











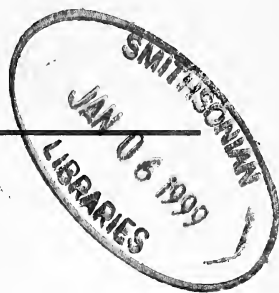




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# CONTRIBUTIONS IN SCIENCE

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OSTEOLOGY AND PHYLOGENY OF THE CUTLASSFISHES  
(SCOMBROIDEI: TRICHIURIDAE)

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F. JAVIER GAGO



NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY



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# OSTEOLOGY AND PHYLOGENY OF THE CUTLASSFISHES (SCOMBROIDEI: TRICHIURIDAE)

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F. JAVIER GAGO<sup>1</sup>

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**ABSTRACT.** This study describes the osteology and otolith morphology of the genera of the Trichiuridae. Evolutionary relationships of the group are investigated based on a cladistic analysis of adult characters. Evidence is provided for the monophyly of the trichiurids. The data support the following phyletic sequence among the genera and clades: *Aphanopus*, *Benthodesmus*, *Lepidopus caudatus*-*L. fitchi* clade, *Lepidopus altifrons*-*Evoxymetopon* clade, *Assurger*, *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*. Osteological data suggest that *Lepidopus* is paraphyletic. In addition, the sister group relationship of a gempylid clade *Diplospinus*-*Paradiplospinus* to the trichiurids is strongly supported. The most parsimonious hypotheses of relationships indicate that the caudal fin has been lost only once during the evolution of the trichiurids, whereas the pelvic fin appears to have disappeared or become reduced twice within the group and independently in the outgroup *Paradiplospinus*. The data of this study are compared with previous studies on trichiurid morphology and analyses of relationships among the scombroids. Prior studies, particularly those based on analysis of ontogenetic characters, support the results of the study reported herein.

## INTRODUCTION

The trichiurids, commonly known as cutlassfishes, hairtails, frostfishes, scabbardfishes, or ribbonfishes, are benthopelagic predators inhabiting the con-

tinental shelf and slope worldwide. Their habitats in tropical and temperate regions range from estuaries to open water 2,000 m in depth. Adults are generally identified by their extremely elongate, laterally compressed bodies; a cluster of long, fang-like teeth on the premaxillary symphysis; presence of a single nostril on each side of the head; a lachrymal that covers most of the descending arms of the maxilla and premaxilla; and reduction or ab-

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sence of the caudal and pelvic fins in some genera. Although not as important commercially as their tuna and billfish relatives, some species of cutlassfishes constitute valuable fisheries in several areas of the world, such as the East China Sea, the North Indian Ocean, and the Mediterranean (Ye and Rosenberg, 1991; Nakamura and Parin, 1993).

Most authors separate the cutlassfishes and the closely related snake mackerels into the Trichiuridae and Gempylidae, respectively. Nakamura and Parin (1993) included the Gempylidae and Trichiuridae within the superfamily Trichiuroidea, suborder Scombroidei.

The Trichiuridae comprises at least 35 species belonging to the following nine genera: *Aphanopus* Lowe 1839, *Assurger* Whitley 1933, *Benthodesmus* Goode and Bean 1882, *Eupleurogrammus* Gill 1862, *Evoxymetopon* Gill 1863, *Lepidopus* Goüan 1770, *Lepturacanthus* Fowler 1905, *Tentoriceps* Whitley 1948, and *Trichiurus* Linnaeus 1758 (Nakamura and Parin, 1993; Parin, 1995). Evidence for the monophyly of the trichiurids has been presented previously (Collette et al., 1984; Johnson, 1986), and most authors have concluded that these fishes represent a highly derived branch of some group of gempylids (Tucker, 1956; Matsubara and Iwai, 1958; Parin and Becker, 1972; Collette and Russo, 1986; Johnson, 1986; Potthoff et al., 1986; Nakamura and Parin, 1993; Carpenter et al., 1995). In a cladistic classification of the scombroids, Johnson (1986) placed the cutlassfishes (his subfamily Trichiurinae) and the snake mackerels (his subfamilies Gempylinae and Lepidocybiinae) as part of his Gempylidae. Throughout this manuscript, the most common usage of the names Trichiuridae and Gempylidae (their limits according to the classification presented by Nakamura and Parin, 1993) is maintained to avoid confusion when reviewing the literature. Thus, unless otherwise indicated, Trichiuridae (cutlassfishes) and Gempylidae (snake mackerels) refer to the Trichiurinae and Gempylinae plus Lepidocybiinae of Johnson (1986), respectively.

In this study, a cladistic hypothesis of relationships among the genera of the Trichiuridae (*sensu* Nakamura and Parin, 1993) is proposed, using a comparative analysis of adult osteology, including otoliths. The hypothesis constructed with adult characters is compared to previous hypotheses of relationships and, in particular, with that of Gago (1997), which was based on larval characters.

## HISTORICAL BACKGROUND

The trichiurids and gempylids were recognized as scombroids by Cuvier (in Cuvier and Valenciennes, 1832). Later workers proposed variations on classifications of the trichiurids and considered the gempylids and trichiurids to be closely related (Swainson, 1839; Günther, 1860; Gill, 1863; Capello, 1868; Goode and Bean, 1895; Boulenger, 1904; Goodrich, 1909).

Since the definition of the Scombroidei proposed

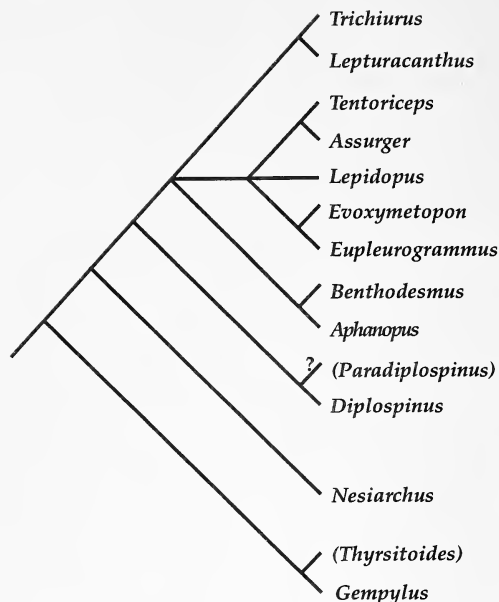


Figure 1. General diagram of the hypothesis of relationships between the trichiurid genera according to Tucker (1956). In parentheses: *Mimasea* (= *Thyrsitoides*) was included in Tucker's (1956) study but is not part of this analysis; *Paradiplospinus* was not recognized at the time of Tucker's (1956) study, but it is included in this analysis.

by Regan (1909), the trichiurids have consistently been included in this suborder. Regan (1909) considered the Scombroidei to comprise the Gempylidae, Istiophoridae, Luvaridae, Scombridae, Trichiuridae, and Xiphiidae. The trichiurids and gempylids were placed within his division Trichiuriformes, characterized by: caudal fin rays not deeply forked at the base; premaxilla beak-like and detached from the nasals; mouth with a lateral cleft and strong anterior canines; epiotic separated by the supraoccipital; gill membranes free from the isthmus; and pectoral fins located low on the body.

Starks (1911) and Gregory (1933) suggested a close relationship between *Gempylus* Cuvier 1829 and the trichiurids. Matsubara and Iwai (1958) suggested that the gempylids *Gempylus* and *Mimasea* (= *Thyrsitoides*) Fowler 1929 are the most closely related genera to the trichiurids and that *Gempylus* approaches the "primitive trichiurid" *Diplospinus* Maul 1948 in several characters.

Tucker (1956) presented the first modern comparative study of the trichiurids, including a more thorough analysis of the gempylid-trichiurid relationships. Figure 1 shows a general diagram of the hypothesis of Tucker (1956) based on his figure 26. He divided the Trichiuridae into three subfamilies: Aphanopodinae (Gill, 1863), including *Aphanopus*, *Benthodesmus*, and *Diplospinus*; Lepidopodinae (Gill, 1863), including *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps*;

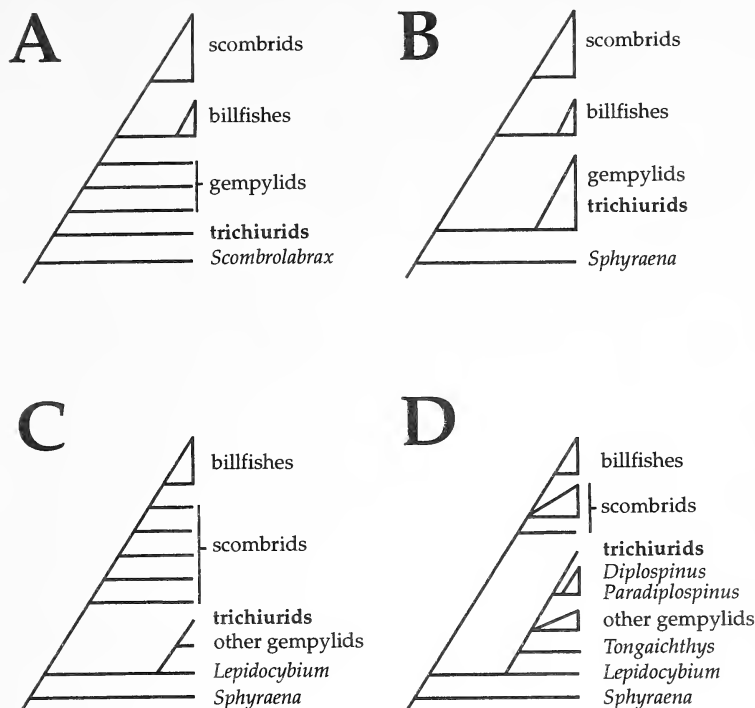


Figure 2. General diagrams of the hypotheses of relationships among the scombroids based on morphological data and following the work of: (A) Collette et al. (1984); (B) Collette and Russo (1986); (C) Johnson (1986); (D) strict consensus tree from figures 5–8 of Carpenter et al. (1995).

Trichiurinae (Swainson, 1839), including *Lepturacanthus* and *Trichiurus*. Tucker (1956) also considered the trichiurids as an offshoot of the gempylids, and he suggested that the gempylids *Gempylus*, *Nesiarchus* Johnson 1862, and *Mimasea* (= *Thyrstitoides*) are the most closely related to the trichiurids. He hypothesized that *Diplospinus* and *Nesiarchus* represent the bridge connecting the two families, and he considered *Diplospinus* as the most primitive trichiurid. However, Tucker (1956: 125) noted that “whether the Trichiurinae crossed the same bridge or by a parallel bridge further downstream is still debatable.” Andriashev (1960) described *Paradiplospinus antarcticus* and considered it the most primitive representative of the Aphanopodinae of Tucker (1956). Parin and Becker (1970) recognized the Aphanopodinae of Tucker (1956) as a natural group excluding *Diplospinus* and *Paradiplospinus*. Parin and Becker (1972) removed *Diplospinus* and *Paradiplospinus* from the Trichiuridae and included them with the gempylids based on the following characters: two external nares on each side; the number of dorsal-fin pterygiophores does not correspond to the number of neural spines; a low number of caudal vertebrae; and a gempylid-like larval morphology. They placed *Diplospinus* and *Paradiplospinus* in the Gempylidae but noted that these two genera occupy an intermediate position between the gempylids

and the trichiurids. Furthermore, they indicated that *Aphanopus* is the most primitive genus within the trichiurids.

Collette et al. (1984) placed the trichiurids as the sister group of all other scombroids, except *Scombrabrax heterolepis* Roule 1921, which they used to root their cladogram (Fig. 2A). In their hypothesis of relationships the gempylids appeared as a paraphyletic group. Collette and Russo (1986) re-evaluated the previous phylogeny and presented a hypothesis of relationships in which the trichiurids appeared to form a monophyletic group with the gempylids *Gempylus*, *Nealotus* Johnson 1865, *Nesiarchus*, *Promethichthys* Gill 1893, *Rexea* Waite 1911, *Thyrstitoides*, and *Tongaichthys* Nakamura and Fujii 1983 (Fig. 2B).

Johnson (1986) discussed the cladistic analysis of Collette et al. (1984) and proposed an alternative hypothesis of scombroid relationships (Fig. 2C). He defined the monophyly of the trichiurids based on nine meristic, osteological, external anatomy, and larval morphology synapomorphies, including two reversals. He recognized three gempylid subfamilies: Lepidocybiinae [including only *Lepidocybium flavobrunneum* (Smith 1849)]; Gempylinae [Gempylidae of Collette et al. (1984), excluding *L. flavobrunneum*]; and Trichiurinae [Trichiuridae of Collette et al. (1984)]. In Johnson’s (1986) hypothesis, *Scombrabrax* Roule 1921 was placed as an

outgroup and *Sphyræna* Röse 1793 was included within the Scombroidei as the sister group to all other scombroidei. Johnson (1986) considered his Gempylidae as the sister group of all other scombroidei, except *Sphyræna*. He also placed *Lepidocybium* Gill 1862 as the sister group of all the other gempylids and trichiurids. He concluded that his monophyletic Trichiurinae represented a highly specialized branch of the Gempylidae with some small group of his subfamily Gempylinae being its sister group. Johnson (1986) noted the need for more systematic work to resolve the precise relationships among gempylids and trichiurids.

Potthoff et al. (1986) described the development of bone and cartilage in several scombroidei groups. They noted that the gempylids and the trichiurids are very closely related and that the trichiurids represent a group derived from the gempylids.

The work of Block (1991), Block et al. (1993), and Finnerty and Block (1995; Fig. 3) and data presented by Finnerty and Block at the 1994 meetings of the American Society of Ichthyologists and Herpetologists addressed the question of scombroidei phylogeny using molecular systematics. Although all of their molecular data sets have consistently supported the monophyly of the billfishes and their separation from the gempylids, scombroidei, and trichiurids, the placement of *Trichiurus lepturus* Linnaeus 1758 and *Gempylus serpens* Cuvier 1829 (the only trichiurid and gempylid used in their analysis) is very unstable.

Carpenter et al. (1995) examined different hypotheses of scombroidei relationships obtained by re-analyzing the data of Johnson (1986), analyzing the revised combined data sets of Collette et al. (1984) and Johnson (1986), and reinterpreting the gill raker character of Johnson (1986: character 44). A summary diagram of Carpenter et al.'s (1995) hypothesis is shown in Figure 2D. The different analyses based on the revision of Johnson's (1986) data set did not change his original hypothesis of relationships among the gempylids and the trichiurids. In these revised analyses the trichiurids always appeared as an offshoot of some group of the gempylids (gempylines of Johnson, 1986), and *Lepidocybium* appeared as the sister group of all the other gempylids and trichiurids. All of the resulting cladograms from the analysis of Carpenter et al.'s (1995) expanded data matrix, which included the data of Collette et al. (1984) and Johnson (1986), also agreed with the hypothesis of relationships among the gempylids and trichiurids proposed by Johnson (1986). The expanded analyses of Carpenter et al. (1995), including their change in the coding of Johnson's (1986) character 44, always resulted in placing *Diplospinus* (which includes *Paradiplospinus* in their data matrix) as the sister group of the trichiurids. The relationships among the rest of the gempylids, except *Lepidocybium* and *Tonigachthys*, which always appear in that phylogenetic order as the sister groups of the gempylids and trichiurids, were unresolved in the unweighted anal-

ysis of Carpenter et al.'s (1995) expanded data matrix (their figs. 5, 7). The placement of *Gempylus* and *Nesiarchus* (two genera that have been previously proposed as being closely related to the trichiurids) in Carpenter et al.'s (1995) weighted analyses was variable. A strict consensus tree of their 142 most parsimonious trees obtained after successive character weighting of their expanded data matrix (their fig. 6) placed *Nesiarchus* as the sister group to an unresolved clade including the gempylids *Epinnula* Poey 1854, *Ruvettus* Cocco 1829, and *Thyrsitoides*. *Gempylus* appeared as part of a trichotomy that includes *Nealotus* Johnson 1865 and a clade including *Epinnula*, *Nesiarchus*, *Promethichthys*, *Ruvettus*, *Thyrsitoides*, and *Thyrsitops* Gill 1862. In their weighted analysis based on a different interpretation of a gill raker character (their fig. 8), *Nesiarchus* appeared as the sister group of a clade that includes *Epinnula*, *Neoepinnula* Matsubara and Iwai 1952, *Ruvettus*, and *Thyrsitoides*. *Gempylus* appeared as part of a trichotomy with *Nealotus* and a clade that includes all of the six taxa above plus *Promethichthys* and *Thyrsitops*. Carpenter et al. (1995) concluded that a data set with more characters that vary within the gempylids and trichiurids would be necessary to resolve the relationships among these groups.

Gago (1997) analyzed the relationships among the trichiurids based on a data matrix of ontogenetic characters. He included most gempylids as the outgroups and rooted the resulting trees at *Lepidocybium*. The results of his analysis did not resolve the relationships among the gempylids. However, the ontogenetic data increased the support for the monophyly of the trichiurids. Within the trichiurids, he found that those genera lacking a well-developed caudal fin complex constitute a clade.

## MATERIALS AND METHODS

### Comparative Material

The comparative material is listed in alphabetical order according to the taxon and the institutions that provided the specimens. The catalogue number is followed by the number of specimens and the range (within parentheses and in mm) of standard lengths (SL; when a caudal fin is present) and total lengths (TL; taxa without a caudal fin). A question mark indicates unknown or unavailable data. All specimens listed are cleared and stained, except those followed by the abbreviation "sk," which indicates skeletonized material. Many radiographs and alcohol-preserved specimens as well as cleared and stained specimens from uncatalogued collections were also studied, but are not listed here. Institutional abbreviations follow Leviton et al. (1985). Species names are those recognized by Nakamura and Parin (1993) and Parin (1995).

### Gempylidae

*Diplospinus multistriatus* Maul 1948: LACM 45450-1 (1; 193 SL), 45604-2 (2; 178, ≈183 SL); USNM 194475 (1; ≈172 SL).

*Gempylus serpens*: LACM 34160-8 (1; 430 SL).



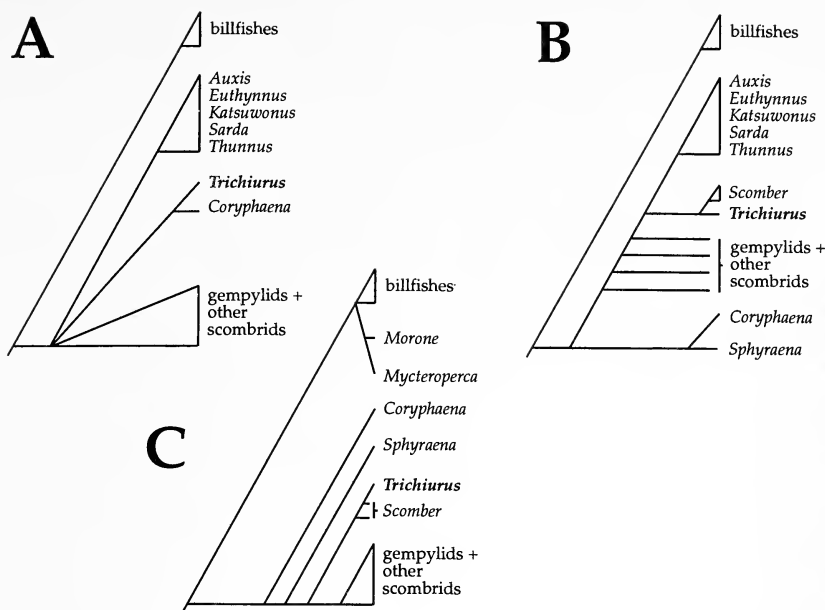


Figure 3. General diagrams of the hypotheses of relationships among the scombroids based on the cytochrome *b* gene data of Finnerty and Block (1995: figs. 2, 4, 7): (A) unweighted analysis of nucleotide substitution data; (B) weighted analysis of nucleotide substitution data; (C) amino acid sequence data.

*Nesiarchus nasutus* Johnson 1862: USNM 236803 (1; 67 SL), 324038 (1; 276 SL).  
*Paradiplospinus antarcticus* Andriashev 1960: LACM 10942 (1; 283 SL), 11325-22 (1; 198 SL), 11511 (1; 278 SL); USNM 208448 (1; 320 SL).

### Trichiuridae

*Aphanopus arigato* Parin 1995: LACM 37113-1 (1; 968 SL), 38240-1 (1; 648 SL).  
*Aphanopus carbo* Lowe 1839: AMS I.25852004 (1; 418 SL).  
*Assurger anzac* (Alexander 1916): SIO 63-229 (1; ≈750 SL).  
*Benthodesmus simonyi* (Steindachner 1891): USNM 292768 (1; 537 SL).  
*Benthodesmus tenuis* (Günther 1877): LACM TC61-117 (1; 522 SL); SIO 82-43 (1; 369 SL).  
*Eupleurogrammus glossodon* (Bleeker 1860): LACM 38131-15 (1; 356 TL), 38134-14 (1; 345 TL).  
*Evoxymetopon taeniatum* Gill 1863: USNM 321690 (1; 190 SL).  
*Lepidopus altifrons* Parin and Collette 1993: USNM 292765 (1; ≈390 SL), 317979 (1; ≈345 SL).  
*Lepidopus caudatus* (Euphrasen 1788): AMS IA.7041 as *L. lex* (1; ?)sk; USNM 268911 (1; ≈246 SL).  
*Lepidopus fitchi* Rosenblatt and Wilson 1987: LACM 31683-1 (1; ≈239 SL), 32684-1 (1; 185 SL), 37102-1 (1; 685 SL)sk, 37102-2 (1; 785 SL)sk, 37103-1 (1; ≈900 SL)sk, 38511-1 (1; 272 SL), 45602-1 (3; 198-223 SL), 45855-1 (1; 275 SL); SIO 72-84 (2; 152-164 SL), 72-209 (1; 237 SL).  
*Lepturacanthus savala* (Cuvier 1829): AMS IB. 1797 (1; ?)sk; LACM 38131-16 (1; 421 TL), 38134-15 (1; >275 TL), 38136-21 (1; 376 TL).  
*Tentoriceps cristatus* (Klunzinger 1884): AMS I.17805002

as *Tentoriceps* sp. nov. (1; 301 TL), I.22830008 (1; 354 TL); LACM 44793-11 (1; 310 TL).

*Trichiurus lepturus*: AMS IB.7447 as *T. coxii* Ramsay and Ogilby 1887 (1; ?)sk; LACM 6945-11 (1; 340 TL), 37104-1 as *T. nitens* Garman 1899 (1; 488 TL)sk, 37906-22 (1; 452 TL)sk, 37955-1 (1; ?)sk, 37955-2 (1; ?)sk, 37955-3 (1; ?)sk, 37956-1 (1; ?)sk, 37957-1 as *Trichiurus* sp. (1; ?)sk, 38117-100 as *T. nitens* (1; 1060 TL)sk, 38117-101 (1; 953 TL)sk, 33807-12 as *Trichiurus* sp. (1; 586 TL)sk, 38130-19 (1; 288 TL); SIO 55-58 (1; 281 TL).

I analyzed 336 sagittae from the Fitch otolith collection at the Natural History Museum of Los Angeles County. They included specimens of the following scombroid genera: *Aphanopus*, *Assurger*, *Benthodesmus*, *Lepidopus*, and *Trichiurus* (Trichiuridae); *Diplospinus*, *Gempylus*, *Lepidocybium*, *Nealotus*, *Paradiplospinus*, *Promethichthys*, *Rexea*, and *Ruvettus* (Gempylidae); *Euthynnus* Lütken 1882 (in Jordan and Gilbert 1882), *Grammatocercus* Gill 1862, *Scomberomorus* Lacepède 1801, and *Thunnus* South 1845 (Scombridae); *Istiophorus* Lacepède 1801, *Makaira* Lacepède 1802, and *Tetrapturus* Rafinesque 1810 (Istiophoridae); *Xiphias* Linnaeus 1758 (Xiphiidae). Six sagittae of the trichiurid species *Lepturacanthus savala* were obtained as a loan from the Australian Museum (I.21955-013). In addition, a drawing of the medial face of a left sagitta of the gempylid *Nesiarchus nasutus* (provided by D. Nolf, Institut Royal des Sciences Naturelles, Belgium), plus several descriptions and drawings of sagittae of other scombroid species (taken from the literature), were compared.

### Comparative Analysis

Osteological characters were examined from radiographs, cleared and stained specimens, and dry skeletal prepara-

tions of adults. I followed the method of Potthoff (1984) for clearing and staining. A Wild M-5 dissecting microscope with a camera lucida was used for the preparation of drawings. Representative drawings of most of the adult osteological characters of each of the trichiurid genera are included for comparative purposes throughout the text. In most cases within the outgroups, I have only included osteological drawings of *Diplospinus* and *Paradiplospinus* since detailed drawings of most gempylids can be found in the work of Russo (1983). Osteological terminology follows mainly the works of Collette and Chao (1975) and Collette and Russo (1984), unless otherwise indicated.

The medial face of the sagittae was lightly rubbed with graphite for enhancement of morphological features. The sagittae were examined under a Wild M-5 dissecting microscope, and scanning electron microscopy was performed on representative specimens. Terminology for the otolith morphology follows Chaine and Duvergier (1934).

## Phylogenetic Analysis

Polarity of the characters was determined by outgroup comparison. Choosing the outgroup is a critical step in cladistic analysis since character argumentation depends heavily on this decision. For the trichiurids this step was facilitated by the large amount of data available regarding scombroid interrelationships. As previously indicated, most workers have proposed a close relationship between gempylids and trichiurids.

Although noncladistic, the works of Tucker (1956) and Parin and Becker (1972) suggested that the gempylids *Diplospinus*, *Gempylus*, *Nesiarchus*, and *Paradiplospinus* are the best candidates for trichiurid outgroups. In addition, prior to the work of Parin and Becker (1972), *Diplospinus* and *Paradiplospinus* were included in the Trichiuridae. The consistent earlier placement of these two genera within the Trichiuridae was based on numerous similarities among these fishes and was interpreted by Tucker (1956) as evidence of common ancestry.

Johnson (1986) concluded that the trichiurids represent a highly derived offshoot of a paraphyletic Gempylidae (his subfamily Gempylinae). The work of Russo (1983) is particularly important because it provides a data matrix of osteological characters for the species of Gempylidae. Russo (1983) could not demonstrate the monophyly of the Gempylidae but concluded that the family comprises six groups. His most derived group was composed of the following genera in phyletic sequence: *Thyrstitoides*, *Nesiarchus*, *Gempylus*, and his *Paradiplospinus*-*Diplospinus* clade. Although *Paradiplospinus* was not recognized at the time of Tucker's (1956) study, *Diplospinus*, *Gempylus*, *Nesiarchus*, and *Mimasea* Kamohara 1936 (= *Thyrstitoides* Fowler 1929) were placed as the basal branches of his trichiurid tree. Furthermore, the results of the work of Carpenter et al. (1995) always placed the *Diplospinus*-*Paradiplospinus* clade as the sister group to the trichiurids.

A preliminary survey of the adult osteology and otolith morphology of the trichiurids and gempylids and its comparison with hypotheses and data sets presented by previous authors (Tucker, 1956; Parin and Becker, 1972; Russo, 1983; Collette et al., 1984; Johnson, 1986; Carpenter et al., 1995) indicate that *Diplospinus* and *Paradiplospinus* are the closest sister groups to the trichiurids. Thus, these two genera, plus *Gempylus* and *Nesiarchus*, are used as the outgroups in this study.

Trees were rooted at a basal polytomy with *Nesiarchus* and *Gempylus*, and following the conclusions of most authors, *Diplospinus* and *Paradiplospinus* were used as a clade representing the sister group to the trichiurids. For

those characters that appear to be heterogeneous among the outgroups and in which the hypothesized state at the outgroup node was equivocal (Maddison et al., 1984), the plesiomorphic condition was determined by comparison to the conditions in other gempylids and scombroids based on information taken from the literature. I agree with the conclusions of Russo (1983), Johnson (1986), and Carpenter et al. (1995) and consider *Lepidocybium* as the most basal gempylid. Thus, the plesiomorphic condition is assumed to be that present in *Lepidocybium*. If the condition in *Lepidocybium* is unknown, the plesiomorphic condition is assumed to be that which is most common among other gempylids or scombroids. Although "most common" does not necessarily indicate plesiomorphy (Maddison et al., 1984; Wiley et al., 1991), "the primitive state of a character for a particular group is likely to be present in many of the representatives of closely related groups" (Kluge and Farris, 1969 p. 5). Maddison et al. (1984) indicated that this form of outgroup methodology can lead to cladograms that are not globally parsimonious. This type of character assessment is used in this study, but more definite conclusions on the polarity of those characters that appear to be equivocal must await the results of a study in progress that includes all gempylids and trichiurids (F.J. Gago and J.L. Russo, unpublished data). The distribution among other gempylids and scombroids of the conditions of those characters that are equivocal is discussed under each of the osteological sections where these characters are described.

A data matrix of characters (Table 1) was constructed using MacClade version 3 (Maddison and Maddison, 1992) and analyzed with PAUP version 3.1.1 (Swofford, 1993). Character states were coded as numerals and "?," where 0 represents the plesiomorphic condition and "?" missing or nonapplicable data

## RESULTS

All multistate characters (Table 1) were considered unordered, and the trees were rooted at a basal polytomy with *Gempylus* and *Nesiarchus*. An analysis using the branch-and-bound algorithm and ACCTRAN transformations resulted in three equally most parsimonious trees. These three trees have 99 steps, a consistency index of 0.869, and a rescaled consistency index of 0.809. All three trees have the same topology as the tree of Figure 4, except for the resolution between *Evoxymetopon*, *Lepidopus altifrons*, *L. caudatus*, and *L. fitchi*. Figure 5 shows the only portion of the topology among the most parsimonious trees that is variable. The variation in the topology of these trees is the result of different interpretations about the evolution of character 36. Figure 5 only includes character 36 since the interpretation of all the other characters analyzed using ACCTRAN is identical for all three trees at these variable nodes.

One tree places *Lepidopus caudatus* and *L. fitchi* as a monophyletic group (node IVa) and *Evoxymetopon* and *L. altifrons* as an unresolved polytomy at node V (Fig. 5A). In this tree the derived condition of character 36 is assumed to have evolved independently in the clade uniting *L. caudatus* and *L. fitchi* (node IVa) and in the monophyletic group above node V. This tree topology also

Table 1. Data Matrix of Adult Characters. 0 = plesiomorphic state; 1, 2, 3, 4 = apomorphic states; ? = missing data or not applicable.

Taxa	Characters					
	10	20	30	40	50	60
<i>Aphanopus</i>	100112000101000211010101001000000000100?01021020110000000212111110					
<i>Assurger</i>	110112011001000211011121111001111101100101021121211001000212111010					
<i>Benthodesmus</i>	120112001001000211010101001000110100100101021020210000000212111100					
<i>Eupleurogrammus</i>	120112010011011321010111101000121211110111121121311114121???????					
<i>Evoxymetopon</i>	120112011001000211011121111001111100100101021021311001000212111???					
<i>Lepidopus altifrons</i>	120112011001000211011121111001111100100101021021311001000212111???					
<i>L. caudatus</i>	120112011001000211010101101001111101100101021021311001000212111010					
<i>L. fitchi</i>	120112011001000211010101101001111101100101021021311001000212111010					
<i>Lepturacanthus</i>	12111211201111321010101101000121210111????21121311112121?????011					
<i>Tentoriceps</i>	12011201000100132101112111100112110111011112121311113111???????					
<i>Trichiurus</i>	12111211201111321010101101000121210111????21121311112121?????011					
<i>Diplospinus</i>	0000110000000002001000010001100000000001000100000000000102100100					
<i>Gempylus</i>	000000000100000100000000000000200200010000000000000000000000000000					
<i>Nesiarchus</i>	00					
<i>Paradiplospinus</i>	000011000000000200100001000110000000000?00010000000000000102100100					

assumes that character 36 reverted to the plesiomorphic condition at node IX.

A second tree places *Evoxymetopon* and *Lepidopus altifrons* as a clade (node Va) and *L. caudatus* and *L. fitchi* as an unresolved polytomy at node IV (Fig. 5B). Finally, the third tree places *L. caudatus* and *L. fitchi* and *Evoxymetopon* and *L. altifrons* in two separate clades, respectively (Fig. 5C, nodes IVa and Va). This last hypothesis of relationships has a “zero length” branch (node IVa), but it is included in the results of the analysis by PAUP to indicate that there is potential support for these monophyletic groups under some “most parsimonious reconstructions” (Swofford, 1993). The trees of Figure 5B and 5C assume that the derived condition of character 36 evolved only once below node IV and was lost independently in the clades including *Evoxymetopon* and *Lepidopus altifrons* (node Va) and *Lepturacanthus* and *Trichiurus* (node IX), respectively. A different interpretation of the third tree using DELTRAN assumes that the derived condition of character 36 evolved independently in the clade above node V and the clade of node IVa. This alternative hypothesis also concludes that character 36 reverted to the plesiomorphic condition in node IX and that the branch leading to node Va is “zero length.”

The tree in Figure 4 is not considered to be the final hypothesis of relationships. One must be aware that there are three equally parsimonious hypotheses as described earlier in this section and the tree of Figure 4 is just one of these hypotheses. However, because the three hypotheses differ only in the interpretation of a single character (character 36), the tree in Figure 4 serves as a good summary of the hypotheses of relationships and character evolution. The description that follows is based on the results of the analysis using ACCTRAN, as pre-

sented in Figure 4. An analysis of the tree in Figure 4 using DELTRAN results in different interpretations of character transformations for 10 of the characters utilized. For comparative purposes, Figure 6 shows the distribution of character states when using DELTRAN.

A monophyletic group including the gempylid genera *Diplospinus* and *Paradiplospinus* (node Ia) is supported by three synapomorphies and appears as the sister group of the trichiurids. The monophyletic group including these two outgroup genera plus the trichiurids (node I) is supported by 10 synapomorphies, including only one homoplasy.

*Aphanopus* appears as the sister group to the rest of the trichiurids at node II. A total of 21 synapomorphies, including only two homoplasies, support the monophyly of the trichiurids (node II).

The monophyly of the group that includes all the trichiurids except *Aphanopus* (node III) is supported by six synapomorphies, including three homoplasies. A monophyletic group including all trichiurids except *Aphanopus* and *Benthodesmus* (node IV) is supported by 10 synapomorphies, including four homoplasies.

As indicated earlier, in the tree of Figure 4 the branch leading to the monophyletic group of *Lepidopus caudatus* and *L. fitchi* is interpreted as having no support in the form of synapomorphies (zero length). However, the results using DELTRAN include character 36 as a synapomorphy at this node (Fig. 6).

The clade including *Evoxymetopon* and *Lepidopus altifrons* appears as the sister group to the monophyletic group that includes *Assurger*, *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, in that phyletic order. The monophyletic group including these seven taxa (node V) is sup-

TL: 99  
CI: 0.869  
RC: 0.809

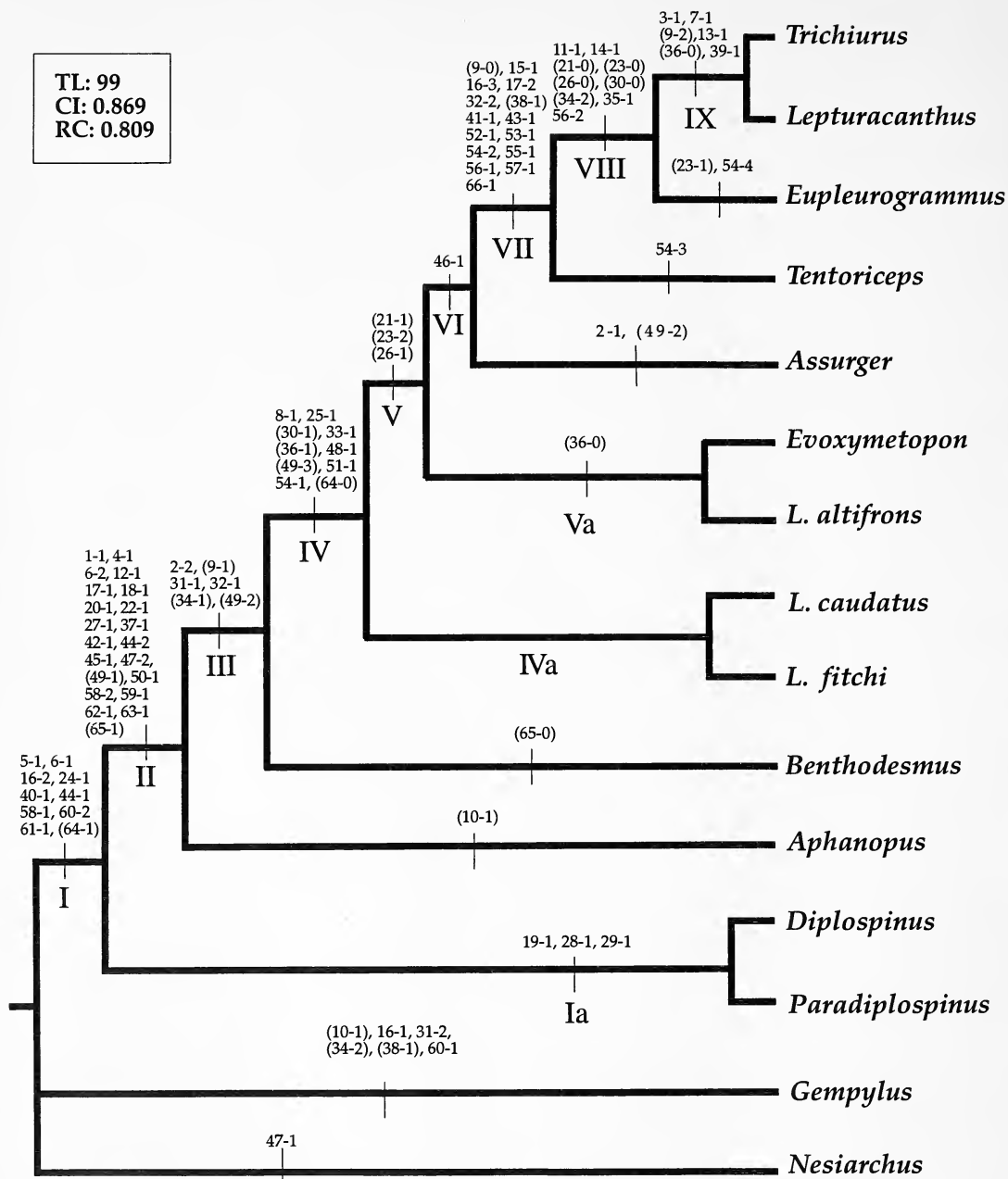


Figure 4. Hypothesis of relationships resulting from the branch-and-bound analysis of the data matrix. Character transformations follow ACCTRAN. Homoplastic characters are enclosed within parentheses; character numbers are followed by the state present at each respective node.

ported by three homoplasies (independent acquisitions).

A clade including *Evoxymetopon* and *Lepidopus altifrons* (node Va) is only supported by a reversal in character 36 (Fig. 5B, C). An analysis using DELTRAN includes this node, although it provides no support for its monophyly (Fig. 6; node Va).

Node VI places *Assurger* as the sister group to

the clade formed by *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, but this is supported by only a single synapomorphy. The sister group relationship between *Tentoriceps* and the clade including *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* (node VII) is supported by 15 synapomorphies, including two homoplasies.

Furthermore, *Eupleurogrammus* appears as the

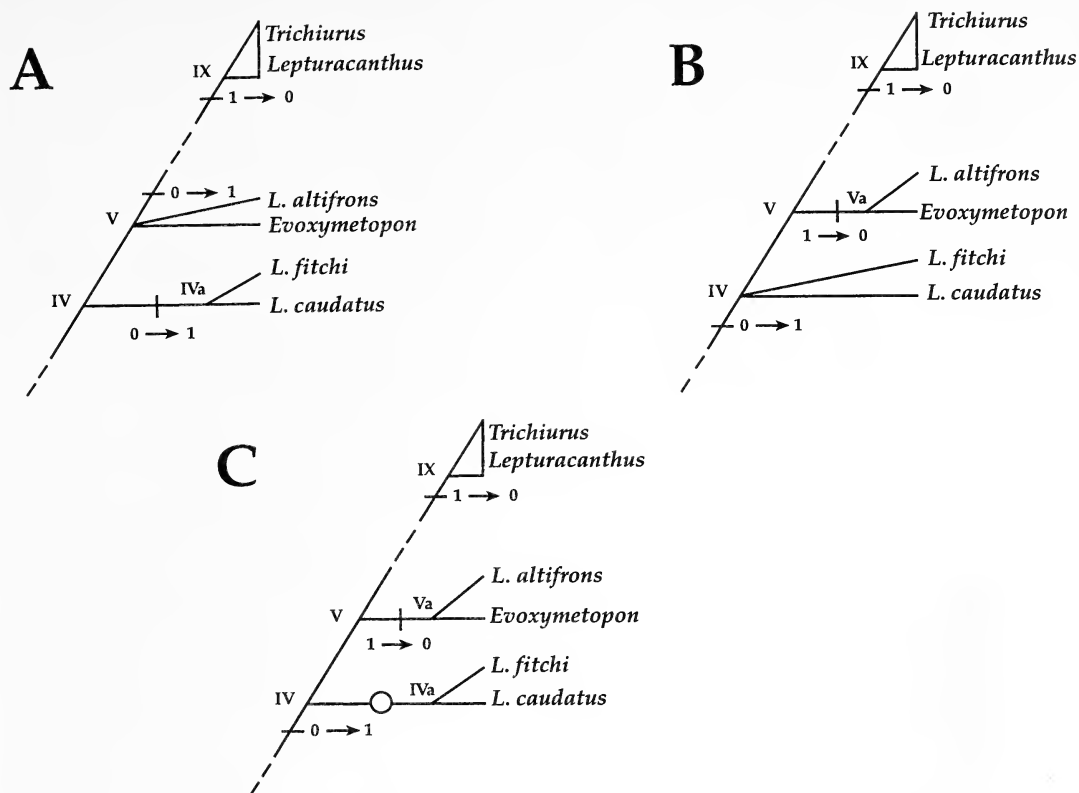


Figure 5. General diagrams of the most parsimonious hypotheses obtained during the branch-and-bound analysis of the adult data matrix (Appendix). Character transformations follow ACCTRAN. The direction of change between the states of character 36 (Appendix) is indicated with an arrow at each of the nodes. Dashed lines above and below nodes IV and V indicate portions of the hypotheses that are identical to those in the tree in Figure 4. Open circle = zero length branch.

sister group to *Lepturacanthus* and *Trichiurus* (node VIII). The monophyletic group including these three genera is supported by nine synapomorphies, including five homoplasies.

*Lepturacanthus* and *Trichiurus* appear as a monophyletic group (node IX). Six synapomorphies, including two homoplasies, support the monophyly of these two genera.

A tree with the topology presented by Tucker (1956; Fig. 1) was created using MacClade and imported into PAUP as a topological constraint for a branch-and-bound search using the data matrix of Table 1, but excluding *Paradiplospinus* and *Thyrstitoides* from the analysis. As mentioned earlier, Tucker's (1956) tree places *Gempylus* (plus *Thyrstitoides*, which was not included in this study), *Nesiarchus*, and *Diplospinus* (*Paradiplospinus* was not recognized at the time of Tucker's 1956 study), in that phyletic order, as the sister taxa of the trichiurids. He proposed three major groups in his tree: *Aphanopus-Benthodesmus* (his subfamily Aphanopodinae minus *Diplospinus*); *Lepturacanthus-Trichiurus* (his subfamily Trichiurinae); *Assurger-Eupleurogrammus-Evoxymetopon-Lepidopus-Tentoriceps* (his subfamily Lepidopodinae). The branches leading to these three groups appear as a trichotomy

above *Diplospinus*. Within his monophyletic Lepidopodinae he shows a trichotomy that included the following groups: *Assurger-Tentoriceps*; *Eupleurogrammus-Evoxymetopon*; *Lepidopus*. A branch-and-bound search with all characters treated as unordered resulted in three equally most parsimonious trees with a length of 134 steps and consistency and rescaled consistency indexes of 0.672 and 0.468, respectively. In all three resulting trees the clades *Aphanopus-Benthodesmus* and *Lepturacanthus-Trichiurus* appear, in that phyletic order, as the sister groups to Tucker's Lepidopodinae. The trees differ in the three possible resolutions among the clades proposed by Tucker (1956) within the Lepidopodinae.

## DESCRIPTIVE OSTEOLOGY OF ADULTS

The characters for the phylogenetic analysis are indicated with numbers that correspond to those in the data matrix (Table 1), list of characters (Appendix), and phylogenies (Figs. 4–6). Character numbers are followed by the state present at each particular node. Character numbers in parentheses represent homoplasies.



TL: 99  
CI: 0.869  
RC: 0.809

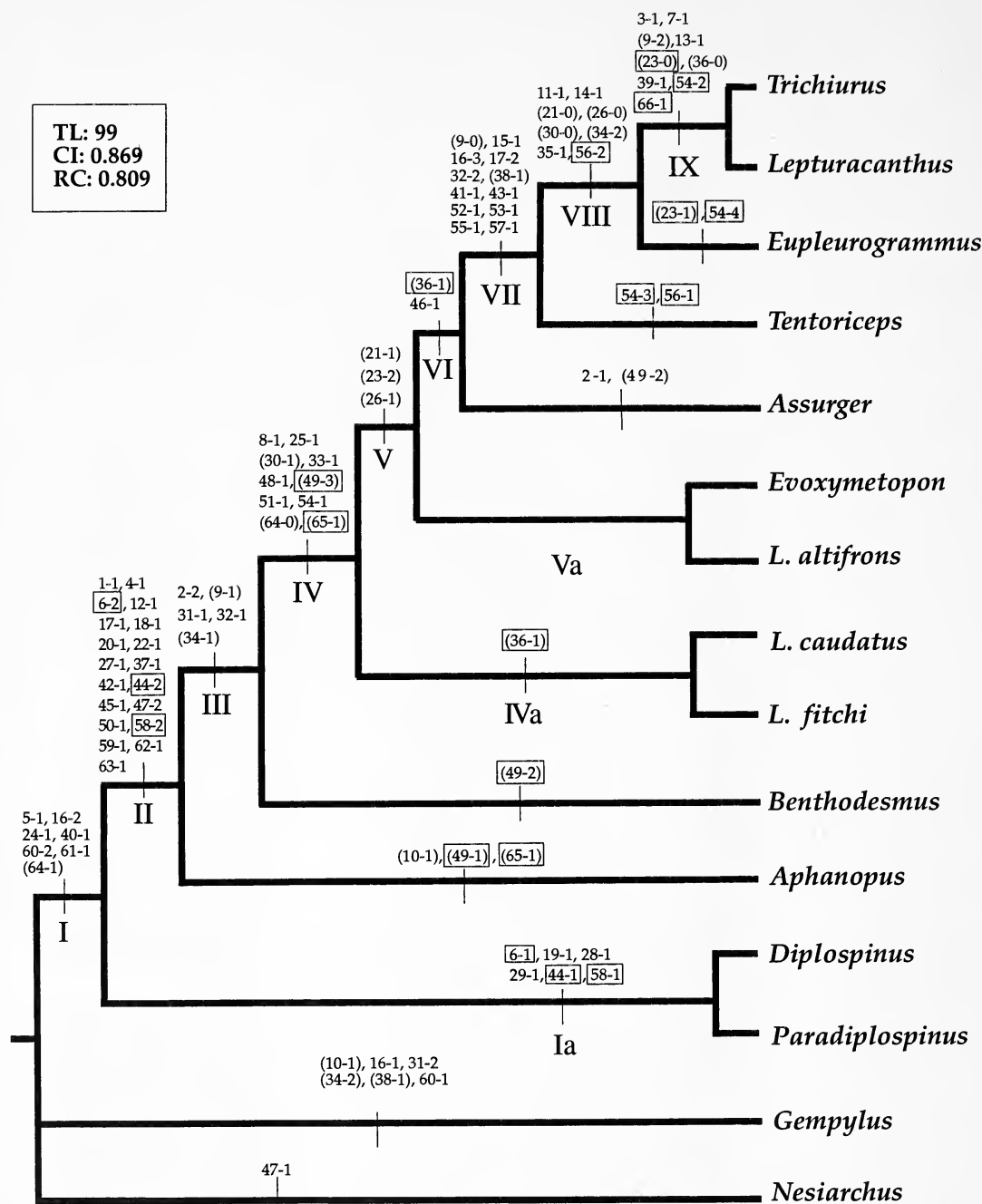


Figure 6. Hypothesis of relationships resulting from the branch-and-bound analysis of the data matrix. Character transformations follow DELTRAN. Homoplastic characters are enclosed within parentheses; character numbers are followed by the state present at each respective node. Those interpretations of character transformations that differ from the results using ACCTRAN (Fig. 4) are enclosed within a rectangle.

## OPERCULAR SERIES

The bones of the opercular series in both the trichiurids and gempylids are poorly ossified. The thickest, most strongly ossified areas, which are the

articular corners of the opercle, subopercle, and interopercle, are spongy in appearance (Fig. 7).

*Character 1.* In the trichiurids, the posterior and ventral margins of the opercle, subopercle, and interopercle (the interopercle to a lesser degree) are

strongly splintered or fimbriated (Fig. 7C–K). Johnson (1986: character 26) considered this condition (including the ventral margins of the lachrymal) as a synapomorphy of his Trichiurinae. In the outgroups, the posterior and ventral margins of the opercle, subopercle, and interopercle are mostly complete (only the dorsal flap of the opercle and the posterior corner of the subopercle may be slightly splintered; Fig. 7A, B).

### Opercle

The opercle of all gempylids and trichiurids is quadrilateral and characterized by the presence of a posterodorsal notch. Russo (1983: character 55) indicated that the posterodorsal notch in all gempylids, except *Gempylus* and *Lepidocybium*, is deep and bordered by a wide dorsal flap. In contrast, *Gempylus* and *Lepidocybium* have shallow opercular notches with a dorsal margin that tapers posteriorly to a point. The trichiurids have a deep dorsal notch and the dorsal flap above it is narrower than that in most gempylid genera, but it is not pointed.

Russo (1983: character 56) noted that all gempylids, except *Diplospinus*, *Gempylus*, *Lepidocybium*, *Nealotus*, *Nesiarchus*, *Rexea*, *Thyrsites* Cuvier (in Cuvier and Valenciennes 1832), and *Thyrstitoides*, bear a spinous ventral margin on the posterodorsal notch of the opercle. All of the trichiurids analyzed here have opercular notches with ventral margins that are not pointed or spinous. Some specimens of *Paradiplospinus* utilized in this study have a small feeble spinous ventral margin on the opercular notch, and one specimen of *Diplospinus multistriatus* has a spinous opercular notch on only one side of the body. The presence or absence of a spinous ventral margin on the opercular notch is variable within these two outgroup genera.

The opercle articulates with the posterior condyle of the hyomandibula by an anterodorsal articular head that houses an articular fossa. All gempylids, except *Lepidocybium*, and the trichiurids share this condition. At its base, the anterodorsal articular head bears one to three struts or ridges that support the main body of the opercle medially. The articular head is short in all the genera studied, except *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, in which it clearly projects from the anterodorsal corner of the opercle by way of an elongate neck-like base. However, it is difficult to categorize this condition objectively because *Assurger*, *Evoxymetopon*, and *Lepidopus* share an intermediate state in the elongation of the articular head.

**Character 2.** The outgroup genera and the trichiurid *Aphanopus* have a lateral plate-like process at the anterodorsal corner of the opercle that covers all or most of the articular head (Fig. 8A). In all the other trichiurids, except *Assurger*, the articular head lacks a lateral plate, but it bears a well-developed elongate lateral process that is round in cross

section (Fig. 8C). *Assurger* also bears an elongate lateral process, but it is flat in cross section (Fig. 8B). In *Gempylus* the plate-like process is dorsally elongate, but the condition is not comparable with that of *Assurger*. The flat process of *Assurger* crosses the articular head of the opercle at about its center (as in those trichiurids with an elongate process that is round in cross section), whereas the flat process of *Gempylus* extends posterodorsally of the articular head and appears to be a modification of the plate covering the dorsal margin of the articular head. The lateral process is longer in *Assurger*, *Eupleurogrammus*, *Lepidopus*, *Tentoriceps*, and *Trichiurus*, but the degree of elongation is difficult to categorize objectively.

### Subopercle

The subopercle of all the genera analyzed in this study is flat and triangular. The dorsal margin of the subopercle abuts the ventral margin of the opercle medially. The subopercle of all trichiurids is poorly ossified and has a strongly fimbriated or splintered ventral margin, whereas the ventral margin of the subopercle in the outgroup genera is mostly complete, and fimbriations, if present, are extremely reduced and restricted to the posterodorsal corner of the bone.

**Character 3.** The fimbriations on the posteroventral corner of the subopercle in the trichiurid genera *Lepturacanthus* and *Trichiurus* are longer than the preceding ventral ones. Thus, the contour formed by the ventral margin of the subopercle and the posteroventral corner of the opercle in these two genera appears to be slightly concave (Fig. 7I, K). Tucker (1956) used this character to group these two genera into his subfamily Trichiurinae. All the other trichiurids and the outgroups have a subopercle which, together with the opercle, forms a convex ventral margin.

**Character 4.** The outgroups and trichiurids are characterized by the presence of an anterodorsal articular process on the subopercle. In the outgroups, the articular process extends dorsally at a right angle to the dorsal margin of the subopercle and articulates mainly with the anteroventral corner of the opercle (Fig. 9A). A much smaller anterior projection on the articular process articulates with the interopercle. All trichiurids possess an articular process that extends anteriorly, articulating mainly with the posterodorsal corner of the interopercle (Fig. 9B). The articular process is short in *Aphanopus*, *Benthodesmus*, and *Lepturacanthus*, whereas it is longer and more pointed in other trichiurids. The degree of elongation of the anterodorsal process seems to vary in a continuous gradient from pointed to rounded and is difficult to categorize.

### Interopercle

The interopercle is triangular and poorly ossified. The dorsal margin is characterized by a shallow lat-

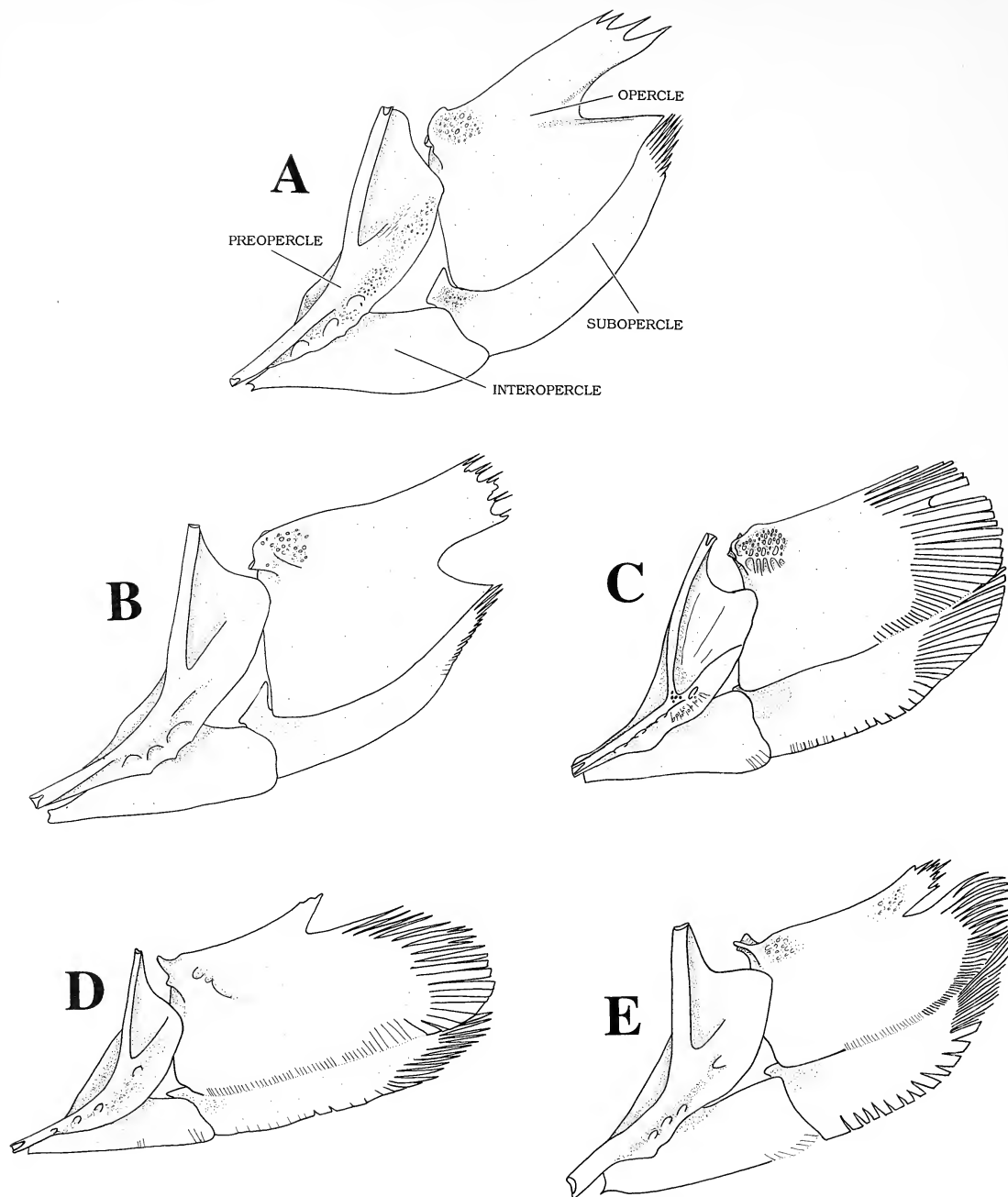


Figure 7. A–E. Lateral view of the left opercular series: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

eral fossa, which serves as a facet for the ventral portion of the posterior wing of the preopercle. Posteriorly, the margin of the interopercle overlaps the anterior margin of the subopercle laterally. The posterodorsal corner of the interopercle articulates with the anterodorsal articular process of the subopercle. Medially, the interopercle has a small anterodorsal fossa that articulates with the posterior

corner of the epihyal and the interhyal. The interopercle is similar among the species studied and differs only slightly in its overall shape.

### Preopercle

The preopercle is crescent-shaped with a longitudinal lateral-line canal on the anterior margin and

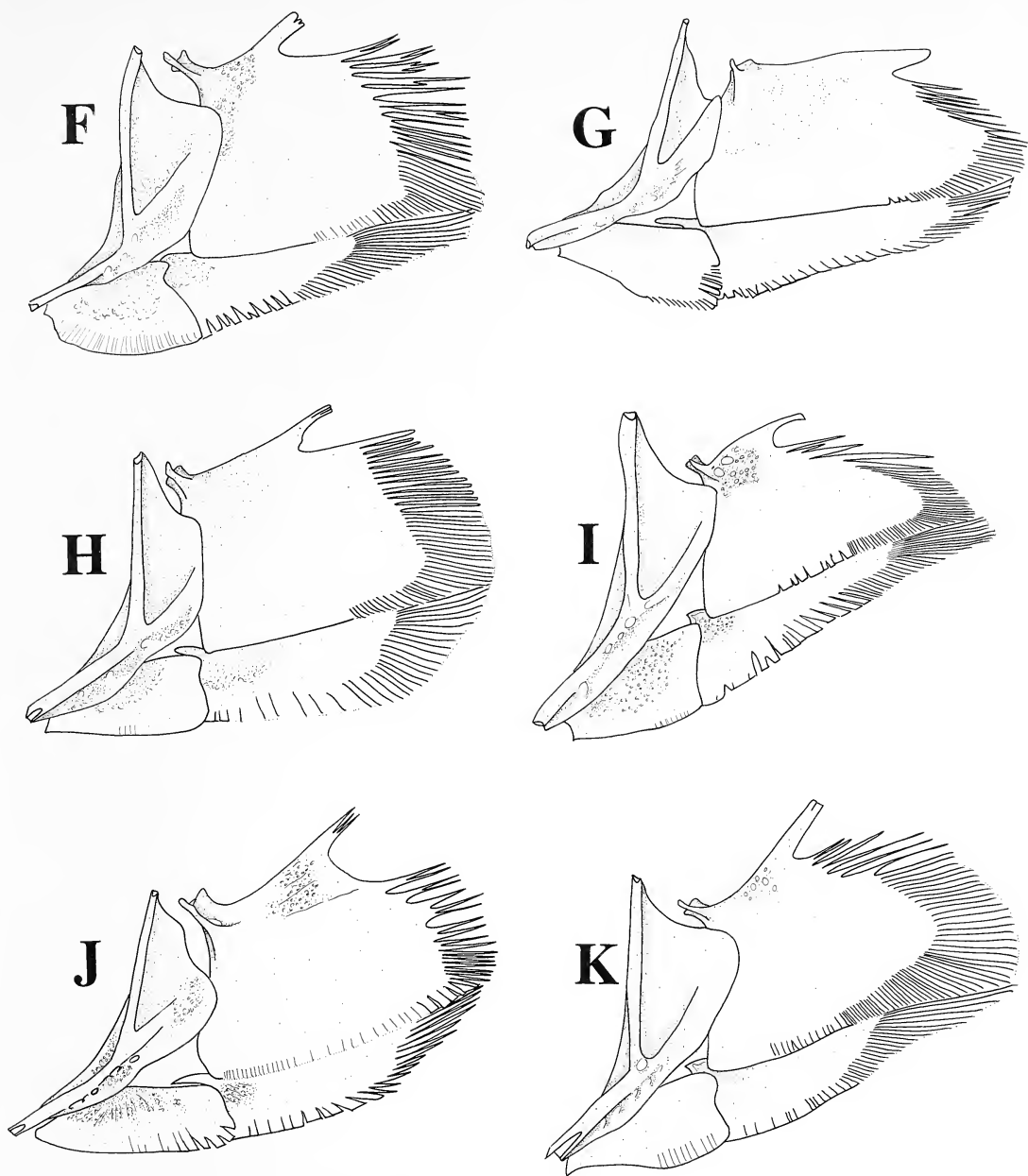


Figure 7. F-K. Lateral view of the left opercular series: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

a posterior strut on the dorsal half of the bone. The canal and the strut converge in the shape of a "Y." The anterior longitudinal canal carries the preopercular branch of the laterosensory canal system (Coombs et al., 1987), which it receives from a lateral pore on the pterotic. This preopercular canal exits the preopercle at the anteroventral tip to enter the articular bone. As it passes along the preopercle, the preopercular canal opens laterally through sensory pores. The preopercle is the most heavily

ossified bone in the opercular series. The posterior wing of the preopercle is less ossified than the central axis, and it overlays the anterior margin of the opercle and a shallow, dorsolateral fossa on the interopercle.

The posterior margin of the preopercle of all adult trichiurids is smooth and devoid of spines. Russo (1983) noted the variability in the posteroventral margin of the preopercle of gempylid genera. He indicated that the preopercular margin of

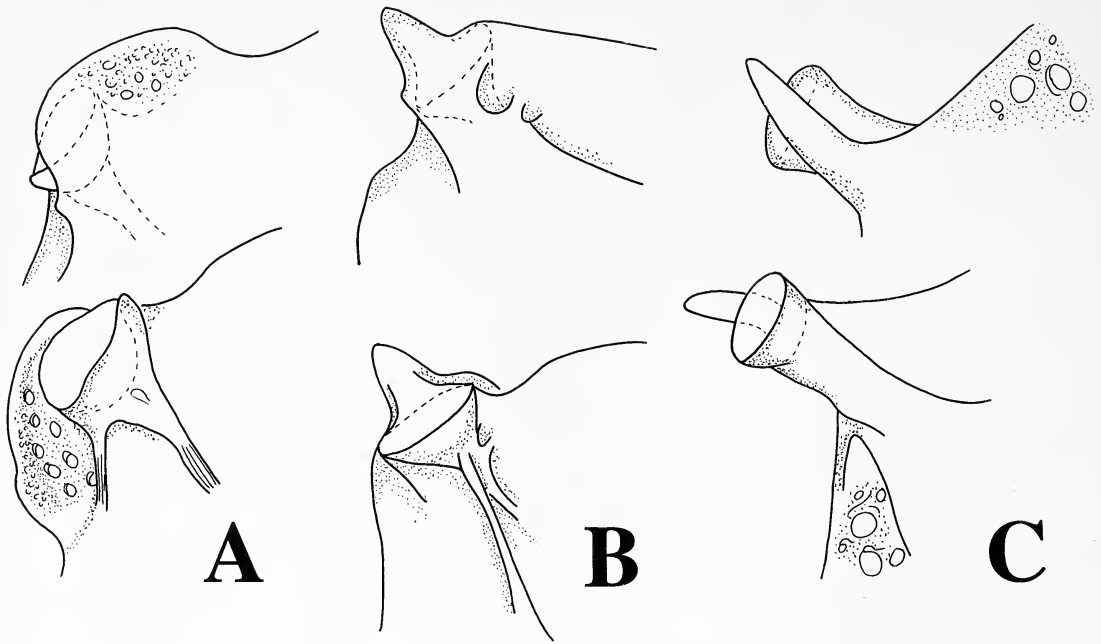


Figure 8. Lateral (top) and medial (bottom) views of the lateral process on the articular head of the left opercle: (A) *Diplospinus multistriatus*; (B) *Assurger anzac*; (C) *Trichiurus lepturus*.

the gempylids can be smooth (*Diplospinus*) or serrate (*Paradiplospinus*), have ventrally or dorsally directed spines (*Gempylus* and *Nesiarchus*), or be irregular in shape because of poor ossification. In some cases, the presence or absence of spines is difficult to evaluate because their recognition depends on the degree of ossification or development. For example, Russo (1983) noted the presence of small spines in *Paradiplospinus*, but concluded that they could be interpreted as serrations because of their poor development. Russo (1983) omitted this character from his analysis because of the difficulty in its interpretation.

**Character 5.** The preopercle of the outgroups *Gempylus* and *Nesiarchus* bears a convex posterodorsal margin. Russo (1983: character 48) identified the presence of a slightly concave posterodorsal margin on the preopercle as a synapomorphy of his gempylid clade comprising *Diplospinus* and *Paradiplospinus*. All trichiurids examined in this study share this feature. Because of the presence of a convex posterodorsal margin in the preopercle of all gempylids, except *Diplospinus* and *Paradiplospinus*, I agree with Russo (1983) and consider the presence of a concave posterodorsal margin as the derived condition.

### CIRCUMORBITAL SERIES

The circumorbital series is a group of poorly ossified, small bones that carry the infraorbital branch of the lateral sensory canal system. Russo (1983) indicated that the numbers of left circumorbital el-

ements present in the gempylids *Diplospinus multistriatus*, *Gempylus serpens*, *Nesiarchus nasutus*, and *Paradiplospinus gracilis* (Brauer 1906) were 26, 29, 21, and 21, respectively. However, he noted that the number of circumorbitals varied not only within species but also between sides of the same specimen. Jollie (1986) indicated that hypotheses of homology concerning the infra- and postorbitals (excluding the lachrymal and jugal) are impossible because of the variation in the number of elements, as well as the arbitrariness of their recognition.

**Character 6.** All of the circumorbital series of the gempylids examined by Russo (1983: character 35) are continuous, except those of *Diplospinus* and *Paradiplospinus*, which have a short gap separating the first infraorbitals from the posterior circumorbitals (Fig. 10A, B). Russo (1983) considered the condition present in *Diplospinus* and *Paradiplospinus* as a synapomorphy uniting these two genera. A further derived condition, as explained by Johnson (1986: character 27), is present in the trichiurids, which have an extremely reduced circumorbital series (only the lachrymal and jugal are present, Fig. 10C–K). Although this character appears equivocal at the outgroup node in this study, I agree with Russo (1983) and Johnson (1986) in their polarization of the character states.

### Lachrymal

The lachrymal constitutes the largest element of the circumorbital series. The ventral wing of the lachrymal is poorly ossified and membranous. The



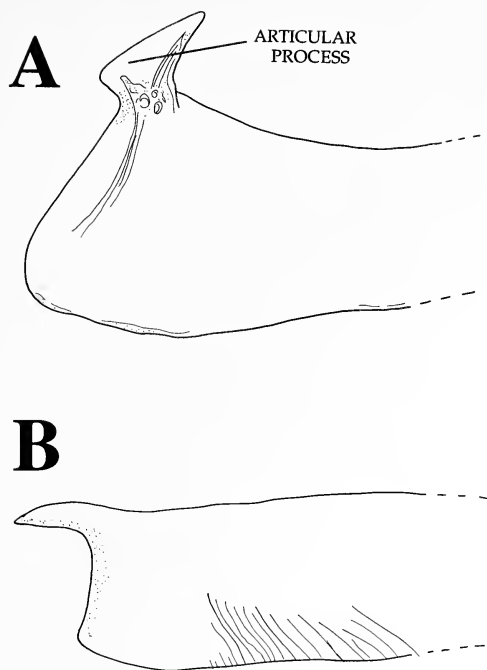


Figure 9. Lateral view of the articular process of the left subopercle: (A) *Paradiplaspinus antarcticus*; (B) *Lepidodiplosis altifrons*.

poorly ossified ventral margin of this wing is fimbriated or splintered in the trichiurids. The latter character state was included by Johnson (1986) as part of his character complex 26. I do not consider this condition to be independent of that present in some of the opercular series (character 1). All trichiurids are characterized by a lachrymal with an extremely large ventral wing that completely covers the descending arms of the maxilla and premaxilla and in some cases extends past the ventral margin of the premaxilla. This character was recognized and used by Regan (1909) to define his family Trichiuridae. In the outgroups, the ventral wing does not cover the descending arms of the maxilla and premaxilla completely, and the ventral margin of the wing is complete. Matsubara and Iwai (1952) noted that the maxilla in *Gempylus* is largely hidden by the infraorbital membrane. However, variation in the extent of the ventral wing is continuous and the character is not included in the analysis since its categorization into objective states is difficult.

The ventral wing of the lachrymal is joined to a dorsal, longitudinal lateral-line canal. A perpendicular dorsal process of this longitudinal canal divides it into an anterior and a posterior section and forms the articular process that joins the lateral ethmoid. All the outgroups and trichiurids are characterized by articular processes that are elongate and pointed.

**Character 7.** In the trichiurids *Lepturacanthus* and *Trichiurus*, the ventral wing of the lachrymal becomes separated from the longitudinal, dorsal lateral-line canal at its anterior and posterior tips. The fimbriations in the anterior and posterior margins of the ventral wing of *Lepturacanthus* and *Trichiurus* extend vertically and are almost perpendicular to the dorsal, longitudinal lateral-line canal. Thus, *Lepturacanthus* and *Trichiurus* have a ventral wing on the lachrymal that appears quadrilateral (Fig. 10I, K). The rest of the trichiurids and all outgroups, except *Gempylus*, have a lachrymal in which the anterior and posterior portions of the ventral wing are connected to the anterior and posterior tips of the dorsal, longitudinal lateral-line canal. In *Gempylus* and *Tentoriceps*, the anterior margin of the ventral wing seems to become slightly separated before its anterior tip. However, this condition is not comparable to that in *Lepturacanthus* and *Trichiurus*, where the anterior tip of the dorsal, longitudinal lateral-line canal extends free of the ventral wing for a longer distance. In the outgroups and the rest of the trichiurids, the fimbriations in the anterior and posterior portions of the ventral wing of the lachrymal are not perpendicular to the dorsal, longitudinal lateral-line canal, and the ventral wing appears ovoid (Fig. 10A–H, J).

**Character 8.** The posterodorsal angle between the articular process and the posterior section of the dorsal, longitudinal lateral-line canal is strengthened by a plate-like ossification. This plate-like ossification extends posteriorly and terminates before or above the posterior pore of the dorsal, longitudinal lateral-line canal in the outgroups and the trichiurids *Aphanopus* and *Benthodesmus* (Fig. 10A–C, E). In the rest of the trichiurids this plate-like ossification extends past the posterior pore of the longitudinal, dorsal lateral-line canal and ends above the jugal (Fig. 10D, F–K).

## Jugal

The jugal is the next bone, posterior to the lachrymal. Russo (1983: character 33) indicated that in all gempylids, except *Lepidocybium* and *Ruvettus*, the articulation between the lachrymal and the jugal is weak and the two elements are not in contact. Although the outgroup specimens analyzed in this study, except *Gempylus* where the jugal and lachrymal are separated, have a weak articulation between the jugal and lachrymal, these elements remain in contact with each other. The contact between the first two infraorbitals seems to be completely lost only in the trichiurids and *Gempylus*. The degree of separation between the lachrymal and the jugal is difficult to interpret and appears to be highly variable. Jollie (1986) considered the term jugal as useful only in its positional reference. Problems of interpretation of the homology of this bone may be, in part, a result of the probable separation of free lateral-line canal units from the posterior end of the lachrymal.

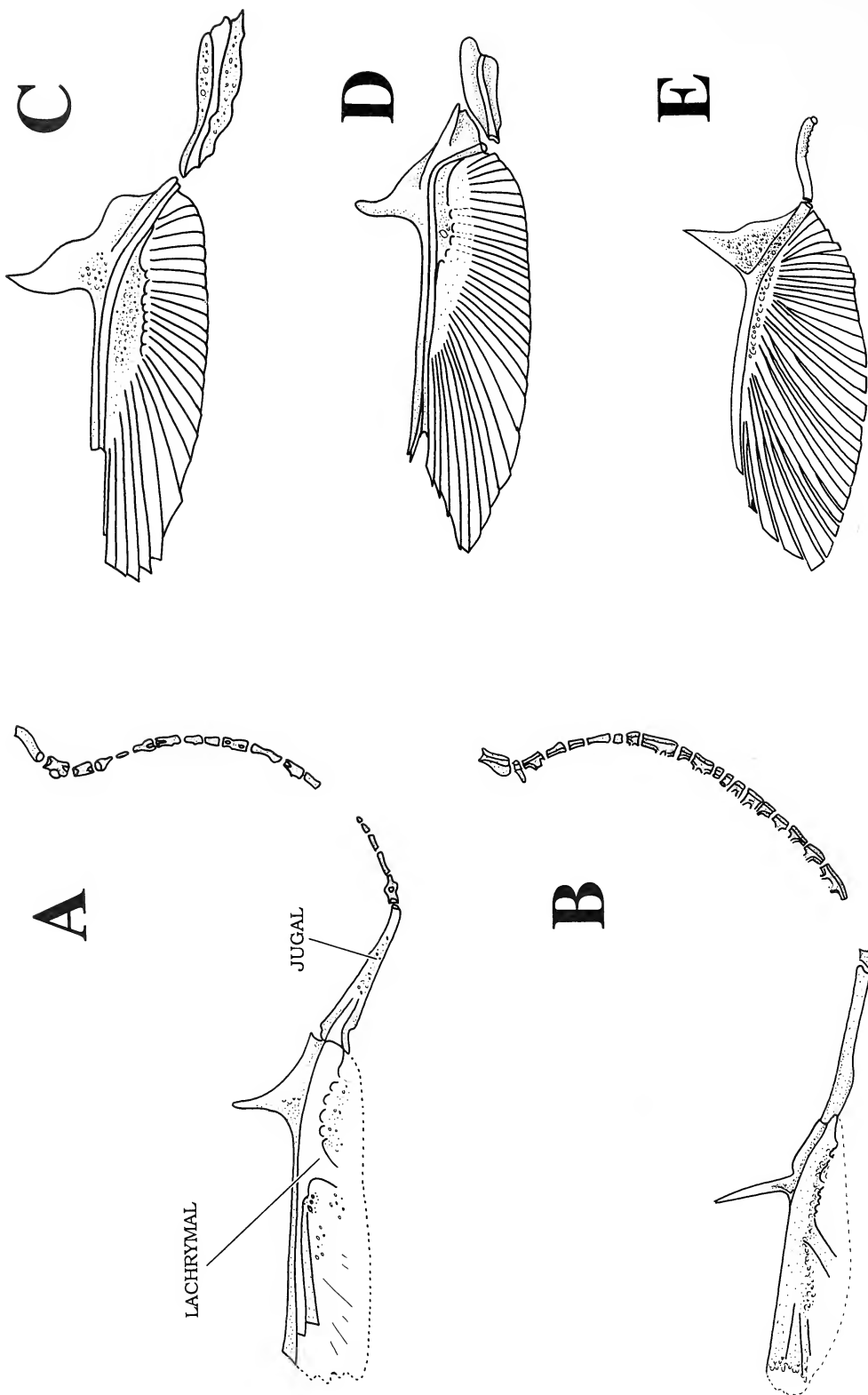


Figure 10. A-E. Lateral view of the left circumorbital series: (A) *Diplospinus multistriatus*; (B) *Paradipllospinus antarcticus*; (C) *Assurger anzac*; (D) *Aphanopus arigato*; (E) *Benthodesmus tenuis*.

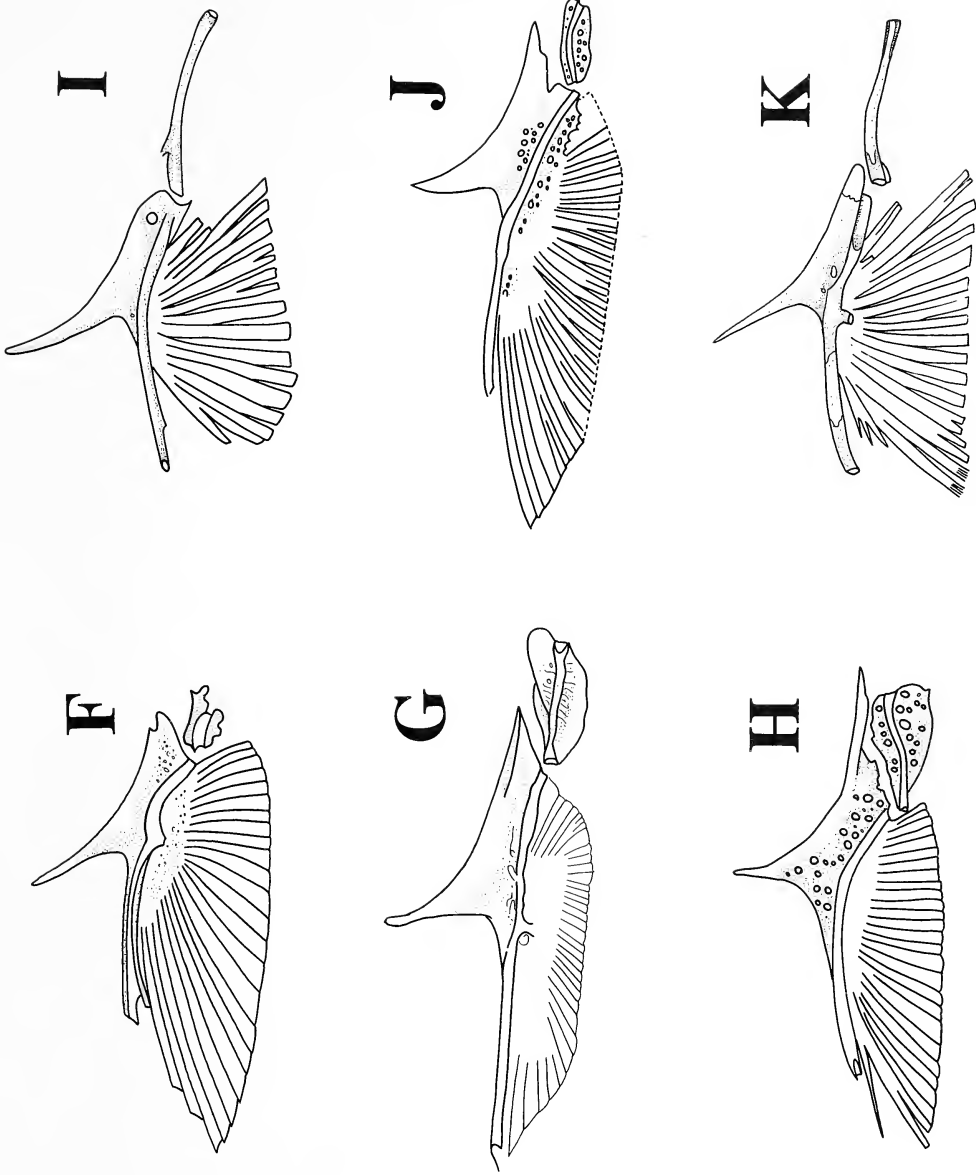


Figure 10. F–K. Lateral view of the left circumorbital series: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatius*; (H) *Lepidopus fitchii*; (I) *Lepturacanthus savala*; (J) *Trichiurus lepturus*; (K) *Trichiurus cristatus*.

The jugal in the gempylids *Diplospinus*, *Nesiarchus*, and *Paradiplospinus* and the trichiurids *Aphanopus carbo*, *Benthodesmus*, *Lepturacanthus*, and *Trichiurus* is a simple tube with ventral and dorsal laminar ossifications that are extremely reduced (i.e., they do not extend along the entire length of the bone) or absent. *Gempylus* and the trichiurids *Aphanopus arigato*, *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps* have a jugal with well-developed ventral and dorsal laminar extensions that extend along the whole or most of the length of the bone. However, the condition is variable within genera (e.g., *Aphanopus*) and difficult to interpret since it depends on the size and degree of ossification of the specimens. The cleared and stained specimen of *Aphanopus arigato* analyzed in this study had well-developed laminar ossifications in the jugal, whereas a smaller specimen of *Aphanopus carbo* lacked the condition. Some specimens of *Diplospinus* and *Trichiurus* have small laminar ossifications anteriorly. Other specimens seem to show the presence of membranous dorsal and ventral extensions, which are not yet ossified.

#### Postorbital Ossification

**Character 9.** *Assurger*, *Benthodesmus*, *Evoxymetopon*, *Lepidopus*, *Lepturacanthus*, and *Trichiurus* have a paired, ossified element suspended in the adipose tissue of the posterior margin of the orbit (Fig. 11). The postorbital ossification in *Lepturacanthus* and *Trichiurus* is large, thick, and strongly ossified, whereas in *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* it is small, thin, and poorly ossified. This element does not appear to have a lateral-line canal. Laterally, it appears as a crescent-shaped ossification, but upon close examination it is plate-like and extends medially as a small postorbital shelf. The posterior face of the postorbital ossification tends to be slightly convex, whereas the anterior face is concave. In anterior view, the postorbital ossification of *Lepturacanthus* and *Trichiurus* appears triangular. The shape of this element in *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* is quite variable and dependent on the size of the specimens. In *Evoxymetopon* and *Lepidopus* the postorbital ossification bears dorsal or ventral processes at the lateral or medial corners. The outgroups and the rest of the trichiurids lack postorbital ossifications. Johnson (1986), Senta (1975), and James (1961) mentioned the presence of these ossifications but did not attempt any hypotheses of homology. Senta (1975) and James (1961) described these ossifications as the dermosphenotic. Although the homology between the conditions observed in *Lepturacanthus* and *Trichiurus* and the rest of the trichiurids having a postorbital ossification is inconclusive, I include this character complex in the data matrix as a multistate character.

#### JAWS

Johnson (1986) indicated that the scombroids are characterized by jaws with teeth that are peripherally ankylosed to the walls of a longitudinal crypt (tooth attachment Type 1 of Fink, 1981). He also indicated that tooth replacement within these longitudinal crypts occurs between the mature ankylosed teeth.

Accurate counts of the actual numbers of mature, ankylosed teeth in trichiurids are difficult because the old teeth are rapidly shed or resorbed after replacement and are easily lost in preserved specimens. There is no apparent systematic pattern of replacement, and within a species, two specimens of the same size may not correspond in their dental formula or arrangement of replacement and mature teeth. Soot-Ryen (1936) indicated that in *Aphanopus minor* Collett 1887 (= *A. carbo*), the number and placement of teeth vary considerably between individuals and so cannot be used as specific characters.

The trichiurids, as well as all the other scombroids, have teeth of reticulate or cancellous appearance internally when viewed in glycerin (Johnson, 1986). A longitudinal crypt extends along the dorsal margin of the dentary and the ventral margin of the premaxilla, serving as the base for a uniserial row of teeth in each of these bones. These teeth are mediolaterally flattened and triangular, with well-developed anterior and posterior cutting edges, except in the dentary of *Nesiarchus* where they are retrorse. Large specimens of *Nesiarchus* and the trichiurids *Lepturacanthus* and *Trichiurus* are distinct in that some of the anterior-most teeth in the longitudinal series of the dentary are barbed. The serial teeth of the trichiurids *Lepturacanthus* and *Trichiurus* have well-developed barbs at their points, whereas those of *Nesiarchus* have no barbs or are extremely reduced in some specimens.

Most trichiurids and outgroups have a pair of small fangs on the dentary (Fig. 12). These fangs are barbed and large in *Lepturacanthus* and *Trichiurus*. Some large specimens of *Lepidopus caudatus* and *Lepidopus fitchi* also bear reduced barbs on the dentary fangs. The condition is also variable within genera. For example, of the two species of *Eupleurogrammus*, only *E. glossodon* has dentary fangs (Nakamura and Parin, 1993).

A pair of small canine teeth on the premaxilla project forward and are visible from a dorsal aspect in *Lepturacanthus*. *Eupleurogrammus*, *Tentoriceps*, and *Trichiurus* also have a pair of small, anteriorly directed teeth on the premaxilla, but these are not visible in dorsal view. Nakamura and Parin (1993) noted the presence of two small canine teeth projecting forward on the premaxillary symphysis as a character that differentiates *Lepturacanthus* and *Trichiurus*. This character is dependent on the size of the specimens, and it is quite variable within genera.

All gempylids and trichiurids in this study had a

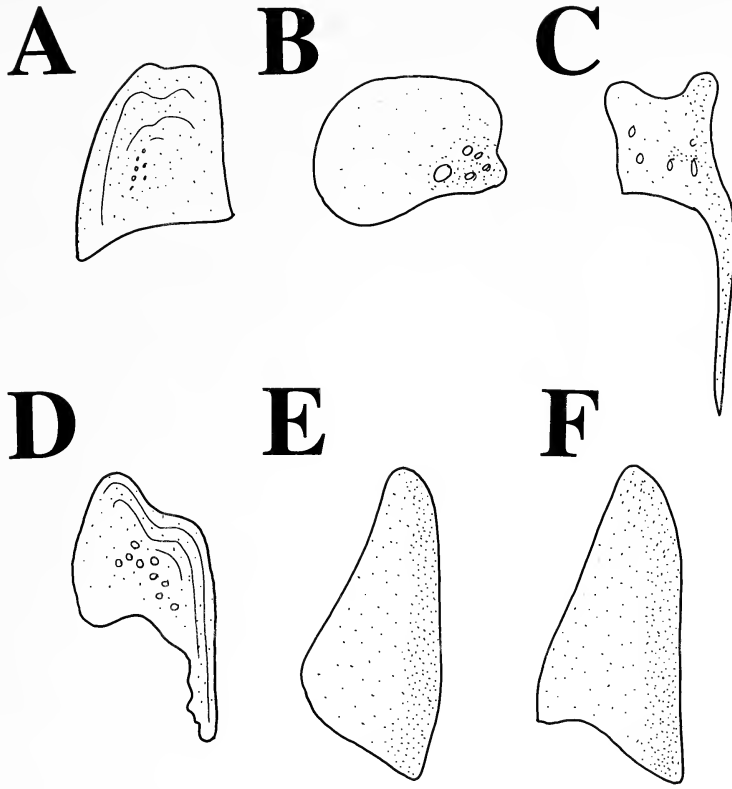


Figure 11. Anterior view of the left postorbital ossification: (A) *Assurger anzac*; (B) *Benthodesmus tenuis*; (C) *Evoxymetopon taeniatum*; (D) *Lepidopus caudatus*; (E) *Lepturacanthus savala*; (F) *Trichiurus lepturus*.

cluster of up to six fangs at the tip of the premaxilla. These teeth are not part of the longitudinal crypt and are rounder in cross section, larger, and stronger than those of the longitudinal series. Some of the teeth in this cluster are depressible. The anterior fangs in *Lepturacanthus* and *Trichiurus* have well-developed barbs. Some large specimens of *Eupleurogrammus*, *Lepidopus caudatus*, and *Nesiarchus* may also bear reduced barbs on their premaxillary fangs. The presence of barbs might represent a more derived condition than that noted by Russo (1983: character 37), where the gempylids *Gempylus*, *Nealotus*, *Nesiarchus*, *Promethichthys*, *Rexea*, and *Thyrstitoides* are characterized by having fangs with an extended, flattened cutting edge on the posterodistal surface. He considered that the condition of simple pointed fangs found in *Diplospinus*, *Paradiplospinus*, and the rest of the gempylid genera represented the plesiomorphic state. However, the presence of barbs on the premaxillary fangs is variable within genera and species. For example, Nakamura and Parin (1993) reported that *Trichiurus auriga* Klunzinger 1884 and most specimens of *Eupleurogrammus* lack barbs on the premaxillary fangs.

**Character 10.** All of the species analyzed in this study have serial teeth with smooth edges, except

for those in the outgroup *Gempylus* and the trichiurid *Aphanopus*, which have serrate edges. The premaxillary fangs of large specimens of *Aphanopus* and the outgroup *Gempylus* are also serrate. Maul (1953) reported the presence of minute serrations along the anterior margin of the premaxillary canines of *Benthodesmus simonyi*. The specimen of *B. simonyi* analyzed in the present study (USNM 292768) has only slight irregularities along the margins of the fangs and serial teeth. These irregularities are not comparable to the serrations of *Aphanopus* or *Gempylus*. Russo (1983) noted that among the gempylids only *Gempylus* and *Thyrstites* have serrate edges on their fangs and serial teeth. However, *Gempylus* has serrations in both the posterior and anterior edges, whereas *Thyrstites* bears serrations only on the anterior edge of the fangs and the posterior edges of the serial teeth. Russo (1983: character 38) considered the presence of serrations on the premaxillary fangs as the apomorphic condition. I agree with Russo (1983), but extend the character to include the presence of serrations on the anterior and posterior edges of the fangs and the serial teeth as the apomorphic condition.

#### Lower Jaw

**DENTARY.** Posteriorly, the dentary is divided into a ventral and a dorsal arm (process). A large

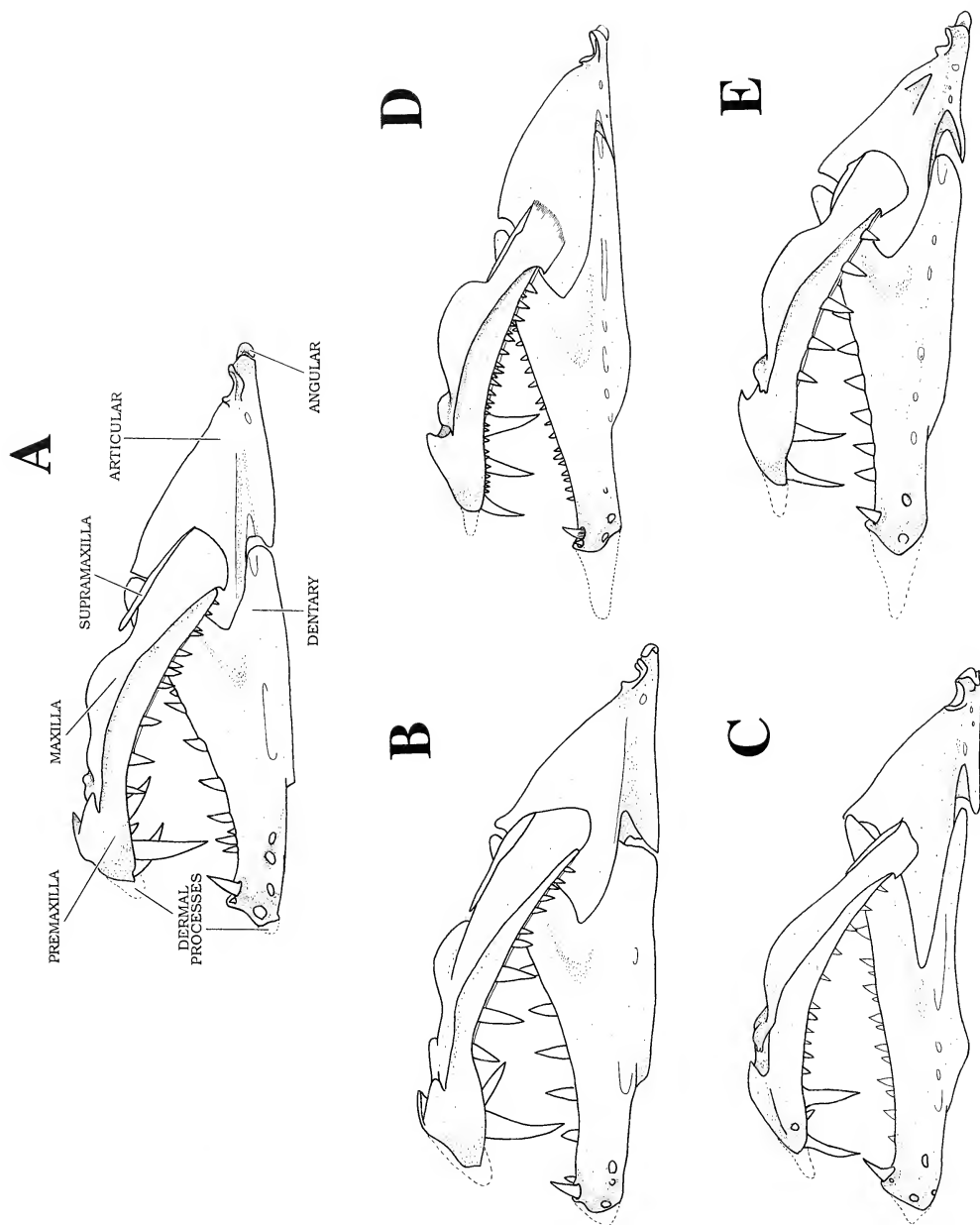


Figure 12. A-E. Lateral view of the left lower and upper jaw bones: (A) *Benthodesmus tenuis*; (B) *Diplospinus multistriatus*; (C) *Paradipliospinus antarcticus*; (D) *Assurger anzac*; (E) *Assurger anzac*.

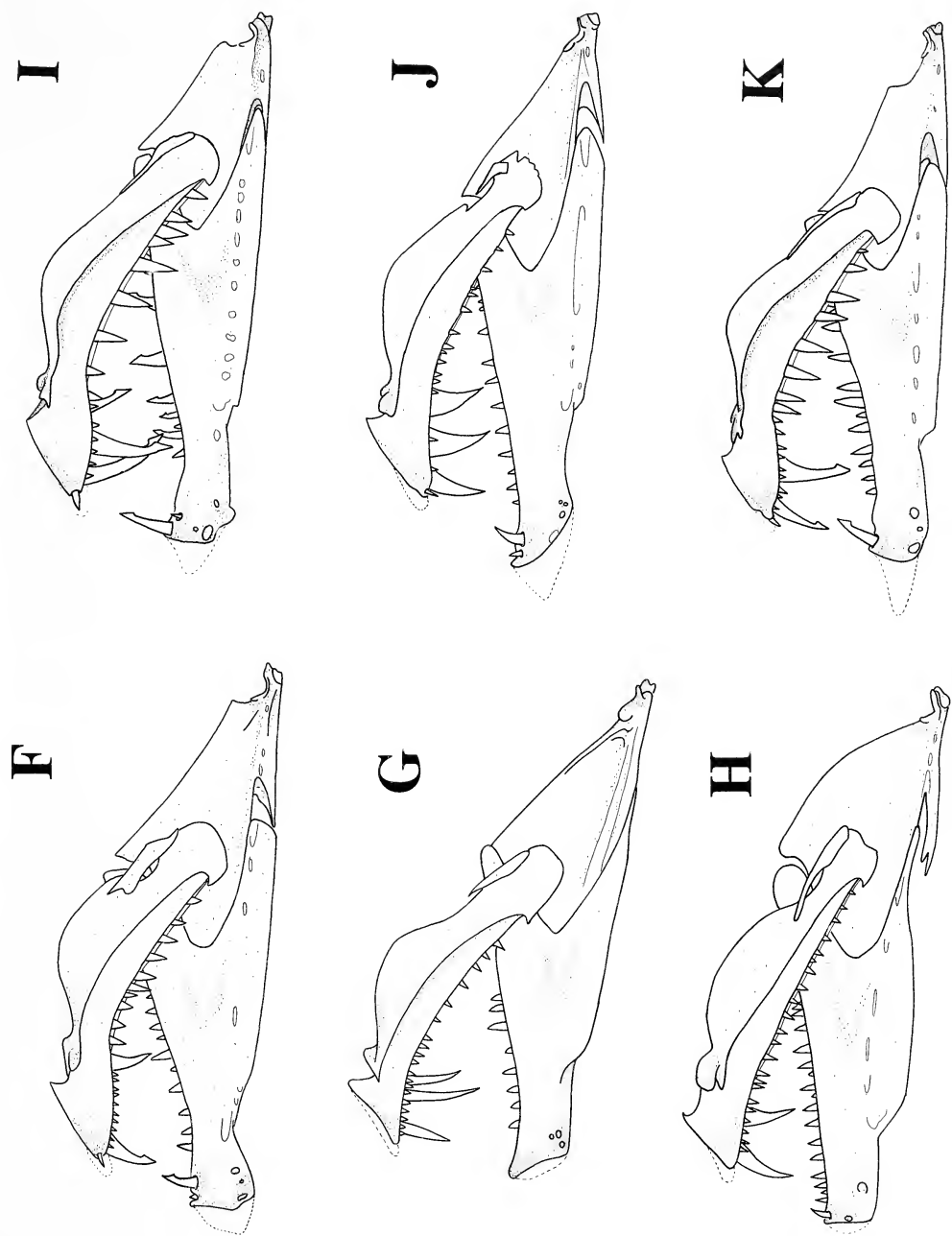


Figure 12. F-K. Lateral view of the left lower and upper jaw bones: (F) *Eupleurogrammus glossodon*; (G) *Euxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriiceps cristatus*; (K) *Trichiurus lepturus*.

anteromedial fossa between the two arms accepts the anterior process of the articular. The dentary is sutured anteriorly with the tip of Meckel's cartilage at the mandibular symphysis.

Russo (1983) noted that the presence of a fleshy conical process at the mandibular symphysis is always correlated with the occurrence of a similar structure at the premaxillary symphysis, and he considered it apomorphic among gempylids. However, there is some disagreement among authors about the presence or absence of these conical processes in the gempylids *Diplospinus* and *Nealotus*. Russo (1983) reported them in *Nealotus*, whereas Parin and Becker (1972) and Nakamura and Parin (1993) did not. Russo (1983) also characterized *Diplospinus* by the absence of such processes, whereas Nakamura and Parin (1993) noted their presence only at the premaxillary symphysis. The confusion may be a result of the reduced condition of these conical processes in some genera. The mandibular symphyses of all the trichiurids and the outgroups analyzed in this study have an anteriorly directed, external conical process (dermal process of Nakamura and Parin, 1993). In the outgroups *Diplospinus* and *Paradiplospinus*, the trichiurid *Evoxymetopon*, and some species of *Lepidopus*, this conical process is extremely reduced, and it is easily overlooked, except in cleared and stained specimens examined through transmitted light. This conical process has been described by some authors (Tucker, 1956; James, 1961; Parin and Becker, 1972; Russo, 1983) as a cartilaginous projection, but it does not stain with alcian blue.

**ARTICULAR.** The articular forms the posterior angle of the lower jaw and couples it to the palatoquadrate. Anteriorly, a large, triangular process fits into the anteromedial fossa of the dentary. Besides this anteromedial process, the articular also bears a dorsal, a ventral, and a posterior process. The dorsal and ventral processes are anteriorly directed and shorter than the anteromedial triangular process of this bone. Their tips abut or approach the posterodorsal and posteroventral arms of the dentary. The posterior process of the articular is hook-shaped, and it bears a transverse dorsal articular fossa for articulation with the quadrate. The ventral corner of this posterior process bears medial and lateral depressions in which the angular fits. The morphology of this bone is similar in all of the species studied.

**ANGULAR.** The angular is a small hook-shaped bone that fits on the posteroventral corner of the articular. A small arm fits laterally on the posteroventral corner of the articular, whereas a longer arm curves around and fits into a depression on the medial side. In all the outgroups and the trichiurids this medial arm extends anteriorly along the medial face of the posteroventral corner of the articular as an elongate, tubular process. The extent of the elongation of the medial arm is variable among genera. In some genera the medial arm extends dorsally, forming a wider, plate-like process that covers

most of the medial face of the posteroventral corner of the articular. The shape of the medial arm of the angular is quite variable and it is difficult to categorize into objective character states.

## Upper Jaw

**PREMAXILLA.** All the trichiurids and the outgroups have an external dermal process at the premaxillary symphysis. As indicated earlier in the description of the dentary bone, this structure is considered together with the presence of a dermal process at the mandibular symphysis. The premaxillary dermal process tends to be smaller than that present at the dentary. This dermal process in the trichiurids is also smaller than that of the outgroups *Diplospinus* and *Paradiplospinus*.

All scombroids are characterized by having a nonprotrusible upper jaw, with the premaxilla strongly attached to the maxilla and the ethmovomerine region of the neurocranium (Collette et al., 1984: character 19; Johnson, 1986: character 9).

A small, ascending process extends dorsally from the anterior tip of the premaxilla. The ascending process abuts the rostral cartilage, which provides a pivot point for the dorsoventral rotation of the premaxilla (Johnson, 1986). The trichiurids are characterized by the presence of a shortened, ascending process on the premaxilla. Russo (1983: character 39) indicated that the gempylids also share the presence of a short, ascending process of the premaxilla.

Posterior to the ascending process, a small, dorsal process serves as the articular condyle for the maxilla. The descending arm of the premaxilla extends posteriorly and medially to the maxilla. The posterior-most margin of the premaxilla does not extend past the descending arm of the maxilla. Russo (1983: character 40) also found that all the gempylids were characterized by a posterior premaxillary arm that does not extend beyond the descending arm of the maxilla.

**MAXILLA.** Anteriorly, the maxilla has a strong, rounded articular head that articulates with the palatoquadrate and the ethmovomerine region of the neurocranium. Ventrally, the articular head is also divided by a notch that accepts the articular condyle of the premaxilla.

Posterior to the articular head, the maxilla becomes narrow, forming a small dorsal depression that accepts the maxillary process of the palatine. The descending arm of the maxilla becomes wider as it extends posteroventrally and completely covers the descending arm of the premaxilla. Dorsally, the descending arm of the maxilla may expand into a dorsal ridge that serves as an attachment point for the adductor mandibulae. Russo (1983: character 42) indicated that all gempylids share the presence of a well-developed dorsal ridge that arches high above the dorsal margin of the maxilla. He also noted that a more derived state was present in the genus *Gempylus*, where the ridge is extremely



large and occupies about two thirds of the anterior half of the maxilla. All the trichiurids, except *Aphanopus*, *Lepturacanthus*, and *Trichiurus*, have well-developed dorsal ridges. The presence of a well-developed dorsal ridge on the maxilla is correlated with a dorsal notch formed between the dorsal ridge and the posterior margin of the maxilla. In those cases where the dorsal notch is present, the posterior margin of the maxilla is dorso-ventrally expanded. The extent of the dorsal ridge of the maxilla is quite variable, and this character cannot be easily categorized.

The posterodorsal corner of the maxilla accepts the posterior half of the supramaxilla, which extends anteriorly and sometimes reaches the posterior margin of the dorsal ridge. The posteroventral corner of the maxilla is hook-shaped and expands beyond the ventral margin of the descending arm of the premaxilla.

**SUPRAMAXILLA.** All the trichiurids, except *Eupleurogrammus*, and outgroups, except *Nesiarchus*, have an extremely reduced, splint-like supramaxilla. Russo (1983: character 43) considered the presence of a reduced splint-like supramaxilla as a derived condition uniting the gempylids *Diplospinus*, *Gempylus*, and *Paradiplospinus*. The trichiurid *Eupleurogrammus* and the outgroup *Nesiarchus* are characterized by having a much wider, well-developed supramaxilla. However, it is difficult to categorize the variation in the size of the supramaxilla into objective character states. In those trichiurids and gempylids having a well-developed dorsal notch on the descending arm of the maxilla (*Asurger*, *Benthodesmus*, *Diplospinus*, *Eupleurogrammus*, *Evoxymetopon*, *Gempylus*, *Lepidopus*, *Nesiarchus*, *Paradiplospinus*, and *Tentoriceps*), the supramaxilla originates laterally on a dorsal plate-like expansion of the posterior margin of the maxilla. In most cases, the supramaxilla extends anteriorly over the dorsal notch of the maxilla and its anterior half remains unattached. In *Eupleurogrammus* and *Lepidopus*, the anterior margin of the supramaxilla reaches and attaches to the dorsal ridge of the maxilla. The central part of the body of the supramaxilla remains free and unattached to the maxilla. The trichiurids *Aphanopus*, *Lepturacanthus*, and *Trichiurus* lack a well-developed dorsal notch, and the supramaxilla simply extends along the dorsal margin of the maxilla to which it attaches.

## SUSPENSORIUM

Collette and Russo (1984) separated the bones of this series into the palatine and hyoid arches. The palatine arch consists of the palatine, ectopterygoid, endopterygoid, and metapterygoid. The hyoid arch includes the hyomandibula, symplectic, quadrate, and hyoid complex. I include the palatine and hyoid arches as part of the suspensorium (Fig. 13) but exclude the hyoid complex, which is discussed separately.

## Hyomandibula

The hyomandibula has a cruciform dorsal process bearing three articular condyles. The anterior and dorsal condyles articulate with the hyomandibular fossa of the otic capsule (formed by the sphenotic, pterotic, and prootic), whereas the posterior condyle articulates with the articular fossa of the opercle.

The hyomandibula bears an elongate ventral arm with a prominent lateral ridge that is pointed at its dorsal tip. The lateral ridge serves as the attachment point to the anterior margin of the preopercle and the posterior margin of the metapterygoid. The angle between the anterior articular condyle and the ventral arm extends as a small plate that is fused medially and laterally to the dorsal corner of the metapterygoid. The morphology of the hyomandibula is similar among the taxa analyzed in this study.

## Symplectic

The symplectic lies between the quadrate, metapterygoid, interhyal, and hyomandibula. It is tube-like, with the ventral half fitting along the postero-medial fossa of the quadrate. Anterodorsally, it has a plate-like extension that abuts the posteroventral corner of the metapterygoid medially. Posterodorsally, the symplectic of all trichiurids and the outgroups bear a spine-like extension that is covered by the posterodorsal process of the quadrate.

## Quadrate

In the trichiurids, the quadrate joins the lower jaw to the rest of the suspensorium. It is triangular and bears a transverse mandibular condyle on the ventral corner that fits on the articular fossa of the articular bone. The anterior margin articulates with the ventral arm of the ectopterygoid, whereas the dorsal margin abuts the metapterygoid. Posteromedially, it bears a depression that accepts the ventral portion of the symplectic.

*Character 11.* The posterior margin of the quadrate is strongly ossified and bears a posterodorsal process. This process is elongate and extends well past the ventral margin of the metapterygoid in all outgroups and trichiurids, except *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*. In *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* the process is shorter and does not extend well past the ventral margin of the metapterygoid. The strong posterior margin serves as an attachment surface for the anteroventral arm of the preopercle.

## Metapterygoid

Anteromedially, the metapterygoid articulates with the ectopterygoid and the endopterygoid. Medially along the posteroventral corner, an extremely shallow fossa accepts the anterodorsal plate-like extension of the symplectic. The dorsal corner is usually divided into a medial and a lateral extension that

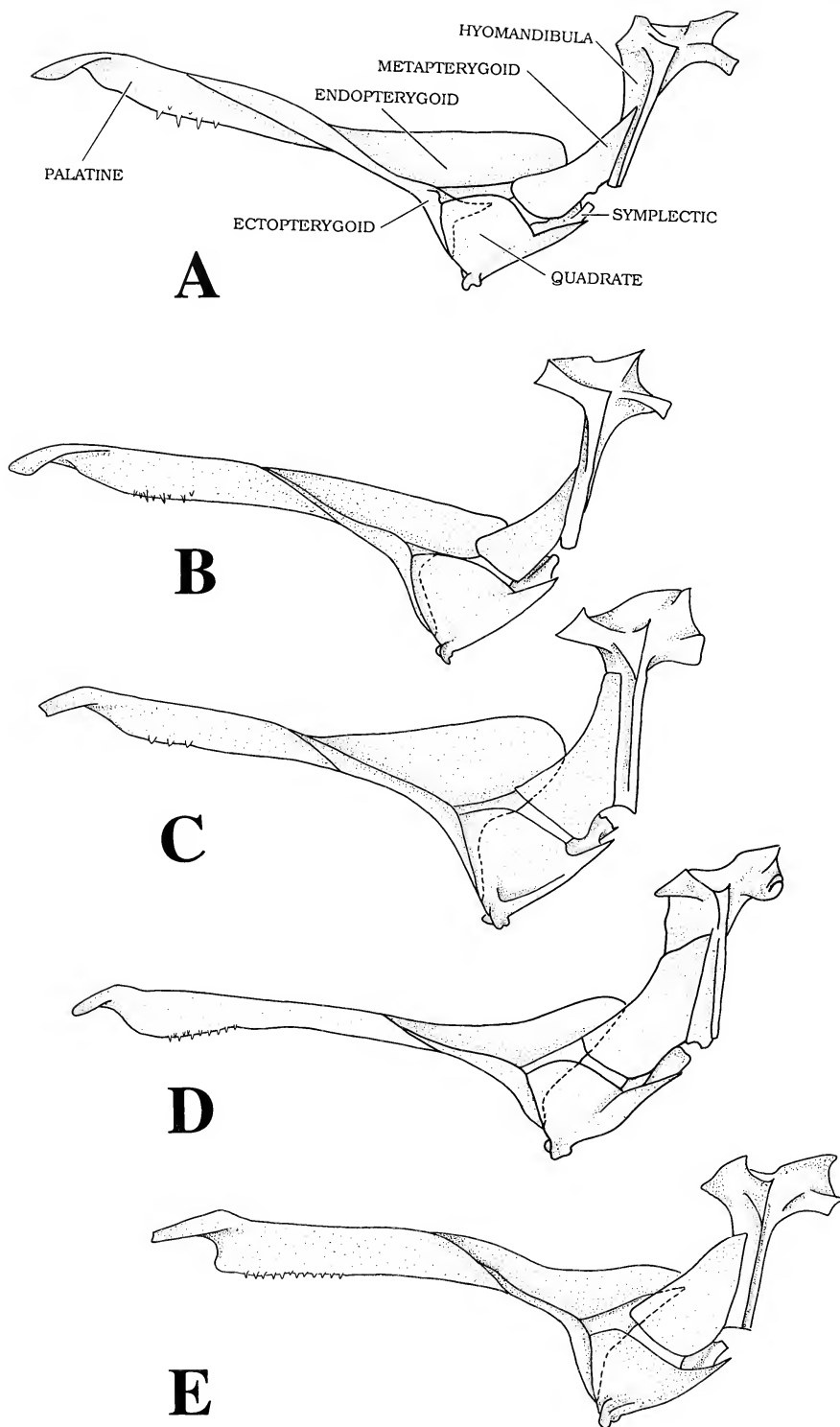


Figure 13. A–E. Lateral view of the left suspensorium: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

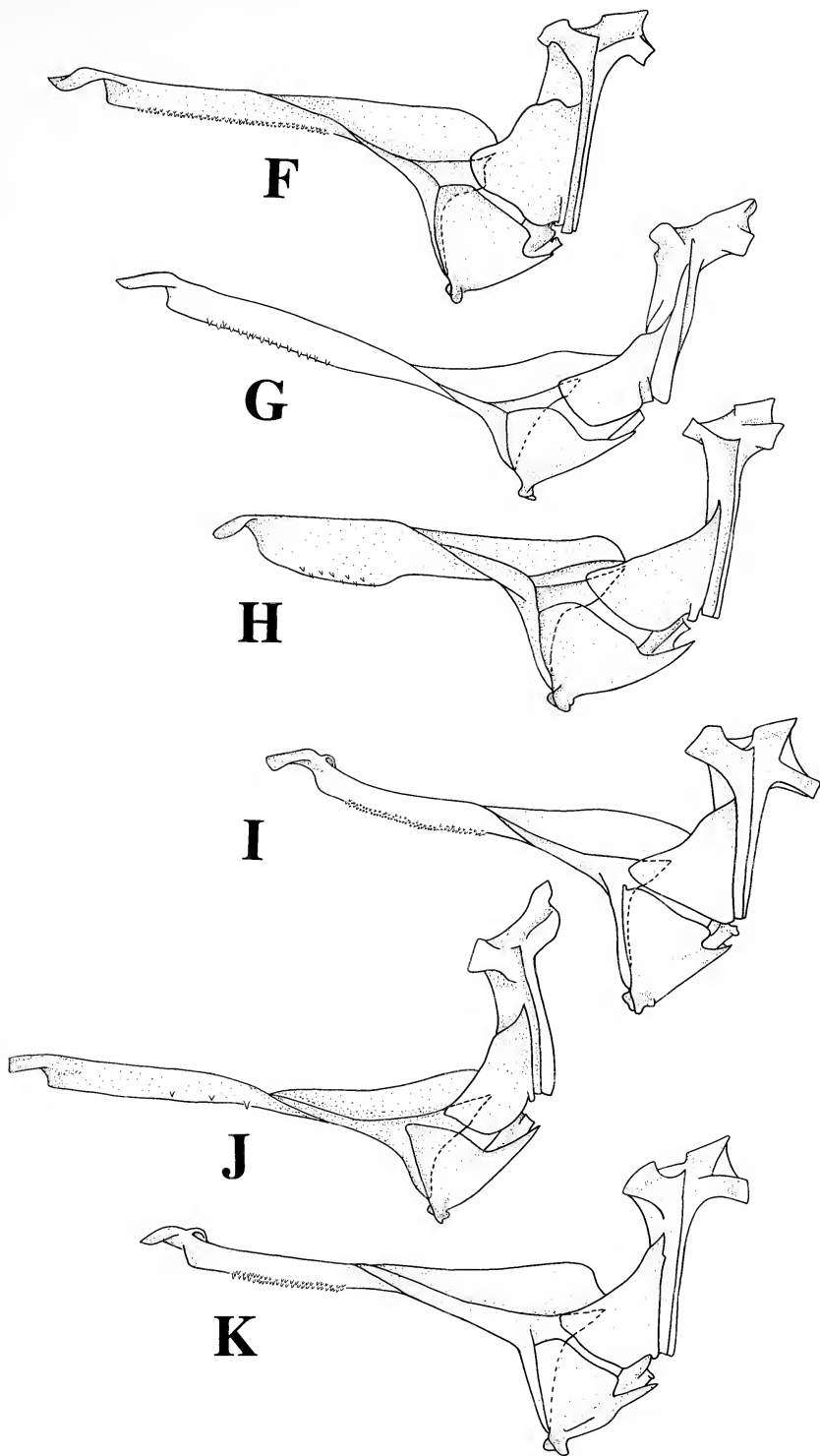


Figure 13. F-K. Lateral view of the left suspensorium: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

are strongly fused to the plate-like process at the angle between the anterior articular condyle and the ventral arm of the hyomandibula. All trichiurids and outgroups, except *Diplospinus* and *Paradiplospinus*, have well-developed lateral and medial processes on the metapterygoid. Russo (1983: character 45) noted that among the gempylids, only *Diplospinus*, *Lepidocybium*, and *Paradiplospinus* bear reduced lateral and medial processes on the metapterygoid. He noted that in these genera the dorsal margin of the metapterygoid appears to come to a single point, giving the bone a triangular appearance. All trichiurids, except some specimens of *Eupleurogrammus*, have a lateral process that comes to a point dorsally. However, the medial process is well developed and flat on its dorsal margin. The lateral shape of the metapterygoid is quite variable and difficult to categorize. This potential character is excluded from the present analysis, although it may prove to be useful in a future study of the gempylids and trichiurids in which its variation can be assessed more extensively.

### Ectopterygoid

The ectopterygoid is composed of three or four arms (anterior, posteromedial, posterolateral, and ventral) that join this bone to the endopterygoid, palatine, quadrate, and sometimes metapterygoid. The posterior margin of the ventral arm articulates with the anterior margin of the quadrate. The anterior arm articulates with the lateral margin of the endopterygoid and fits into the longitudinal fossa of the palatine. *Nesiarchus* bears both a posterolateral and a posteromedial arm. These posterior arms articulate with the lateral margin of the endopterygoid and the anterodorsal corner of the quadrate. The posteromedial arm of *Nesiarchus* is much longer than the posterolateral arm, but it never reaches the anteroventral corner of the metapterygoid. In *Diplospinus*, *Gempylus*, *Paradiplospinus*, and all trichiurids only the posteromedial arm is present.

**Character 12.** In the outgroups, the posteromedial arm of the ectopterygoid articulates only with the lateral margin of the endopterygoid and the anterodorsal corner of the quadrate. All trichiurids are characterized by having a much longer posteromedial arm that extends up to and articulates with the anteroventral corner of the metapterygoid.

### Endopterygoid

The lateral margin of the endopterygoid articulates anteriorly with the ectopterygoid and palatine and posteriorly with the metapterygoid. The endopterygoid of *Lepturacanthus* has a tuberculous patch anteriorly that bears a few small teeth. Although the anterior portion of the endopterygoid is better ossified than the posteromedial shelf, none of the outgroups or the rest of the trichiurids bear any teeth on this bone.

### Palatine

The palatine attaches to the maxilla, the ethmoid, and the lateral ethmoid. Posteriorly, it bears a longitudinal fossa that serves as the surface for articulation with the anterior arm of the ectopterygoid and the lateral margin of the endopterygoid. Anteriorly, a hooked maxillary process fits above the dorsal depression that is present posterior to the articular head of the maxilla.

**Character 13.** A small, medially directed shelf that serves as an articulation point with the ethmoid is evident in the trichiurids and outgroups. Posterior to this small medial shelf, *Lepturacanthus* and *Trichiurus* also bear a well-developed, medially directed condyle at the dorsal corner between the maxillary process and the main body of the palatine. This condyle abuts the posterior margin of the palatal process of the ethmoid and is visible in lateral view.

**Character 14.** All of the outgroups and most of the trichiurids are characterized by having only a few teeth arranged uniserially and not covering the whole length of the ventral margin of the palatine. A few replacement teeth are usually present on the medial face of the palatine above and between the teeth in the main ventral series. Of the trichiurids, only *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* bear large numbers of teeth arranged in several rows and covering most of the length of the ventral margin of the palatine. In *Lepturacanthus* the condition is further modified and part of the medial side of the palatine is covered by a patch of small teeth. Maul (1953) noted that the palatine teeth in *Benthodesmus simonyi* are covered by a fleshy fold and that, in preserved specimens, the fold closes up so tightly that the presence of palatine teeth can be easily overlooked. The case is similar for the preserved specimens of the other trichiurid genera, which may explain previous reports of the absence of palatine teeth in some taxa. Tucker (1956) noted the difficulty in finding the palatine teeth in trichiurids and suggested that reports on their absence should not be taken too seriously.

### HYOID COMPLEX

The hyoid complex is composed of a series of bones that articulate with the suspensorium and support the branchiostegal rays (Fig. 14).

### Interhyal

The interhyal connects the hyomandibula to the epihyal. It is a small, cylindrical bone that is usually constricted in the middle and expanded at the tips. The morphology of this bone is similar among the taxa analyzed in this study.

### Epihyal

The anterior margin of the epihyal is broad and articulates with the posterior margin of the ceratohyal. This anterior articulation includes blocks of

cartilage at the dorsal and ventral corners and suturing by way of odontoid processes in the middle. The posterior end of the epihyal narrows into an apex that bears a dorsal articular fossa for articulation with the interhyal. In the trichiurids, the three posterior-most branchiostegal rays attach laterally to the ventral margin of this bone. The morphology of the epihyal is similar among the taxa analyzed in this study.

### Ceratohyal

The ceratohyal is a flattened bone that articulates posteriorly with the epihyal via blocks of cartilage and suturing by way of odontoid processes. The three anterior-most branchiostegals articulate medially on the ventral margin of this bone, whereas the fourth branchiostegal articulates laterally at the posteroventral corner. The hyoidean groove (Collette and Russo, 1984) runs longitudinally along the lateral face of the ceratohyal. A small slit on the hyoidean groove (the beryciform foramen of McAllister, 1968; or ceratohyal window of Collette and Chao, 1975) is present in *Eupleurogrammus*, *Evoxymetopon*, *Lepturacanthus*, *Tentoriceps*, and the outgroups *Diplospinus* and *Nesiarchus*. This interpretation differs from the observations of Russo (1983), who indicated that *Diplospinus* and *Nesiarchus* lack a ceratohyal window. Collette and Russo (1984) noted that the presence of a ceratohyal window within the Spanish mackerels (*Scomberomorus*: Scombridae) is quite variable.

Anteriorly, the ceratohyal articulates with the dorsal and ventral hypohyals by way of a layer of cartilage; the anteroventral corner of the ceratohyal projects anteriorly to articulate with the posteroventral notch of the ventral hypohyal.

**Character 15.** In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the anterodorsal corner of the ceratohyal is pointed and extends anteriorly, abutting the dorsal margin of a layer of cartilage on the posterior margin of the dorsal hypohyal. All other trichiurids and outgroups lack this anterodorsal extension of the ceratohyal. In *Aphanopus* and some specimens of *Lepidopus fitchi*, the anterodorsal corner extends only slightly anteriorly, but it is not pointed and does not abut the dorsal margin of the cartilage of the dorsal hypohyal.

### Dorsal Hypohyal

Anteriorly, the dorsal hypohyal articulates with the ventral hypohyal by suturing with odontoid processes, whereas posteriorly it articulates via a block of cartilage. The posterior margin articulates with the anterior margin of the ceratohyal by way of a layer of cartilage. The anterodorsal corner bears a medial projection that forms a symphysis with the opposing dorsal hypohyal, the anterior tip of the first basibranchial, and the posterior margin of the glossohyal.

The dorsal hypohyal of the trichiurid *Leptura-*

*canthus* is unique in that it bears teeth along the anterior half of its dorsal margin. These teeth are not part of a dermal plate or patch, and they are fused to the bony element. *Eupleurogrammus* bears longitudinal patches of teeth on the dorsal margin of the dorsal hypohyal. However, these tooth patches are part of the epithelium covering the bone and they are not fused to it.

### Ventral Hypohyal

The ventral hypohyal is joined dorsally to the dorsal hypohyal. The posteroventral corner forms a longitudinal notch where the elongate anteroventral corner of the ceratohyal fits. The anteroventral corner bears a ventral projection that serves as the site for attachment of the ligaments coming from the articular head of the urohyal. The morphology of the ventral hypohyals is similar among the taxa analyzed in this study.

### Glossohyal

The glossohyal is a median bone supporting the tongue. It is covered with flesh, and in the trichiurid *Eupleurogrammus*, it is unique in that it bears two elongate, dermal tooth patches dorsally. *Evoxymetopon* bears a few minute teeth on the lateral margins of the tongue. In both *Eupleurogrammus* and *Evoxymetopon*, the tooth patches are part of the flesh covering the glossohyal; they are not fused to the bone. All other trichiurids and outgroups analyzed in this study lack glossohyal teeth. Posteriorly, the glossohyal articulates with the anterodorsal corner of the dorsal hypohyals and the anterior margin of the first basibranchial. The dorsal face of this bone is flat or slightly concave in all the taxa analyzed in this study. Posteroventrally, the trichiurids and the outgroups, except *Gempylus*, have two lateral processes that converge anteriorly by way of a longitudinal keel. *Gempylus* bears these posteroventral processes but lacks a longitudinal keel.

**Character 16.** Russo (1983: character 51) considered the presence of quadrilateral posteroventral processes on the glossohyal as a derived condition among gempylids. I agree with Russo (1983) and consider the condition observed in *Nesiarchus* and most of the gempylids including *Lepidocybium*, in which the posteroventral processes do not appear quadrilateral, as the plesiomorphic state. He separated the condition observed in *Gempylus* as a different character. As indicated by Russo (1983: character 50), the posteroventral processes of the glossohyal in *Gempylus* are wing-like and have the distal ends pointing posteriorly. In this study, the conditions regarding the shape of the posteroventral processes are combined into a single multistate character. There are three derived conditions regarding the shape of the posteroventral processes relative to the state found in *Nesiarchus* and most of the gempylids: triangular, quadrilateral, and wing-like with the distal ends pointing posteriorly. *Diplospinus*, *Paradiplospinus*, and all trichiurids,

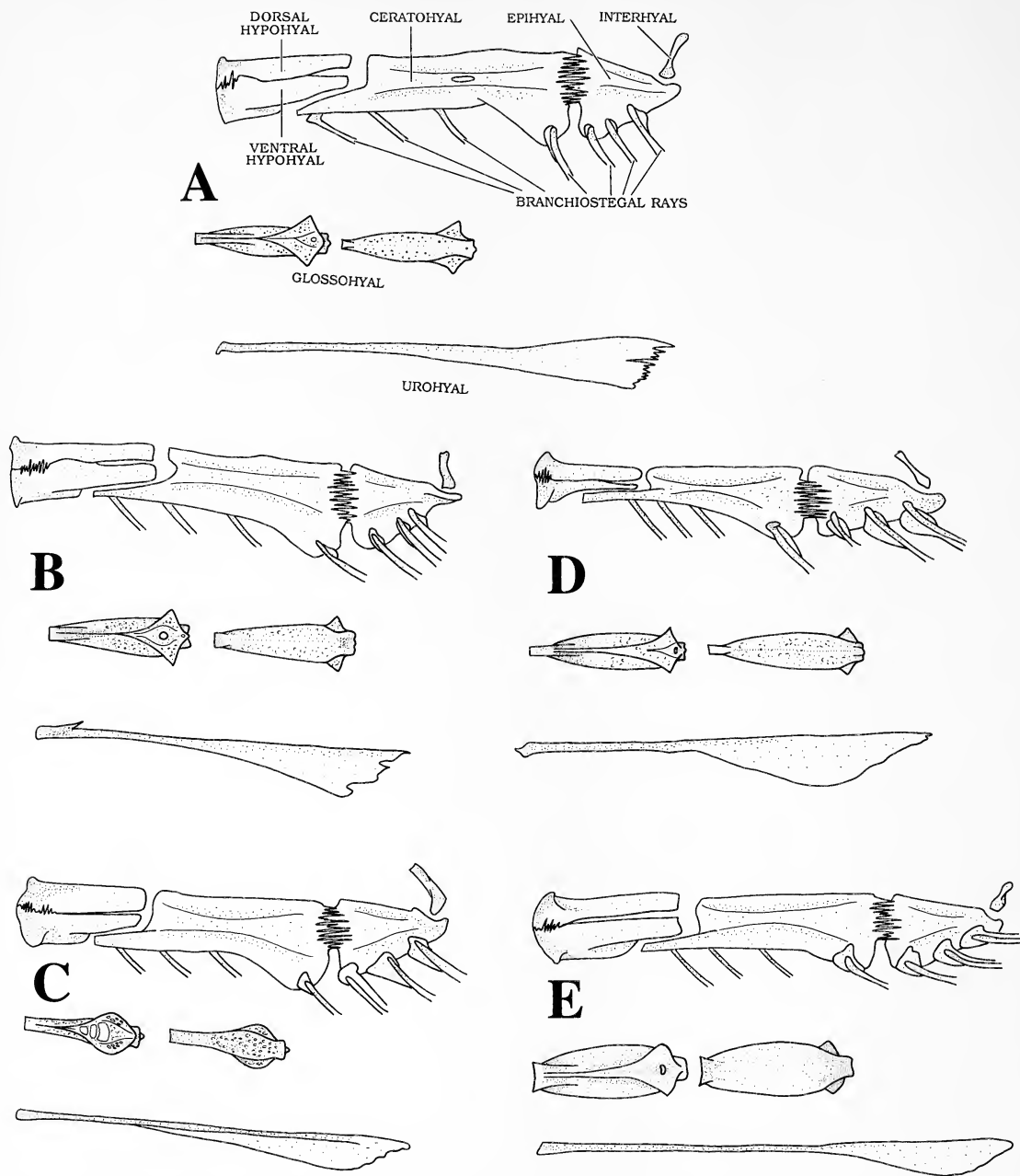


Figure 14. A-E. Lateral view of the left hyoid complex; the glossohyal is represented from left to right in ventral and dorsal views, respectively: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

except *Eupleurogrammus*, *Lepturacanthus*, *Tentoriiceps*, and *Trichiurus*, have ventral processes that appear quadrilateral in ventral view. The trichiurids *Aphanopus* and *Benthodesmus* bear posteroventral processes that appear quadrilateral, although not as pronounced as those in *Diplospinus* and *Paradiplospinus*. In some large specimens of *Aphanopus* and *Benthodesmus*, the lateral corners of the pos-

teroventral processes are rounded. The glossohyal of *Eupleurogrammus*, *Lepturacanthus*, *Tentoriiceps*, and *Trichiurus* bears triangular posteroventral processes. Furthermore, the posteroventral processes in *Gempylus* and *Nesiarchus* are located more anteriorly, leaving a well-developed posterior articular head in the glossohyal. In all trichiurids and the outgroups *Diplospinus* and *Paradiplospinus*,

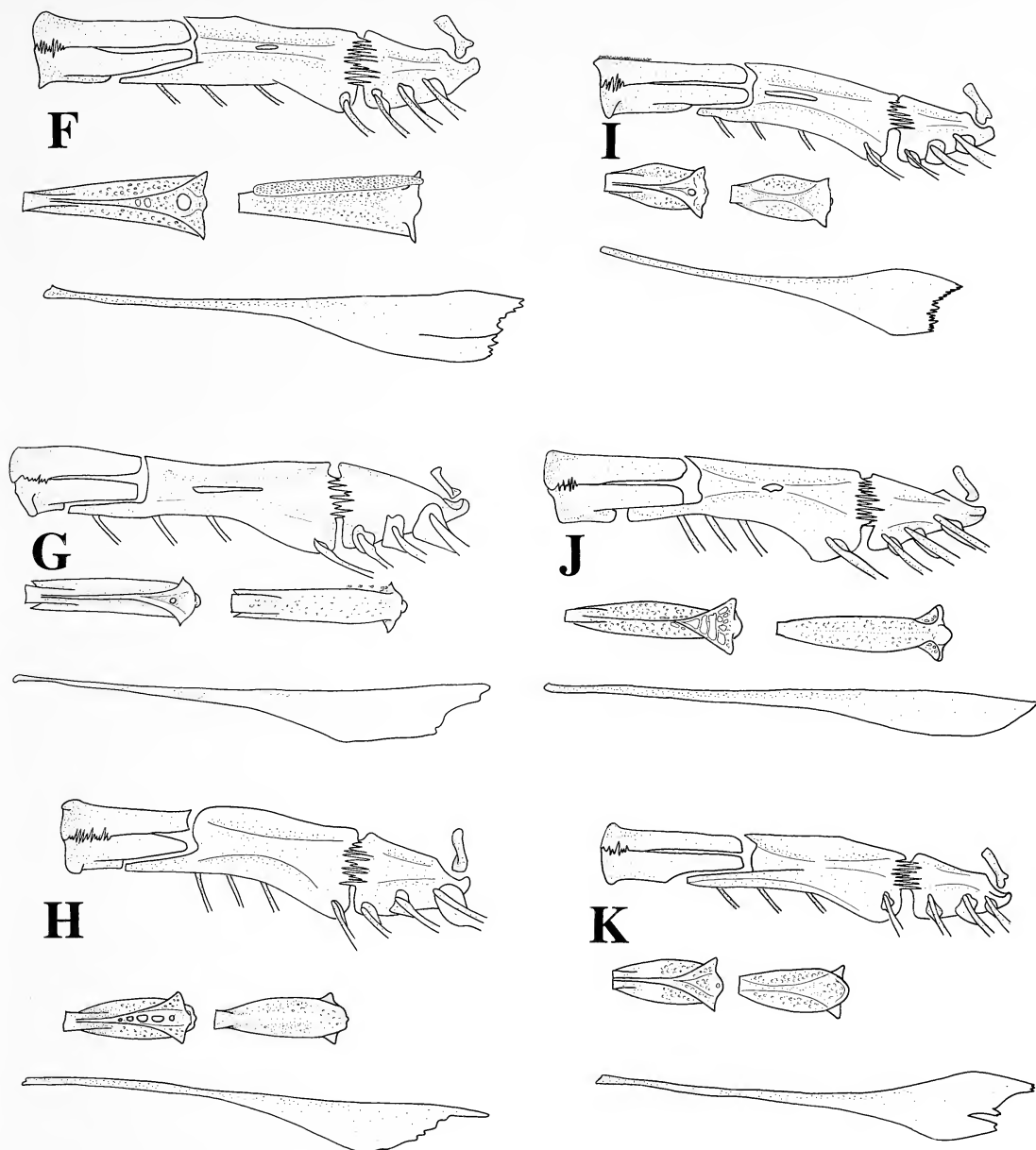


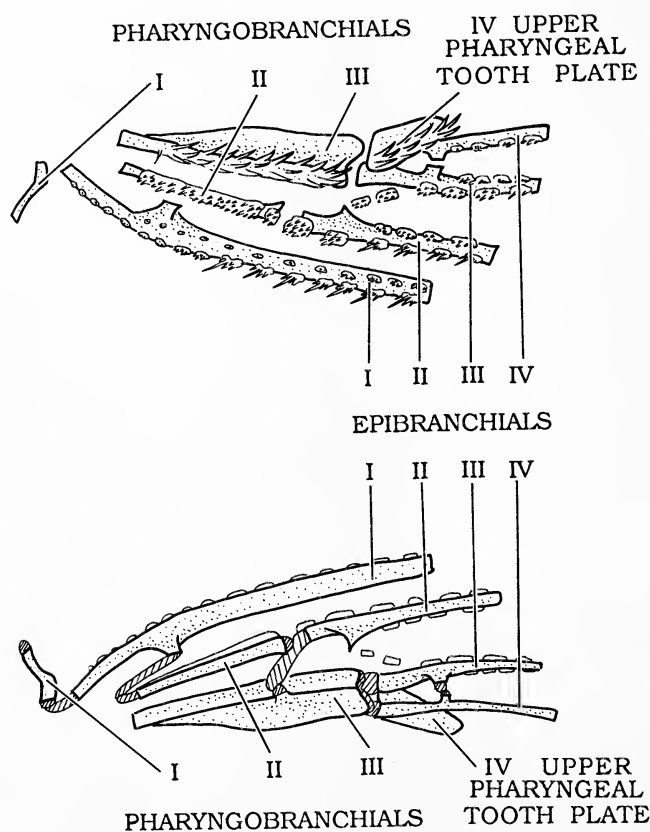
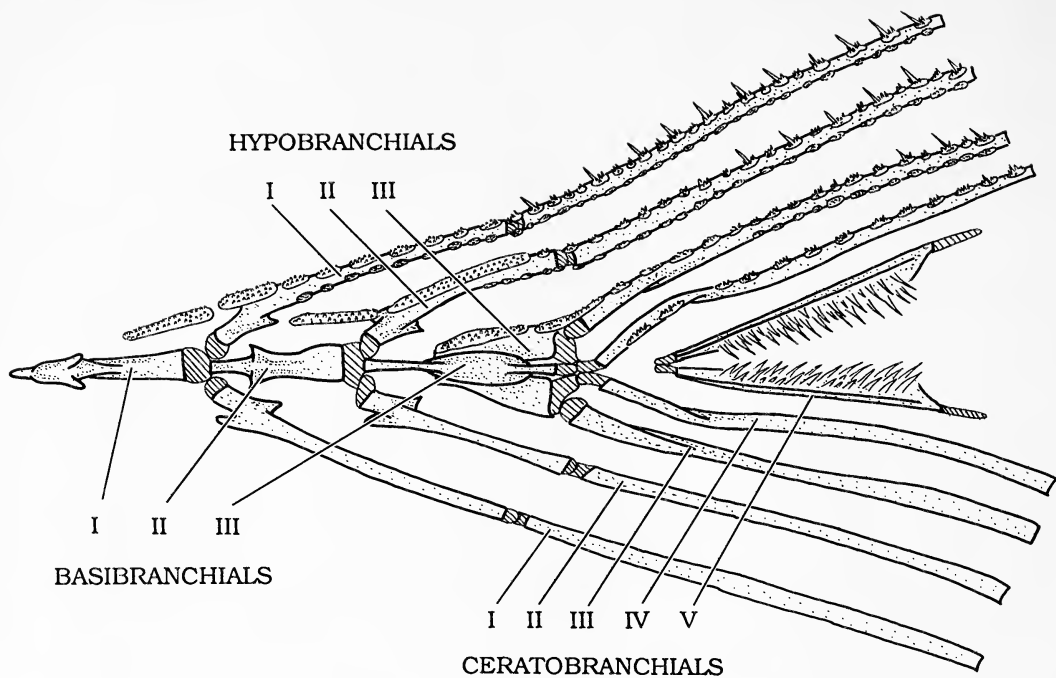
Figure 14. F–K. Lateral view of the left hyoid complex; the glossohyal is represented from left to right in ventral and dorsal views, respectively: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lep-turacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

the posteroventral processes are located farther posteriorly and the glossohyal bears a more reduced posterior articular head.

### Urohyal

The urohyal is a median bone with an anterior end that is a thin rod bearing a small articular head. This articular head is generally forked and is connected to the ventral hypohyals by two strong lat-

eral ligaments. Posterior to the articular head, the outgroup *Paradiplospinus antarcticus* bears a small posteriorly directed dorsal process (the basibranchial attachment of Kusaka, 1974). This interpretation differs from Russo's (1983: character 54) observations, which indicated that such a dorsal process is absent in all gempylids, except *Epinnula*, *Lepidocybium*, *Thyrsitoides*, and *Thyrsitops*. All trichiurids and the rest of the outgroups in this study lack this dorsal process on the urohyal. Pos-





teriorly, the urohyal is poorly ossified and laterally compressed into a plate-like process that is attached to the cleithrum and coracoid by the sternohyoideus.

### Branchiostegal Rays

Seven acinaciform branchiostegal rays (McAllister, 1968) are associated with each side of the hyoid complex. The articular heads are spatulate and expanded to a greater degree in the posterior-most three rays. The three anterior rays are the shortest, and they articulate medially with the ventral margin of the ceratohyal. The fourth branchiostegal ray articulates laterally at the posteroventral corner of the ceratohyal, whereas the three posterior rays articulate laterally with the ventral margin of the epihyal. This distribution of the branchiostegal rays was interpreted by Russo (1983: character 53) as a synapomorphy uniting all gempylids. Johnson (1986: character 10) concluded that the articulation of the fifth branchiostegal on the anteroventral corner of the epihyal represents a synapomorphy for the Scombroidei.

### BRANCHIAL COMPLEX

Only the branchial complex of *Trichiurus lepturus* is drawn (Fig. 15) because most of the characters differ only slightly in magnitude and can be easily identified on *Trichiurus*. The first and second basibranchials are also drawn separately for all the genera analyzed, except *Gempylus* and *Nesiarchus* (Fig. 16). Collette et al. (1984: character 1) and Johnson (1986: character 6) indicated that in the scombroids the cartilaginous anterior tip of the second epibranchial articulates with the second pharyngobranchial. A medial cartilaginous process of the second epibranchial extends well beyond the lateral margin of the third pharyngobranchial and articulates with a small cartilaginous condyle at the anterior tip of a longitudinal column that runs along the dorsal surface of the third pharyngobranchial.

Scombroids are also characterized by the absence of the fourth pharyngobranchial cartilage (Johnson, 1986: character 7). The fourth epibranchial articulates with a more extensive posterior cartilage of the third pharyngobranchial. The extensive posterior cartilaginous tip of the third pharyngobranchial fits into the dorsal surface of the fourth pharyngeal tooth plate.

In addition, scombroids are characterized by the presence of fourth pharyngeal tooth plates and by having extremely elongate third pharyngobranchials. The third pharyngobranchial bears a reduced

lateral shelf that has a straight medial margin (Johnson, 1986: character 8).

### Lower Branchial Apparatus

**BASIBRANCHIALS.** The basibranchials are median bones arranged in a longitudinal series. The first basibranchial articulates anteriorly with the posterior margin of the glossohyal and lies between the left and right dorsal hypohyals. The second serves as the point of articulation for the first hypobranchial. In all outgroups and trichiurids, the third basibranchial has a tubular central axis with lateral shelves that cover the medial margins of the third hypobranchial.

*Character 17.* All of the trichiurids are characterized by the presence of a well-developed, knob-like, anterior articular head on the first basibranchial. In addition, in all trichiurids, except *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*, the articular head has small dorsolateral processes or wings. All outgroups have a first basibranchial with a broad base that gradually tapers to a point anteriorly.

*Character 18.* The second basibranchial in the outgroups has an expanded posterior margin and elongate anterior end. Russo (1983: character 62) considered this condition as a synapomorphy uniting the gempylids *Diplospinus*, *Gempylus*, *Nesiarchus*, and *Paradiplospinus*. In the trichiurids, the second basibranchial bears two small, laterally pointed processes posterior to the place of articulation with the heads of the first hypobranchial.

**HYPOBRANCHIALS.** The hypobranchials are three pairs of bones that form part of the lower arms of the gill arches; their dorsal heads articulate with the ceratobranchials. The ventral heads of the first and second hypobranchials articulate with the cartilaginous junction between the first and second and second and third basibranchials, respectively. The third hypobranchial is triangular and smaller than the first and second hypobranchials, and it has an elongate anterior process that extends under the lateral shelves of the third basibranchial.

The first hypobranchial has a medially curved articular head that may bear a lateral or a medial process, or both. Russo (1983: character 63) noted the absence of an anterior (lateral) process in the first hypobranchial of all gempylids, except *Diplospinus*, *Gempylus*, *Lepidocybium*, and *Tongaichthys*. He considered the presence of an anterolateral process to be plesiomorphic. All trichiurids, except *Aphanopus* and *Benthodesmus*, and outgroups, except *Nesiarchus*, have a medial and a lateral process on the anterior articular head of the first hypobranchial. The cleared and stained specimens of

Figure 15. Dorsal view of the lower branchial apparatus of *Trichiurus lepturus* (top), the left side does not include the gill rakers or tooth patches; cartilaginous articulations striped. Right upper branchial apparatus of *Trichiurus lepturus*: ventral view (center); dorsal view showing the cartilaginous articulations (bottom).

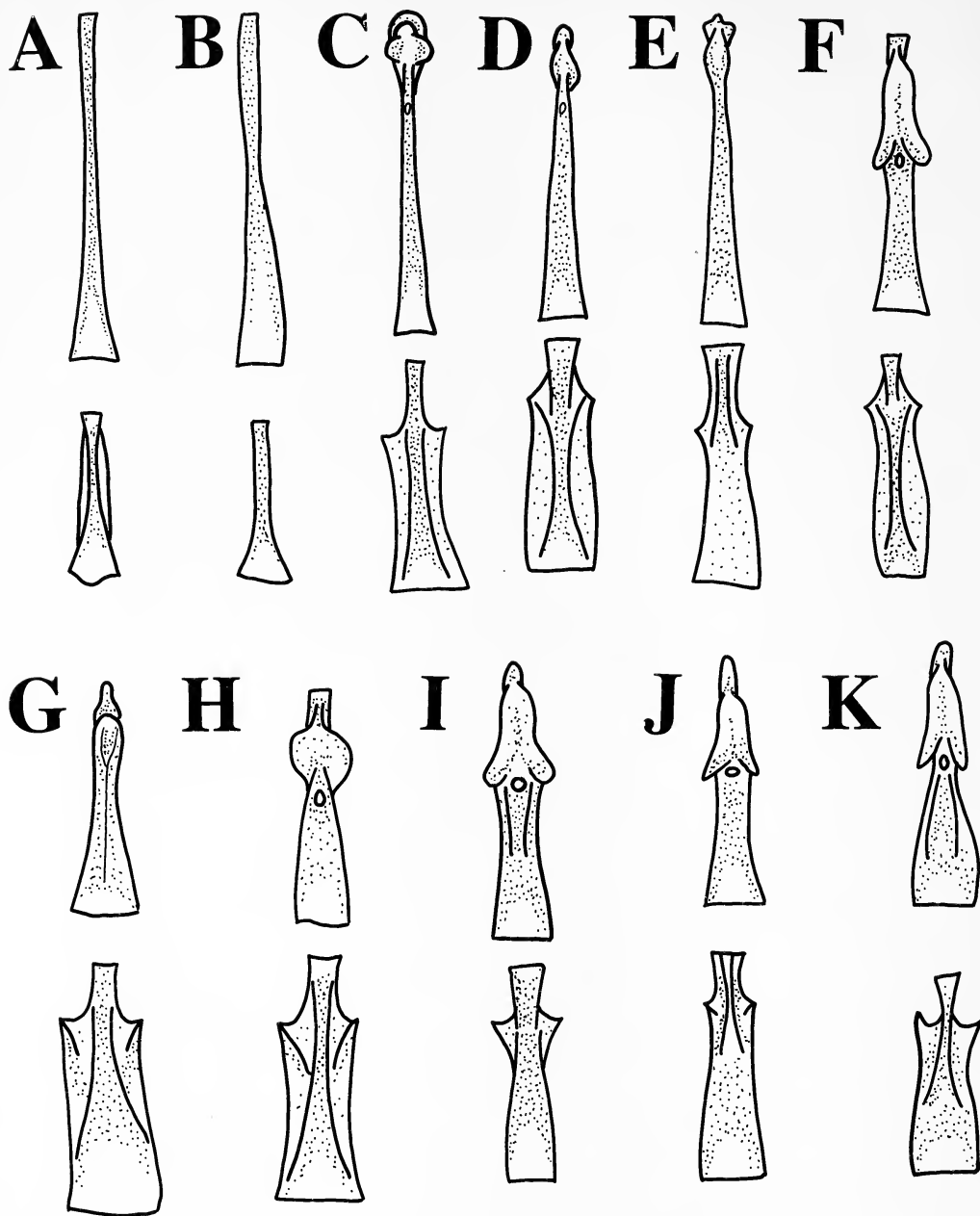


Figure 16. Dorsal views of the first basibranchial (top) and second basibranchial (bottom) of: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*; (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

*Benthodesmus tenuis* and *Nesiarchus* analyzed in this study lacked both lateral and medial processes on the first hypobranchial. The specimens of *Aphanopus* and *B. simonyi*, however, had only well-developed medial processes. The medial and lateral processes are well developed in the rest of the trichiurids analyzed, where they clearly extend far from the lateral and medial margins of the first

hypobranchial. *Diplospinus* and *Paradiplospinus* also bear well-developed medial processes on the first hypobranchial, but their lateral processes are reduced and appear as rounded outgrowths that may extend only slightly past the margin of the first hypobranchial. This condition differs from the observations of Russo (1983) who noted that, whereas *Diplospinus* bears a lateral process on the first

hypobranchial, *Paradiplospinus* lacks such a structure.

The second hypobranchial has a slightly curved articular head and bears no distinct lateral or medial processes in the outgroups, except *Gempylus*, which seems to bear a reduced lateral process on the second hypobranchial. All trichiurids are characterized by the presence of distinct lateral and medial processes in the second hypobranchial. These processes are usually pointed and well defined, except in *Aphanopus* and *Benthodesmus* where they may be reduced. The specimens of *Benthodesmus tenuis* have reduced medial and lateral processes, whereas those of *B. simonyi* have well-developed medial processes. The presence or absence of lateral and medial processes in the first and second hypobranchials is quite variable among and within genera, and its categorization into objective character states is difficult.

The third hypobranchial is triangular, with the tubular anterior end curving medially under the lateral wings of the third basibranchial. In all trichiurids and outgroups, except *Aphanopus*, *Benthodesmus*, *Gempylus*, and *Nesiarchus*, the posterolateral corner of this bone usually bears pointed projections. This condition varies between specimens of the same species, and it is dependent on the size of the specimens available and the degree of ossification of this bone in any given specimen. In some species, the posteromedial corners of this paired bone cover the posterior end of the third basibranchial.

**CERATOBANCHIALS.** The ceratobranchials are pairs of bones that form the lower arms of the gill arches. These are the longest bones in the gill arches, and they support most of the gill filaments and rakers. The anteroventral heads of the first, second, and third ceratobranchials articulate with the first, second, and third hypobranchials, respectively. The anteroventral head of the fourth ceratobranchial articulates with the third basibranchial. The posterior tip of the fifth ceratobranchial has an elongate cartilaginous cap that lies within the epithelium of the branchial cavity. The anterior cartilaginous tips of the paired elements of the fifth ceratobranchial may be fused at their tips and articulate with the complex of the fourth ceratobranchial and third basibranchial by ligaments. The fifth ceratobranchial bears dorsal tooth plates. The morphology of the fifth ceratobranchial is similar among the taxa analyzed in this study.

*Character 19.* The outgroups and trichiurids have straight first, second, and third ceratobranchials. Russo (1983: character 64) considered the sigmoid shape of the fourth ceratobranchial to be a synapomorphy uniting the gempylids *Diplospinus* and *Paradiplospinus*. In the trichiurids and the rest of the outgroups and gempylids, the anteroventral head of the fourth ceratobranchial is twisted medially, but the bone does not appear sigmoidal. Although this character appears equivocal at the out-

group node, I agree with Russo (1983) and consider the presence of a sigmoidal fourth ceratobranchial as a synapomorphy uniting *Diplospinus* and *Paradiplospinus*.

## Upper Branchial Apparatus

**EPIBRANCHIALS.** The epibranchials are four pairs of bones that form part of the upper arms of the gill arches. The posteroventral ends of the epibranchials articulate with the posterodorsal ends of the ceratobranchials. The anterodorsal head of the first epibranchial articulates with the first pharyngobranchial and bears an uncinate process that articulates with the second pharyngobranchial by way of an interarcual cartilage. The anterodorsal head of the second epibranchial articulates not only with the second pharyngobranchial but also with the third pharyngobranchial via an elongate medial cartilaginous process. This medially elongate cartilaginous process joins a small articular condyle on a longitudinal ridge of the dorsal face of the third pharyngobranchial. Posterior to this cartilaginous head, all gempylids and trichiurids, except *Lepturacanthus* and *Trichiurus*, have a truncated dorsomedial process that bears a ligamentous attachment to the third epibranchial. *Lepturacanthus* and some specimens of *Trichiurus* are characterized by having a second epibranchial in which the dorsomedial process is pointed. The third epibranchial also bears a dorsomedial process that connects it to the fourth epibranchial and a cartilaginous knob at the anterior tip that attaches it to the third pharyngobranchial. In *Diplospinus* and *Paradiplospinus*, a shelf-like dorsomedial plate extends longitudinally between the anterodorsal process and the posterior end of the third epibranchial. The rest of the outgroups and the trichiurids lack such a modification or have a partial shelf that does not extend along the entire posterior half of the third epibranchial. However, the extent of this shelf is variable and difficult to categorize into well-defined character states. A dorsolateral process on the fourth epibranchial articulates with the third epibranchial.

**PHARYNGOBRANCHIALS.** The pharyngobranchials are three pairs of small bones that are attached to the anterodorsal heads of the epibranchials. The first pharyngobranchial articulates dorsally with the prootic. In all trichiurids and outgroups, the first pharyngobranchial is a small, tubular, edentulous bone. In *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, the first pharyngobranchial is strongly curved, whereas in the rest of the trichiurids and the outgroups, the bone is straight or slightly curved. The degree of curvature on the first pharyngobranchial is highly variable and difficult to categorize.

The second and third pharyngobranchials bear well-developed tooth plates ventrally. The third pharyngobranchial is the largest, and it bears a small dorsolateral cartilaginous knob that articulates with the cartilaginous tip of the second epi-

branchial. The posterior margin of the third pharyngobranchial bears a large cartilaginous cap that articulates with the third and fourth epibranchials.

**GILL RAKERS.** Gill rakers tend to be more reduced and poorly ossified in the outgroups *Diplospinus*, *Nesiarchus*, and *Paradiplospinus*. The better ossified gill rakers of the trichiurids can be spinous, tuberculous, or a combination of both, with the spinous ones usually at the posterior end of the hypobranchials. Trichiurids have two rows (lateral and medial) of gill rakers on the first and second hypobranchials, except *Benthodesmus*, which bears a single row on the first hypobranchial. All outgroups have a single row of gill rakers on the first hypobranchial and two rows on the second hypobranchial, except *Gempylus*, which has single rows on the first and second hypobranchials. In all trichiurids and outgroups, except *Nesiarchus*, the lateral rows of gill rakers on the first and second hypobranchials extend anteriorly past the articular head of the bone as part of the epithelial covering of the branchial arches. The third hypobranchials bear small tuberculous gill rakers, which are extremely reduced in *Diplospinus* and *Paradiplospinus*.

The outgroups and trichiurids have first, second, and third ceratobranchials bearing two longitudinal (lateral and medial) series of gill rakers on the anterior margins. The lateral series of gill rakers are spinescent, with spine length increasing toward the posterodorsal end where these bones articulate with the epibranchials. The medial series of gill rakers tend to be smaller and more tuberculous in nature. The fourth ceratobranchial may bear one or two rows of gill rakers. The medial row is present only in the largest specimens, and it is extremely reduced and nonspineous.

All the epibranchials in most of the taxa analyzed have either one or two series of gill rakers or tooth plates along their ventral margin. In *Diplospinus*, *Nesiarchus*, and *Paradiplospinus*, the fourth epibranchial is edentulous. The size and number of gill rakers and tooth plates on the other epibranchial bones are reduced in the outgroups *Diplospinus* and *Paradiplospinus*. The trichiurids and the rest of the outgroups have epibranchials bearing gill rakers or tooth plates with stronger spination.

All trichiurids and *Gempylus* have two ventral series of gill rakers on the third epibranchial. In *Diplospinus*, *Nesiarchus*, and *Paradiplospinus*, there is only a single series of reduced gill rakers on this bone. Russo (1983: character 65) indicated that all gempylids have two rows of tooth plates on the third epibranchial, except *Epimula*, *Paradiplospinus*, and *Thyrsitops*, which bear one row, and *Ruvettus* and *Thyrsites*, which bear no rows. The observation of a single row of gill rakers on the third epibranchial of *Diplospinus* differs from the condition noted by Russo (1983). However, the presence or absence of gill rakers on these bones is difficult to evaluate since the gill rakers are ex-

tremely reduced and could easily be lost during handling and dissection.

Matsubara and Iwai (1958) noted that *Gempylus* differs from other gempylid genera in that the gill raker at the angle of the first gill arch is small, triangular, and exposed at its tip. The rest of the gempylids have a gill raker at the angle of the arch that is T-shaped, larger, and more exposed. In the diagrams of Nakamura and Parin (1993: figs. 26, 27), it is evident that some trichiurids share, with *Gempylus* and *Paradiplospinus*, the presence of a small gill raker at the angle of the first gill arch. The gill raker at the angle between the first ceratobranchial and the first epibranchial in *Aphanopus*, *Assurger*, and *Benthodesmus* has a longer spine with an expanded tip. Tucker (1956) described the morphology of the gill rakers in *Benthodesmus tenuis*, noting that some of the gill rakers toward the angle of the gill arches have one large barbed spine. However, the size and shape of the spines on the gill rakers is quite variable between specimens. The gill raker at the angle between the first epibranchial and first ceratobranchial in *Diplospinus* and *Paradiplospinus* is characterized by having a base that bears a small root-like process extending toward the articulation of the ceratobranchial and epibranchial bones. In *Nesiarchus*, the tips of the base in this gill raker bend toward the first epibranchial-first ceratobranchial junction, giving it the appearance of a tri-rooted element. *Gempylus* is characterized by having an angular gill raker with a triangular base that lacks these root-like processes. The angular gill raker in the trichiurids has a circular base bearing one larger spine surrounded by smaller spinules, and it lacks the root-like process observed in *Diplospinus* and *Paradiplospinus*. Although the difference in morphology of the angular gill raker between the trichiurids and the outgroups is obvious, the condition at the outgroup node appears equivocal, and the character is uninformative within the trichiurids. Thus, the morphological features of the angular gill rakers are excluded from this analysis, but they remain as a potentially informative character, or characters, for a future study in which both the trichiurids and gempylids are analyzed together.

## NEUROCRANIUM

In dorsal view, the neurocranium of the trichiurids and outgroups is triangular, being narrow anteriorly and wider posteriorly (Fig. 17). The skulls of most gempylids and all trichiurids are mainly characterized by the elongation of some of their bones. Posterodorsally, the neurocranium bears three prominent ridges. Medially, a single supraoccipital ridge is formed by the confluence of two frontal ridges onto the supraoccipital. Lateral to the supraoccipital ridge, a pair of epiotic ridges extends through the parietal and the posterior edge of the frontal. Lateral to the epiotic ridge, a pair of pter-

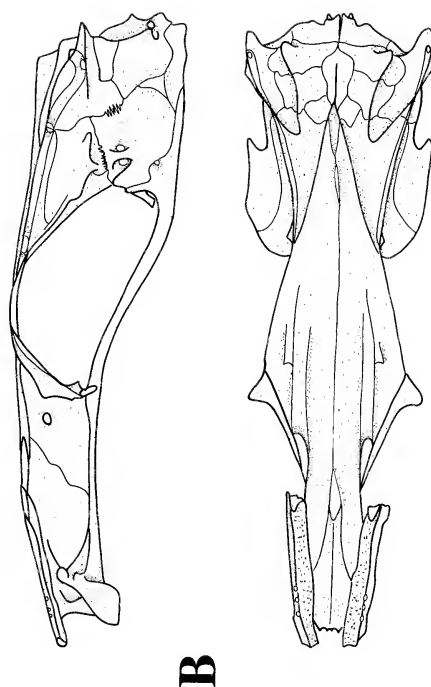
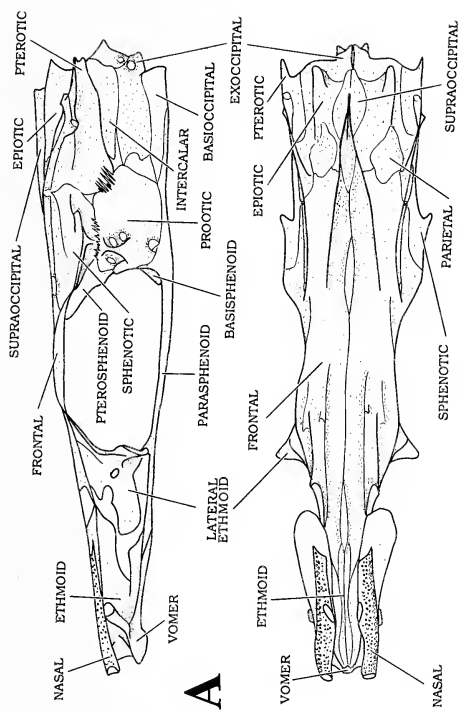


Figure 17. A–B. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*.

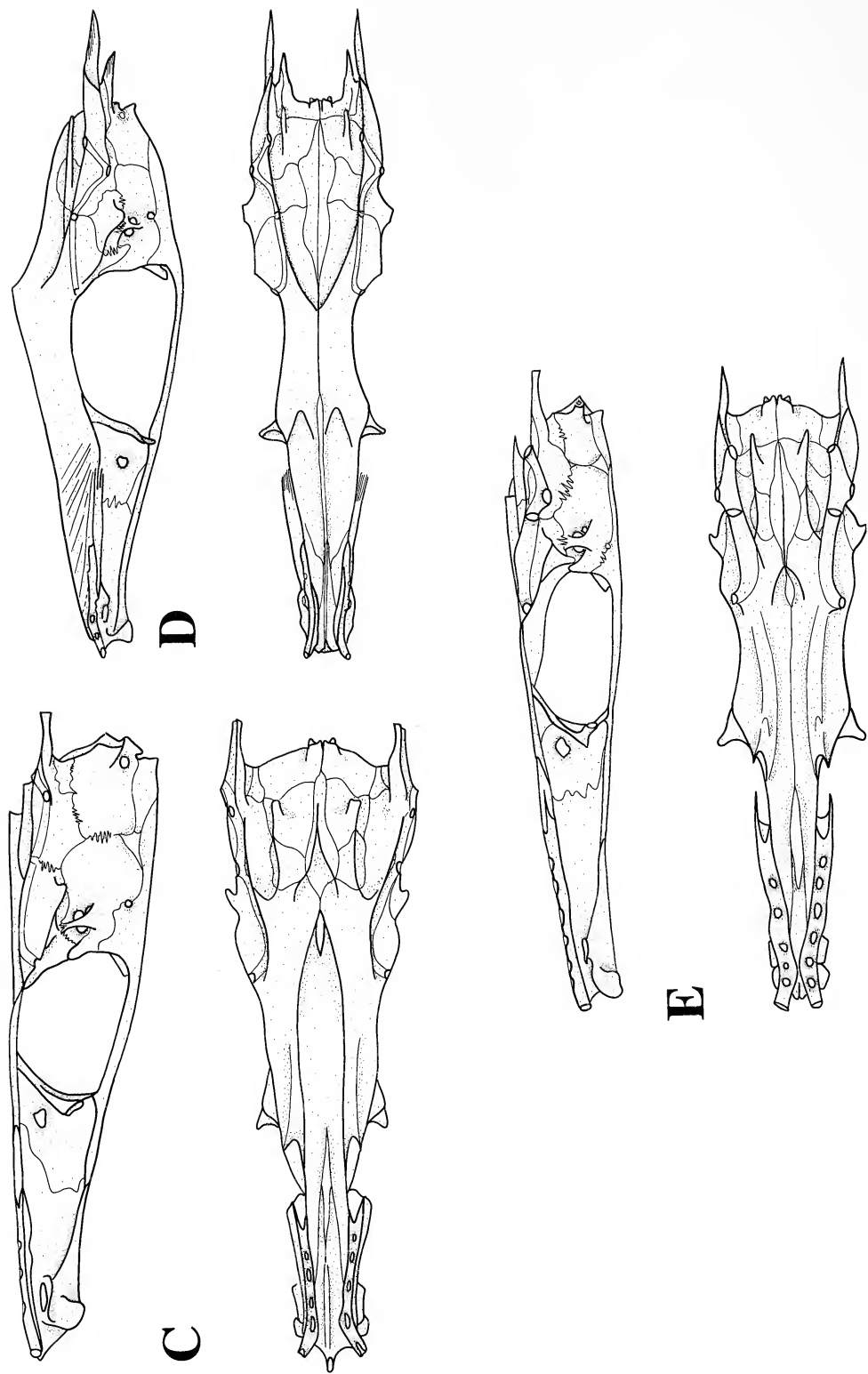


Figure 17. C-E. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

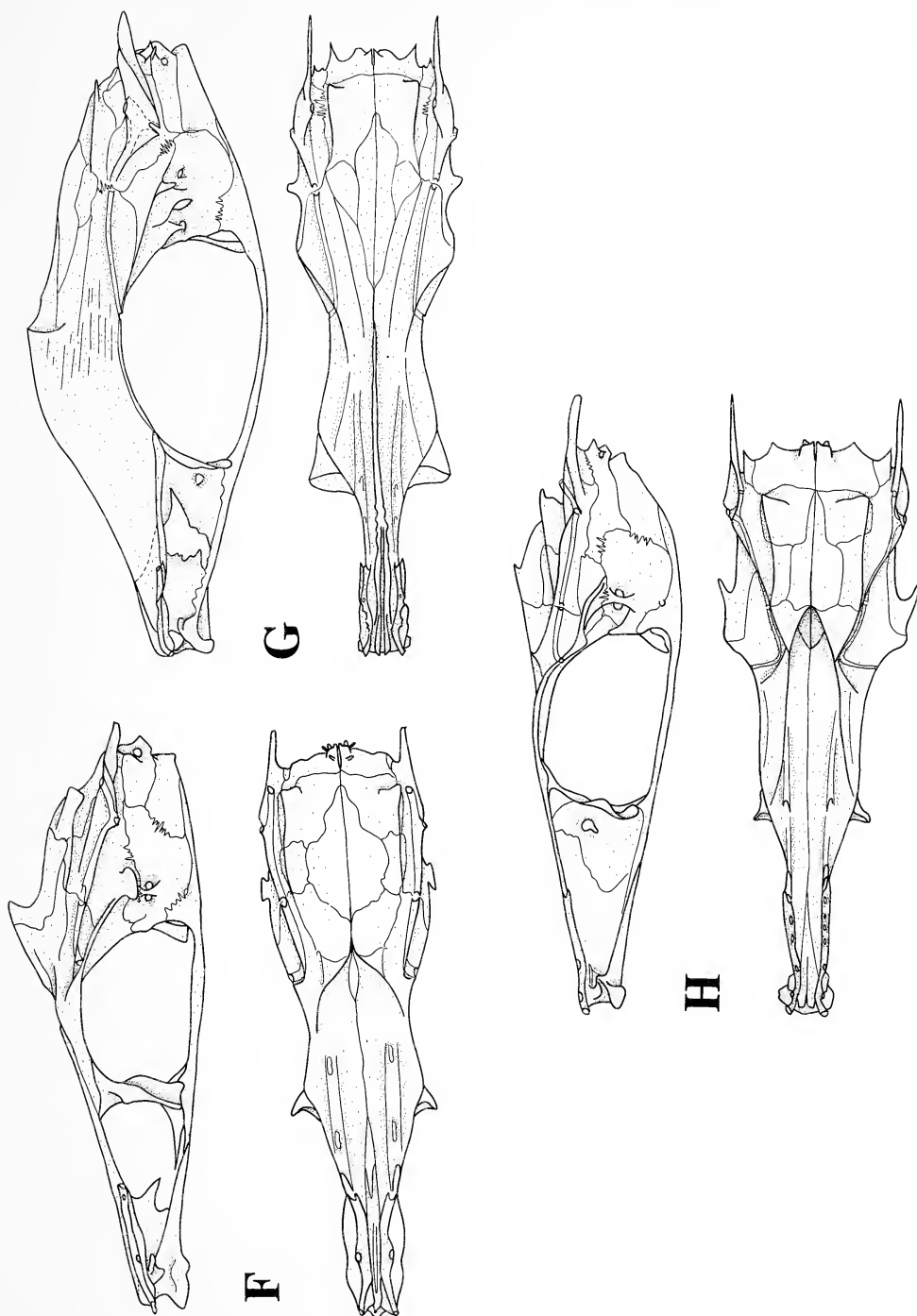


Figure 17. F-H. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (F) *Eupleurogrammus glossodon*; (G) *Eroxymetopon taeniatus*; (H) *Lepidopus fitchi*.

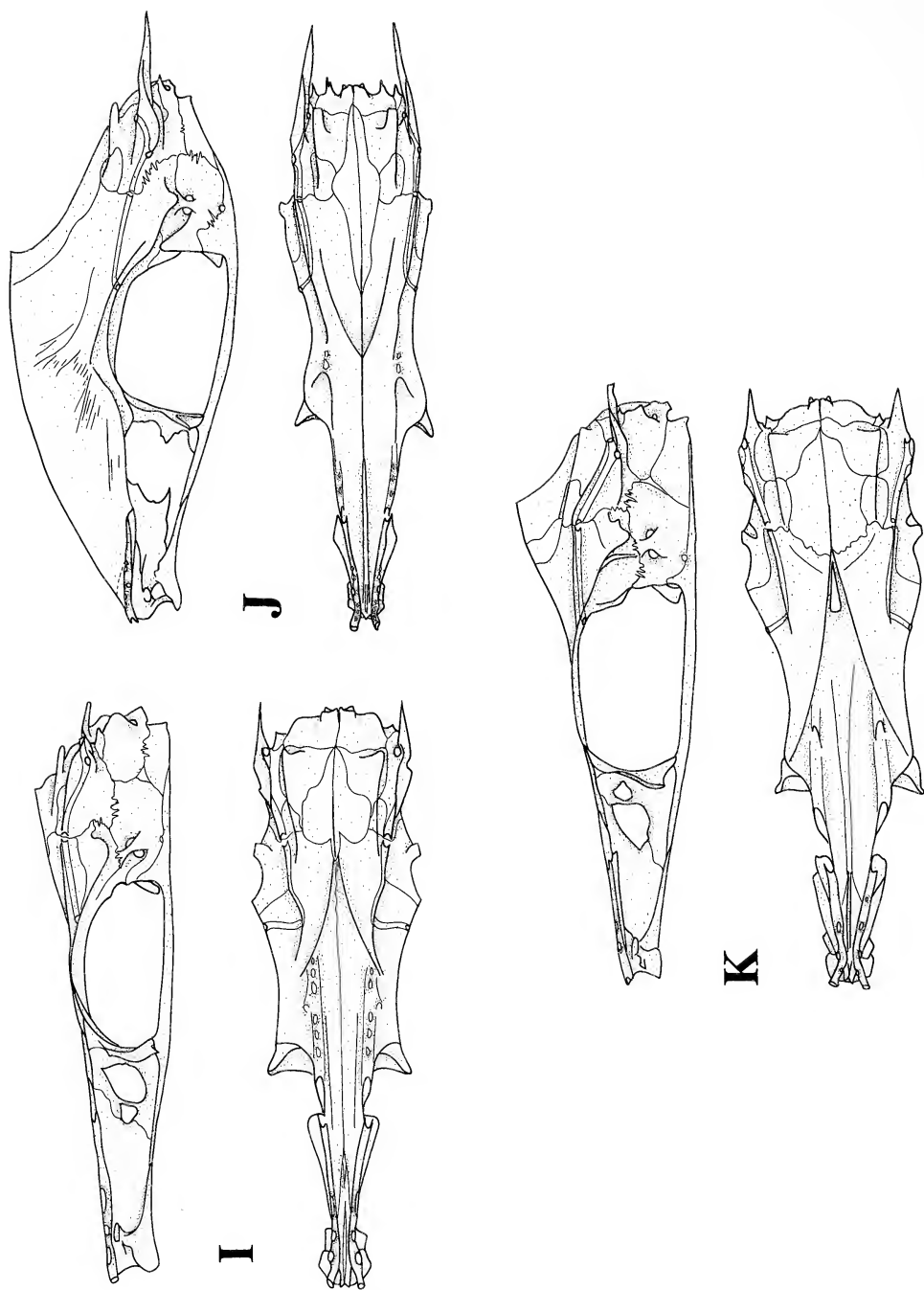


Figure 17. I-K. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.



otic ridges extends through the pterotic and the frontal.

### Ethmoidal Region

**NASAL.** The nasal appears as a simple tube in the outgroup *Nesiarchus* and the trichiurids *Benthodesmus* and *Lepidopus*. Ossified, lateral laminar extensions are present on the nasal and cover the lateral palatal processes of the ethmoid in the outgroups *Gempylus* and *Paradiplospinus* and the trichiurids *Assurger* and *Eupleurogrammus*. The rest of the trichiurids and outgroups bear laminar extensions that do not cover the palatal processes of the ethmoid. *Eupleurogrammus*, *Evoxymetopon*, *Gempylus*, and *Paradiplospinus* are characterized by lateral laminar extensions that extend along the whole length of the nasal. In addition, *Eupleurogrammus* bears smaller medial extensions anteriorly. The lateral extensions are restricted to the posterior half of the nasal in the outgroup *Diplospinus* and the trichiurids *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*. This potential character is difficult to evaluate because the detection of such lateral extensions depends on the degree of ossification of the lateral membrane on the nasal. For example, whereas some specimens of *Diplospinus*, *Lepidopus*, and *Paradiplospinus* seem to show the presence of well-developed, ossified lateral extensions, others are characterized by their reduction or absence.

**Character 20.** The nasal is straight and runs parallel to the ethmoid and frontal in the outgroups. The anterior head of the nasal is curved laterally in all the trichiurids. The anterior head of the nasal in one of the specimens of *Nesiarchus* appeared to be slightly curved, but the condition is not comparable to that of the trichiurids, in which the anterolateral margin of the nasal appears concave in dorsal view and clearly extends past the lateral margin of the ethmoid.

**ETHMOID.** Anterodorsally, the ethmoid supports the nasal and bears two lateral processes, that are attached to the palatine (the palatal processes of Russo, 1983). Anteroventrally, the ethmoid articulates with the dorsal edge of the vomer. Posteriorly, it abuts the lateral ethmoid and articulates with the anterior margin of the frontal. The ethmoid is elongate in all trichiurids and the outgroups.

**Character 21.** In *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps*, the ethmoid bears two dorsally expanded ridges that extend well above the dorsal margin of the nasal in lateral view. The dorsal ridges on the ethmoid of *Evoxymetopon* and *Tentoriceps* are more elevated and appear triangular in lateral view. *Aphanopus*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* are characterized by the presence of two longitudinal ridges on the dorsal face of the ethmoid. However, these ridges do not extend well above the nasal in lateral view. Russo (1983: character 2) not-

ed that the presence of a medial ridge on the dorsal surface of the ethmoid represented a synapomorphy uniting the gempylid genera *Diplospinus* and *Paradiplospinus*. This ridge is reduced and does not extend well above the nasal. The other outgroups in this study, plus *Benthodesmus*, *Lepidopus caudatus*, and *L. fitchi*, lack a dorsal ridge on the ethmoid.

**LATERAL ETHMOID.** Anteriorly, the lateral ethmoid joins the vomer and the ethmoid. It attaches to the frontal dorsally and the parasphenoid ventrally. The posterior margin of the lateral ethmoid forms a lateral process that is divided into a ventral and a dorsal articular head. The ventral articular head attaches to the palatine, whereas the dorsal articular head joins the dorsal articular process of the lachrymal.

The articulations of the lachrymal and palatine with the ethmoid are by way of cartilaginous knobs that may or may not be separated by a bony ridge. Russo (1983: character 8) considered the absence of a bony ridge as the apomorphic condition among some of the gempylids in his study. All of the outgroups and the trichiurids share this derived condition.

**VOMER.** The vomer articulates anterodorsally with the ethmoid and posteriorly with the lateral ethmoid and the parasphenoid. The trichiurids and all outgroups have a vomer with an expanded anteroventral head that lacks teeth. In all trichiurids, except *Assurger* and *Eupleurogrammus*, the anterior margin of the head of the vomer appears flat in ventral view. *Eupleurogrammus* and *Gempylus* are similar in that the anterior margin of the ventral head bears an anteriorly elongate process. *Assurger* and *Paradiplospinus* tend to have a rounded anterior margin on the head of the vomer, whereas *Nesiarchus* and some specimens of *Diplospinus* bear a flat anterior margin. However, the condition seems variable within species. For example, Russo (1983: character 10) noted that the anterior margin of the vomer in the gempylids *Diplospinus*, *Gempylus*, *Neoepinnula*, *Nesiarchus*, *Paradiplospinus*, *Ruvetus*, *Thyrsites*, and *Thyrsitops* is rounded in ventral view. In this study, however, one specimen of *Diplospinus multistriatus* has a rounded head on the vomer; another has a flat anterior margin.

Anteriorly, the vomer has a process that extends anterodorsally and attaches to the anterior tip of the ethmoid. All the trichiurids and the outgroups, except *Aphanopus*, have a vomer in which the anterior tip of this process terminates below or slightly anterior to the ethmoid. In *Aphanopus*, this process is extremely elongate and extends slightly past the anterior margin of the rostral cartilage.

### Orbital Region

**FRONTAL.** Anteriorly, the frontal attaches to the nasal, ethmoid, and lateral ethmoid. Posteriorly, it articulates with the pterosphenoid, sphenotic, parietal, and supraoccipital. Medially, the frontals are

joined to each other. A pineal foramen appears as a gap in this medial junction and is located anterior to the supraoccipital. The pineal foramen is not evident in some large specimens and those trichiurids with a well-developed frontal crest. Russo (1983) noted that there are variations in the size of the pineal foramen among gempylids and indicated that in some genera, such as his outgroup *Pomatomus* Lacepède 1802, the pineal foramen is not present because the supraoccipital crest is carried forward as a ridge onto the frontal. Ventrally, there are short, poorly developed sheets of bone (the orbital lamellae of Collette and Russo, 1984) that abut the lateral ethmoid anteriorly and the pterosphenoid posteriorly. Anterolaterally, the frontal carries the supraorbital canal of the laterosensory canal system, and posterolaterally it carries the anterior half of the otic canal (Coombs et al., 1987). Johnson (1986: character 3') noted that, in the scombroids, the frontosphenotic shelf is horizontal and has a sharp edge. The supraorbital canal is separated from the dorsolateral margin of the orbit by a large fossa that houses the dilatator operculi. The infraorbital canal passes over the sharp edge of the frontosphenotic shelf and joins the supraorbital canal medially.

**Character 22.** Johnson (1986: character 29) noted that in the trichiurids the supra- and infraorbital canals are joined by way of a bony tube that extends laterally from the supraorbital canal. This condition is present in all the trichiurids studied. The plesiomorphic condition observed in all other scombroids is characterized by the presence of an elongate dilatator operculi fossa that separates the junction of the infra- and supraorbital canals, which communicate through a dorsally or laterally directed pore on the frontal ridge (Johnson, 1986).

**Character 23.** Two frontal ridges become confluent posteriorly, forming the supraoccipital ridge. In *Assurger*, *Evoxymetopon*, and *Tentoriceps*, the frontal ridges become confluent well anterior to the supraoccipital (on the ethmoidal region) and form an extremely well-developed frontal crest that appears as laterally flat sheets. *Lepidopus altifrons* is unique among the species of this genus in having a well-developed frontal that is similar to that of *Assurger*, *Evoxymetopon*, and *Tentoriceps*. Tucker (1957: 426), in his description of a specimen of *Evoxymetopon taeniatus* (= *L. altifrons*), noted that the ridge-like elevation of the ethmofrontal region "is not so much an osseous elevation but an outgrowth of soft tissue, normally increasing with age as in numerous other percomorph fishes." The frontal crest present in the ethmofrontal region of *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps* is flexible, but it represents an ossified extension of the frontal ridges. In *Eupleurogrammus*, the frontal ridges become confluent anterior to the supraoccipital and form a frontal crest that is elevated above the interorbital space. These ridges in *Eupleurogrammus* are laterally convex. In the rest of the trichiurids and the outgroups, the frontal

ridges are not elevated as a frontal crest, and they do not become confluent until they reach or are close to the supraoccipital.

The frontal crest in *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps* extends above the orbits making the interorbital space convex. *Lepidopus dubius* Parin and Mikhailin 1981 is the only species within the genus that is similar to *L. altifrons* in the morphology of the frontal region. However, in *L. dubius*, the frontal ridges are not as elevated as in *L. altifrons*, do not extend far onto the ethmoidal region, and become confluent closer to the posterior margin of the orbits. The rest of the trichiurids and the outgroups have an interorbital space that is concave or flattened. Parin and Collette (1993) warned that the presence of a convex interorbital space and a sagittal crest that extends onto the ethmoidal region are characters that seem to change in a gradual manner in the series *L. manis* Rosenblatt and Wilson 1987 and *L. fitchi*, *L. caudatus*, and *L. calcar* Parin and Mikhailin 1982, *L. dubius*, and *L. altifrons*. *Assurger*, *Evoxymetopon*, and *Tentoriceps* could be added to this series as a more derived condition.

**PTEROSPHEOID.** The pterosphenoid forms the margins of the pterosphenotic window (Collette and Chao, 1975). The pterosphenoid articulates with the frontal dorsally and the basisphenoid ventrally. Ventrolaterally it joins the sphenotic and the prootic. The morphology of this bone is similar among the taxa analyzed in this study.

**BASISPHEOID.** The basisphenoid is a Y-shaped median bone. The elongate ventral process, or base, of the basisphenoid extends toward the parasphenoid and bisects the entrance of the posterior myodome (Russo, 1983). Dorsally, it joins the posteroventral edges of the pterosphenoid, whereas laterally it attaches to the prootic. The morphology of this bone is similar among the taxa analyzed in this study.

**SLEROTICS.** The sclerotics are ossifications of the cartilaginous or fibrous regions on the sclera of the eyes. Nakamura and Yamaguchi (1991) found that the 21 teleost species analyzed in their study had at most two sclerotics occupying the anterior and posterior poles of the scleral equator.

**Character 24.** No ossified sclerotics are present in the trichiurids and the outgroups *Diplospinus* and *Paradiplospinus*. However, the outgroups *Nesiarchus* and *Gempylus* have anterior and posterior sclerotics on the scleral equator. I have found no information in the literature about the presence of these ossifications among the rest of the gempylids. Nakamura and Yamaguchi (1991) included two scombroids in their analysis: *Thunnus thynnus* (Linnaeus 1758) and *Trichiurus lepturus*. They indicated that *Thunnus thynnus* has sclerotics that grow to form a complete ring around the sclera, whereas *Trichiurus lepturus* lacked paired sclerotics. Although they did not consider them scombroids, Nakamura and Yamaguchi (1991) also described the sclerotics of a marlin and a barracuda.

They noted that both of these species have a pair of sclerotics. Collette and Chao (1975) described the presence of sclerotics in all the genera of the tribe Sardini within the family Scombridae. Furthermore, Collette and Russo (1984) also noted the presence of sclerotic bones in the genera *Acanthocybium* Gill 1862, *Grammatorcynus*, and *Scomberomorus*. Although the character is variable within the outgroups, I consider the absence of sclerotics as the apomorphic condition since the presence of these ossifications seems to be widely distributed among the scombroids. The presence of sclerotics in the sphraenids might be a good indicator of the plesiomorphic state of this condition because the barracudas have been proposed as the sister group to the rest of the scombroids (Collette and Russo, 1986; Johnson, 1986; Carpenter et al., 1995).

## Otic Region

**SUPRAOCCIPITAL.** The supraoccipital is a median bone forming the posterodorsal corner of the neurocranium. A supraoccipital crest, which originates posterior to the pineal foramen, is formed by the confluence of two ridges from the frontal. The supraoccipital articulates anteriorly with the frontal, posteriorly with the exoccipital, and laterally with the parietal and the epiotic.

Starks (1911) described a specimen of *Trichiurus lepturus* in which the epiotic, frontal, parietal, and supraoccipital were covered by a spongy, bony substance. James (1960) and Nakamura and Parin (1993) reported that some specimens of *T. lepturus* from waters around India show extreme ossification (hyperostosis of Barnard, 1948) of the supraoccipital bone. James (1960) indicated that, in those specimens of *T. lepturus* with extreme hyperostosis of the supraoccipital, the whole occipital region of the neurocranium may be covered by a thickened bony mass, which may extend to the first or second vertebral elements. He remarked that in those specimens the preoccipital profile of the head approaches the orbital region steeply. Some of the specimens of *T. lepturus* analyzed in this study also show the presence of hyperostosis on the supraoccipital. No instances of hyperostosis on the supraoccipital have been noted in any other trichiurid or gempylid. Smith-Vaniz et al. (1995) listed the presence of hyperostotic bones on 92 species belonging to 22 teleost families and concluded that hyperostosis has arisen independently many times among the teleosts.

**Character 25.** Russo (1983: character 20) noted that the supraoccipital of *Diplospinus*, *Nealotus*, *Nesiarchus*, and *Paradiplospinus* is a small thin ridge, low on the cranium. He noted that all the other gempylids in his study, except *Lepidocybium* and *Ruvettus*, have a moderately high supraoccipital crest, extending well above the epiotic ridges. Russo (1983) described the supraoccipital crest of *Gempylus* as being moderate to low in height. In contrast to Russo's (1983) observation, the speci-

men of *Gempylus* analyzed in this study has a supraoccipital crest that is higher than in the other outgroups, but it runs parallel to the epiotic ridges. The other outgroups, plus the trichiurids *Aphanopus* and *Benthodesmus*, are characterized by having a supraoccipital crest that is reduced and runs close and nearly parallel to the epiotic ridges. In lateral view, the rest of the trichiurids have a higher supraoccipital crest that does not run parallel to the epiotic ridges and that extends posterodorsally, diverging at an angle from the epiotic ridges. Thus, the outgroups and the trichiurids *Aphanopus* and *Benthodesmus* have a neurocranium with a dorsal profile that appears flat in lateral view.

**Character 26.** In *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps*, the highest point of the supraoccipital crest ends above the orbits. In all other trichiurid and outgroup genera, the highest point of the supraoccipital crest ends posterior to the orbits and above the otic or occipital regions of the neurocranium.

**PARIETAL.** The parietal articulates with the frontal anteriorly and the epiotic posteriorly. Laterally, the parietal joins the pterotic bone. A ridge that originates on the frontal, lateral to the supraoccipital ridge, continues across the parietal and onto the epiotic. The morphology of this bone is similar among the taxa analyzed in this study.

**EPIOTIC.** The epiotic articulates anteriorly with the parietal and posteroventrally with the exoccipital. It joins the pterotic laterally and the supraoccipital medially. The epiotic is the posterior-most bone forming the epiotic ridges, which also cross the parietal and extend onto the frontal in the outgroups and most trichiurids. In the trichiurids, the epiotic ridges usually become confluent with the pterotic ridges above the parietal or slightly anterior to it on the frontal. The epiotic serves as the site of attachment for the dorsal articular process of the posttemporal, uniting the neurocranium and the pectoral girdle. The posterior margin of the epiotic appears more pointed and posteriorly elongate in dorsal view in *Assurger*, *Benthodesmus*, *Gempylus*, and *Nesiarchus* and some specimens of *Diplospinus*, *Lepidopus*, and *Trichiurus*. In contrast, the posterior margin of the epiotic does not become extremely elongate posteriorly and appears to be flat or rounded in the rest of the outgroups and trichiurids. However, the shape of the epiotics is quite variable among and within species. The conditions described above are difficult to categorize objectively and are dependent on the size of the specimens available.

**PTEROTIC.** The pterotic articulates anteriorly with the frontal and the sphenotic and posteriorly with the exoccipital and the intercalar. It articulates ventrally with the prootic and intercalar and medially with the epiotic and the parietal. Ventrolaterally, the pterotic forms a fossa that serves as the articular facet for the dorsal articular condyle of the hyomandibula. Another fossa at its junction with the sphenotic accepts part of the anterior articular

condyle of the hyomandibula. The posterior portion of the otic branch of the laterosensory canal system (Coombs et al., 1987), the pterotic canal, crosses the pterotic longitudinally. Russo (1983) identified the complete enclosure of the canal as a synapomorphy of the gempylids. The same condition characterizes the trichiurids, although the canal tends to be wider and less ossified in *Aphanopus* and *Benthodesmus*.

Posteriorly, the pterotic bears two pores of the laterosensory canal system. The dorsal pore receives the postotic canal from the anteroventral branch of the supratemporal, and the lateral pore connects to the preopercular canal on the preopercle (Coombs et al., 1987). Russo (1983: character 23) noted that in all gempylids, except *Diplospinus*, *Lepidocybium*, *Nesiarchus*, *Paradiplospinus*, and *Thyrsoitoides*, the dorsal pore extends as a separate canal in a bony shelf away from the main pterotic canal. In *Gempylus*, this shelf appears as a dorsal ridge that runs throughout the whole length of the pterotic canal and completely separates the dorsal and lateral pores. In *Aphanopus*, *Benthodesmus*, and the outgroups, except *Gempylus*, the dorsal pore originates directly from the main pterotic canal, and the dorsal ridge separating the dorsal and lateral pores is extremely reduced or absent. In the rest of the trichiurids, the dorsal pore also originates directly from the main pterotic canal, but the dorsal ridge separating the dorsal and lateral pores is restricted to the posterior portion of the pterotic canal. *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps* bear a well-developed, laterally flattened, porous wall separating the dorsal and lateral pores. However, the extent of the dorsal ridge, as well as the presence of a small porous wall separating the dorsal and lateral pores, is quite variable and difficult to categorize objectively. This potential character is not included in this analysis and must await a future study that incorporates all gempylids and trichiurids.

**Character 27.** In the outgroups, the posterior tip of the pterotic terminates in front of the posterior margin of the neurocranium. Trichiurids have a longer pterotic with the posterior tip terminating beyond the posterior margin of the neurocranium. In *Lepturacanthus* and *Trichiurus*, the pterotic extends as far as the first vertebra and, in some specimens, past the anterior margin of the second vertebra. All specimens of *Aphanopus*, *Benthodesmus*, *Eupleurogrammus*, *Evoxymetopon*, and *Lepidopus* analyzed have a pterotic extending as far as the second vertebra. Senta (1975) noted that in *Tentoriceps*, the pterotic processes are well developed and extend beyond the posterior end of the supraoccipital. In fact, the pterotic of *Assurger* and *Tentoriceps* extends as far as the third vertebral element. However, the length of the pterotic among the trichiurids is variable and dependent on the size of the specimens. In this study I use this character as a dichotomy in which the states are categorized ac-

cording to whether the pterotic extends past the posterior margin of the neurocranium or not.

**INTERCALAR.** The intercalar serves as the point of attachment for the ligament connecting the anteroventral articular process of the posttemporal to the neurocranium. Ventrally, it joins the exoccipital and is overlapped by the anterolateral corner of this bone. It is strongly fused to the pterotic dorsally, and it may articulate with the posterodorsal corner of the prootic anteriorly.

In the trichiurids and outgroups analyzed, the intercalar varied in shape from truncated to pointed. In *Assurger*, the exoccipital and the intercalar form a plate that appears pointed. *Tentoriceps* has an intercalar that is pointed but separate from a posteriorly directed projection on the exoccipital. Russo (1983: character 27) also noted that among the gempylids, *Diplospinus*, *Lepidocybium*, *Neoepinula*, *Paradiplospinus*, *Ruvettus*, *Thyrsoites*, *Thyrsoitops*, and *Tongaichthys* have an intercalar with a flat or slightly rounded posterior end. However, the shape of the posterior margin on the intercalar is highly variable and dependent on the size and degree of ossification of the specimens. In the trichiurids, except *Assurger*, and the outgroups, the intercalar is flat posteriorly and does not extend past the posterior margin of the neurocranium. *Assurger* is unique in that the intercalar is extremely long and extends posteriorly to reach a position above the second vertebra.

**Character 28.** Russo (1983: character 26) noted that the intercalar on *Diplospinus* and *Paradiplospinus* is confined to the ventral surface of the neurocranium and is not visible in dorsal view (a unique condition among gempylids). In *Gempylus*, *Nesiarchus*, and the trichiurids, the intercalar is reduced but visible dorsally. Although the condition at the outgroup node is equivocal, I follow the conclusion of Russo (1983) and consider the condition present in all gempylids, except *Diplospinus* and *Paradiplospinus*, to be plesiomorphic.

**SPHENOTIC.** The sphenotic joins the frontal anteriorly forming the frontosphenotic shelf. Posteriorly, the sphenotic joins the pterotic, whereas anteromedially it joins the pterosphenoid. Ventrally, the sphenotic articulates with the prootic. In dorsal view, the lateral margin of the sphenotic shelf bears a laterally directed process that accepts the anterior articular condyle of the hyomandibula. The morphology of this bone is similar among the taxa analyzed in this study.

**PROOTIC.** The prootic is a paired bone; each unit articulates anteriorly with the basisphenoid and with each other. The juncture of the two units of the prootic along their ventral margins forms the anterior portion of the posterior myodome (Collette and Chao, 1975). The prootic joins the basioccipital, exoccipital, and intercalar posteriorly. It articulates dorsally with the pterotic and sphenotic and ventrally with the parasphenoid. Allis (1903) described the trigeminofacial chamber as the area under the lateral arch of the prootic, which encases

the prootic foramen. All trichiurids and outgroups bear a prootic arch forming a foramen that connects the trigeminofacial chamber with the anterior half of the myodome. The morphology of this bone is similar among the taxa analyzed in this study.

### Basicranial Region

**EXOCCIPITAL.** The exoccipital is a paired bone partially forming the foramen magnum. It bears an occipital condyle, which articulates with the atlas vertebra. This bone articulates with the basioccipital ventrally, the intercalar and supraoccipital dorsally, and the prootic anteriorly. Dorsally, it also joins the pterotic and the epiotic. In most trichiurids, the dorsomedial margins of the exoccipital do not meet each other, leaving an opening that runs from the posterior tip of the supraoccipital to the dorsal margin of the foramen magnum. In some specimens the dorsomedial margins bear cartilaginous edges that abut each other. An anterior glossopharyngeal foramen (Allis, 1903) is present close to the prootic, whereas posterior to this a second foramen is present for the vagus nerve (Russo, 1983).

The exoccipital ridge of the genus *Assurger* appears as an extremely elongate process. This elongate process is formed by the posterior extension of the intercalar and the exoccipital; its posterior tip reaches above the second vertebral element. Although it is possible that the extreme elongation of the exoccipital is not independent of the elongation of the intercalar, both conditions are treated separately and considered autapomorphies for the monotypic genus *Assurger*.

The exoccipital of *Eupleurogrammus* is unique in that it has two small, laterally directed processes on the dorsal face of the occipital condyle. The ventral process bears a small and poorly ossified intermuscular bone (the cephalic intermuscular bone of Collette and Chao, 1975). None of the outgroups, or the rest of the trichiurids, has such a modification on the exoccipital.

*Character 29.* Russo (1983: character 29) noted that *Diplospinus*, *Nealotus*, and *Paradiplospinus* are characterized by the presence of a ridge on the exoccipital, which is short and does not reach the vagus foramen. This ridge extends from the pterotic, crosses the intercalar, and reaches the exoccipital. In the rest of the gempylids and the trichiurids, the exoccipital ridge extends as a shelf-like structure over the intercalar, reaching the vagus foramen on the exoccipital. Although the condition at the outgroup node appears to be equivocal, I consider the presence of an exoccipital ridge that reaches the vagus foramen to be the plesiomorphic condition because it is present in all gempylids, except *Diplospinus*, *Nealotus*, and *Paradiplospinus*.

**BASIOCCIPITAL.** The basioccipital is a median bone forming the posteroventral corner of the neurocranium and the saccular bulla. Internally, it forms the lateral and ventral walls of the posterior

myodome (Collette and Russo, 1984). The basioccipital also forms the ventral edge of the foramen magnum and bears a concave facet for articulation with the atlas vertebra. It articulates anteriorly with the prootic and the parasphenoid. Dorsally, it joins the exoccipital. The morphology of this bone is similar among the taxa analyzed in this study.

**PARASPHENOID.** The parasphenoid joins the vomer anteriorly, and it articulates with the lateral ethmoid on the posterior wall of the ethmoidal region. Posteriorly, it articulates with the basisphenoid, the prootic, and the basioccipital, in that order. Its articulation with the prootic is by two dorsolateral extensions that form part of the anteroventral wall of the posterior myodome (Collette and Chao, 1975). The morphology of the parasphenoid is similar among the trichiurids and outgroups.

### PECTORAL GIRDLE

The pectoral girdle is formed by those bones that support the pectoral fin rays and connect the pectoral fin to the neurocranium (Fig. 18).

#### Supratemporal

The supratemporal is positioned ventrolaterally to the dorsal articular process of the posttemporal (Fig. 19). The supratemporal of the trichiurids is characterized by three branches that bear laterosensory canals. The posterior branch forms the junction between the temporal canal in the posttemporal bone and the system of canals in the skull (Coombs et al., 1987). The anteroventral branch joins the temporal canal with the dorsal pore in the pterotic bone. The anterodorsal branch carries the supratemporal division of the temporal canal (Coombs et al., 1987) onto the parietal region. All the trichiurids and outgroups have a tripartite supratemporal bone with an elongate anterodorsal arm. However, the supratemporal of the specimens of *Tentoriceps* examined have a poorly developed partition between the two anterior canals. One specimen of *Tentoriceps* has a simple, longitudinal, tube-like supratemporal on the right side followed anteriorly by another unbranched, longitudinal, tube-like ossification. In contrast, the left side of the supratemporal shows a tube with three pores, but the anterodorsal branch is not extremely elongate. Russo (1983) indicated that in the gempylids, the elongate dorsal branch on the supratemporal represents the medial extrascapular, which has become fused to the dorsal branch of the supratemporal. The morphology of this bone is similar among the taxa analyzed in this study.

#### Posttemporal

The posttemporal has three arms or articular processes: the dorsal articular process attaches to the dorsal surface of the epiotic; the anteroventral articular process bears a ligamentous attachment to the intercalar; the posteroventral articular process

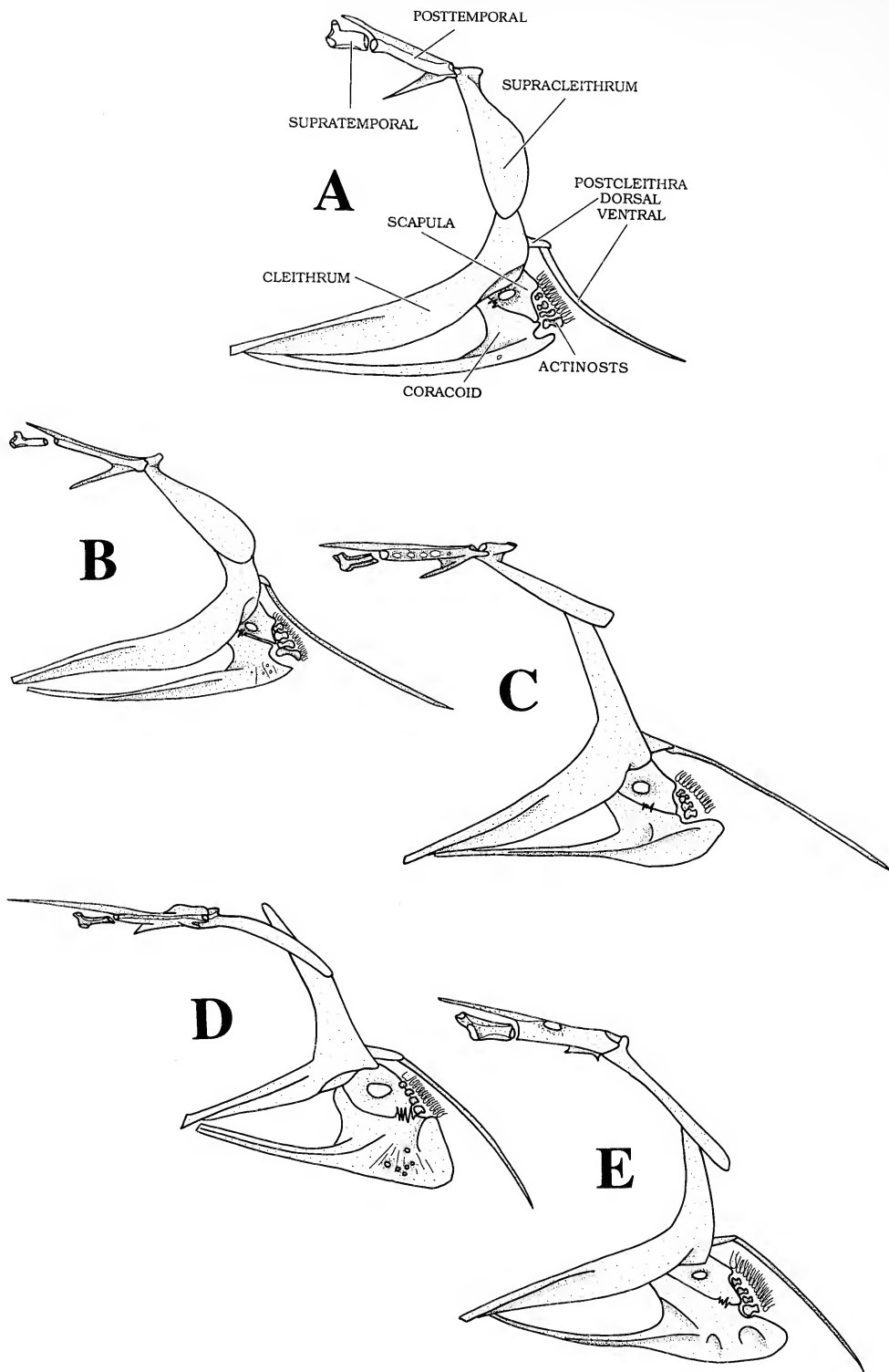


Figure 18. A-E. Lateral view of the left pectoral girdle: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus carbo*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

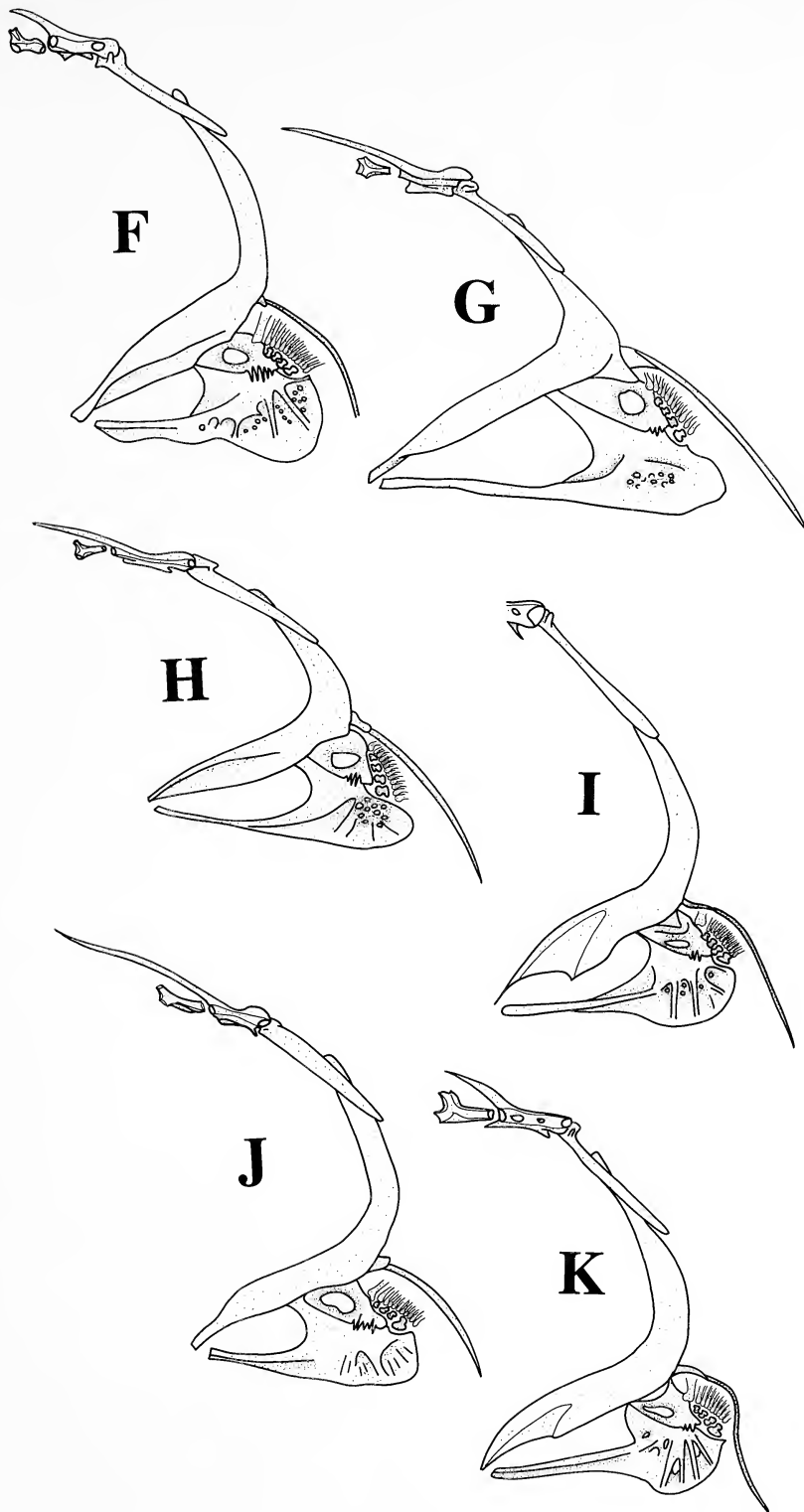


Figure 18. F-K. Lateral view of the left pectoral girdle: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

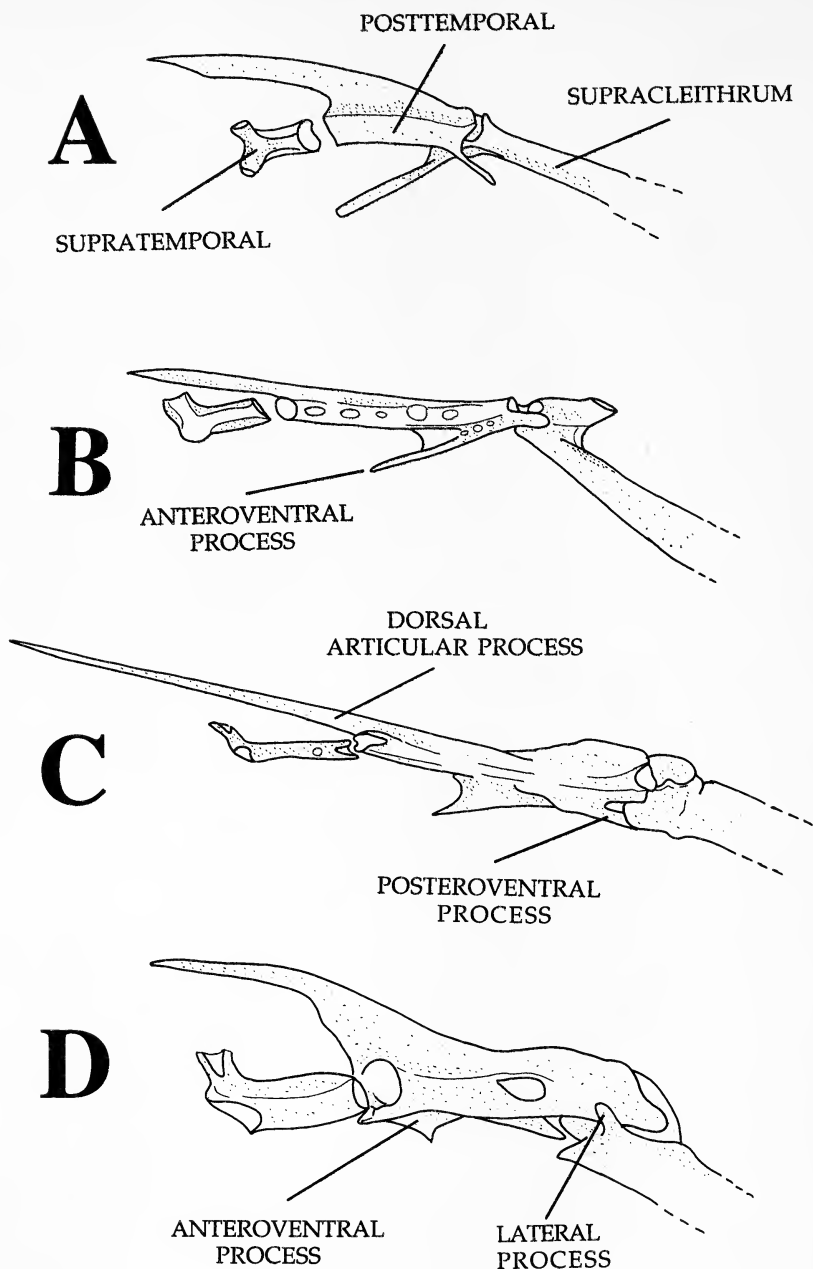


Figure 19. Lateral view of the left supratemporal, posttemporal, and the articular head of the supracleithrum: (A) *Gempylus serpens*; (B) *Aphanopus carbo*; (C) *Assurger anzac*; (D) *Eupleurogrammus glossodon*.

overlaps, or is attached by ligaments, to the dorsal articular head of the supracleithrum laterally. The posterior margin of the posttemporal overlaps the articular head of the supracleithrum laterally. This bone carries the temporal canal of the laterosensory canal system. It joins the canals in the supratemporal with the system of trunk canals in the body (Coombs et al., 1987).

Character 30. *Assurger*, *Evoxytmetopon*, *Lepi-*

*dopus*, and *Tentoriceps* are characterized by having an extremely elongate dorsal articular process, which extends past the anterior margin of the supratemporal and is at least twice the length of that bone (Fig. 19C). All the other trichiurids and the outgroups have a dorsal articular process that is short and terminates before or shortly after the anterior tip of the supratemporal (Fig. 19A, B, D).

Character 31. All the trichiurids, except *Aphan-*



*opus*, share the presence of a short posteroventral process on the posttemporal that is in direct contact, or in contact via ligamentous association, with the articular head of the supracleithrum (Fig. 19C, D). *Gempylus* bears a well-developed rod-like posteroventral process, but this condition is not comparable to that described for most trichiurids (Fig. 19A). In the trichiurids, the process is flat in cross section, further reduced in size, and more posteriorly directed and abuts the supracleithrum medially or bears a ligamentous connection with its articular head. In contrast, in *Gempylus* the posteroventral process is round in cross section and well developed and extends ventrally, and it is not in contact or close association with the articular head of the supracleithrum. *Aphanopus*, *Diplospinus*, *Nesiarchus*, and *Paradiplospinus* lack a posteroventral process (Fig. 19B).

**Character 32.** Russo (1983: character 69) identified the presence of a thin, rod-like anteroventral articular process as a synapomorphy of *Diplospinus*, *Gempylus*, and *Paradiplospinus*. He concluded that the presence of this process represents the plesiomorphic state characteristic of all the other gempylids, including *Nesiarchus*. The difference in the shape of the anteroventral articular process between *Nesiarchus* and the other outgroups (robust versus thin and rod-like) is difficult to evaluate. However, the anteroventral articular process of the trichiurids, except *Aphanopus*, is clearly different. It is elongate and well developed in the outgroups plus *Aphanopus*, and it is reduced in the rest of the trichiurids. In addition, the process originates at the posterior corner of the posttemporal of the outgroups plus *Aphanopus* (Fig. 19A, B), whereas in the trichiurids it originates close to or on the anterior half of the canal portion of the posttemporal, never at the posterior corner of the bone (Fig. 19C, D). Within the trichiurids, *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus* have an anteroventral process that originates separately from the origin of the posteroventral process. In contrast, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* bear a reduced anteroventral process that originates from a common ventral ridge with the posteroventral process.

**Character 33.** The posterodorsal corner of the posttemporal in all the trichiurids, except *Aphanopus* and *Benthodesmus*, is expanded and plate-like (Fig. 19C, D). In *Aphanopus*, *Benthodesmus*, and the outgroups, the posterior end of the posttemporal is tube-like and does not have a plate-like expansion (Fig. 19A, B).

### Supracleithrum

The posterior half of the supracleithrum in all the outgroups is expanded; the space between the margins of the supracleithrum is narrow anteriorly and wide posteriorly, giving the bone an ovoid appearance. All the trichiurids are characterized by having a supracleithrum with a posterior half that is not

expanded and in which the margins are nearly parallel throughout its length. Russo (1983: character 71) noted that *Gempylus* is characterized by having a supracleithrum with an elongate shape more similar to that described for the trichiurids in this study. He warned, however, that assignment of shapes to discrete categories and their subsequent polarization may be unwarranted. In addition, he suggested that ontogenetic changes in the shape of this bone weaken the argument for the categorization of this character. I agree with Russo (1983) that the categorization of this character is difficult, and I do not include it in the data matrix of this study.

**Character 34.** Russo (1983: character 72) noted that the gempylids *Diplospinus*, *Paradiplospinus*, *Promethichthys*, and *Thysites* have a posteriorly expanded process on the head of the supracleithrum, which bears a canal and transmits the lateral line to the posttemporal. The specimens of *Nesiarchus* examined in this study also have a canal bearing a posteriorly expanded process, whereas those of *Gempylus* and the trichiurids *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* lack a canal (Fig. 19A, D). The rest of the trichiurids, except *Aphanopus*, bear a posteriorly expanded head on the supracleithrum, with a semienclosed canal (Fig. 19C). *Aphanopus* shares a condition similar to that of the outgroups, except *Gempylus*, in which the articular head of the supracleithrum is posteriorly expanded and bears a completely enclosed canal (Fig. 19B).

**Character 35.** *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* bear a lateral process on the articular head of the supracleithrum that extends dorsally (Fig. 19D). This dorsally directed lateral process is well developed in *Lepturacanthus* and *Trichiurus*, but extremely reduced in *Eupleurogrammus*. The lateral process is absent in all the other trichiurids and the outgroups (Fig. 19A–C).

**Character 36.** The articular head of the supracleithrum in *Assurger*, *Eupleurogrammus*, *Lepidopus caudatus*, *L. fitchi*, and *Tentoriceps* bears a small anteroventral process (Fig. 19C, D). The rest of the trichiurids and the outgroups lack this process (Fig. 19A, B). However, although this condition is included as a character in the analysis, the validity of this character is questionable because the anteroventral process is quite variable in size within the five taxa above.

### Cleithrum

The main body of the cleithrum is formed by two longitudinal shelves that meet along their anterior margins and run parallel to each other. The scapula, coracoid, and dorsal postcleithrum articulate on the medial longitudinal shelf of the cleithrum. The two units of the cleithrum meet at their anteroventral tips.

The medial shelf of the cleithrum extends posteriorly and overlaps the anterior margin of the scapula laterally. This extension varies in shape from

round to triangular. Starks (1911) described a thickening on the lower part of the cleithrum in an Atlantic specimen of *Trichiurus lepturus*. He concluded that the bone structure was not similar to that of the hyperostosis of the supraoccipital.

### Scapula

The scapula supports three of the four actinosts on its posterior margin. A scapular foramen is present and variable in size and shape within species. An actinost process or posterodorsal facet accepts the first fin ray of the pectoral fin. The morphology of this bone is similar among the genera analyzed in this study.

### Coracoid

The coracoid is a paired bone that articulates dorsally with the scapula and anteriorly with the cleithrum. It bears an elongate anteroventral process, which attaches to the anteroventral tips of the cleithrum. It supports the fourth actinost on its posterodorsal corner.

*Character 37.* Posteroventrally, all trichiurids have a coracoid with a well-developed plate bearing a convex ventral margin that extends beyond the posterior margin of the fourth actinost. The outgroups lack a posteroventral plate, and they have a flat ventral margin on the coracoid that ends before the fourth actinost.

### Actinosts

The actinosts are four pairs of bones that support the bases of the pectoral fin rays. The dorsal-most actinost is numbered as the first and is the smallest of the series. The other three actinosts are each greater in size, with the fourth being the largest. The first three articulate with the posterior margin of the scapula, whereas the fourth articulates with the posterodorsal corner of the coracoid, or partially between the coracoid and the scapula. The morphology of these bones is similar among the genera analyzed in this study.

### Postcleithrum

The postcleithrum includes two pairs of elongate bones. The first pair, or dorsal postcleithrum, attaches to the posteromedial surface of the cleithrum above the scapula. The second pair, or ventral postcleithrum, attaches to the posterior tip of the dorsal postcleithrum and extends posteroventrally into the hypaxial musculature.

The trichiurids and the outgroups have a dorsal postcleithrum that is short and crooked, or sigmoid-shaped, and a ventral postcleithrum with a broad lamellar articular head and a long, styliform descending process. *Gempylus* is characterized by a ventral postcleithrum that is longer than the height of the pectoral girdle (i.e., from the dorsal margin of the posttemporal to the ventral margin of the cleithrum), whereas all the trichiurids and the rest

of the outgroups bear a shorter ventral postcleithrum.

### Pectoral Fin Rays

Nakamura and Parin (1993) noted that *Trichiurus gangeticus* Gupta 1966 bears serrations on the first pectoral ray. They considered the first pectoral ray in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* to be a spine. However, cleared and stained specimens show that the first ray of all the trichiurids and the outgroups is bilaterally divided and that it has an open base that embraces a cartilaginous knob above the first actinost. These characteristics identify this first pectoral element as a soft ray.

*Character 38.* The relative lengths of the pectoral fin rays vary among genera and account for the differences in shapes of the pectoral fin. In the outgroup genera *Diplospinus* and *Paradiplospinus* and in the trichiurids *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*, the posterior rays are longer. In contrast, in the outgroup *Gempylus* and in the trichiurids *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the anterior rays are the longest. The specimens of *Nesiarchus* analyzed in this study have pectoral fins with longer posterior rays. However, in the drawing of an adult *Nesiarchus* presented by Nakamura and Parin (1993: 35), the condition appears to be reversed. I have not been able to confirm the variation in this condition, and so I consider the state present in the specimens used in my study as characteristic of this genus.

### PELVIC GIRDLE

The pelvic girdle is composed of the basipterygium, which supports the fin rays (Fig. 20). Stiassny and Moore (1992) divided the basipterygium into a central part, anterior and posterior processes, and ossified wings. The central part bears cartilaginous tips anteriorly and an articular surface for the fin rays posteriorly. The posterior and anterior processes extend posteriorly and anteroventrally from the articular surface, respectively. The central part might bear four wings of membranous origin: external dorsal, external ventral, internal, ventral.

All the taxa analyzed in this study, except *Benthodesmus*, *Evoxymetopon*, *Lepidopus*, and *Nesiarchus*, have a posterior process that is extremely elongate and extends well past the distal tip of the pelvic scale or spine. In all of these taxa, the posterior process is about the same length as the central part. This process is greatly reduced in size in *Benthodesmus* and *Nesiarchus*, and it does not extend past the tip of the external fin rays. The posterior process is of about the same length as the central part in *Benthodesmus*, whereas it is about one-third the length of the central part in *Nesiarchus*. The posterior process of *Evoxymetopon* and *Lepidopus* is elongate and about the same length as the central part. In *Evoxymetopon*, *L. caudatus*, and *L. fitchi*, it is about the same length as the

scale-like spine. In *L. altifrons*, the posterior process is slightly larger than the scale-like spine. The length of the posterior process relative to the central part is quite variable and difficult to categorize objectively.

In all the taxa analyzed, except *Aphanopus*, the anterior process appears to be absent or extremely reduced. The length of the external ventral wing and the degree of thickness of its ventral margin are variable. It is well ossified and thick in the outgroups *Diplospinus*, *Gempylus*, and *Paradiplospinus* and the trichiurids *Benthodesmus tenuis*, *Eupleurogrammus*, and *Tentoriceps*. In contrast, it is not well ossified in *Assurger*, *Evoxymetopon*, *Lepidopus*, and the outgroup *Nesiarchus*. The length of the external ventral wing is quite variable and varies from less than half of the length (*Diplospinus* and *Paradiplospinus*) to more than half and up to about equal the length of the central part (all other taxa analyzed). Some specimens of *Tentoriceps* have an external ventral wing that extends only half the length of the central part, whereas in others it extends throughout the whole central part. The length of the external ventral wing is also variable among the species of *Benthodesmus*.

The degree of extension of the ventral margin of the external ventral wing is extremely variable and dependent on the degree of ossification and size of the specimens. Potthoff (1980) reported that in *Coryphaena* Linnaeus 1758, the structures of membranous origin in the pelvic girdle (anterior process and wings) develop last, after the ossification of the central part. Thus, categorization of the extent and degree of ossification of the external ventral wing is difficult, and the character is not included in this analysis.

**Character 39.** The outgroups are characterized by the presence of a well-developed basipterygium. In the trichiurids, the basipterygium has become extremely reduced or completely lost as it occurs in *Lepturacanthus* and *Trichiurus*.

Although the basipterygium of *Aphanopus* is reduced to a small internal plate, some parts are discernible under the microscope. Anteriorly the basipterygium bears what appears to be an extremely reduced central part. The central part appears as two unfused, short processes that are slightly inclined dorsally. In *Aphanopus* and the outgroup *Paradiplospinus*, the pelvic girdle bears a single spine in the juveniles, but the spine becomes extremely reduced in the adult where only the internal basipterygium remains.

**Character 40.** *Diplospinus* bears a pelvic fin with an ornamented scale-like element and no soft rays. The lateral margins of the scale-like element in *Diplospinus* are serrate. However, although this condition is described as different from that present in the trichiurids with a pelvic fin (i.e., presence of an unornamented scale-like element), one must be careful because the largest specimen of *Diplospinus* available in this study was only 193 mm SL. Nakamura and Parin (1993) reported that this species

is common up to 200 mm and that it reaches a maximum of 330 mm SL. It is possible that larger specimens of *Diplospinus* have lost the ornamentation of the lateral margins of this scale-like element. In contrast, *Gempylus* and *Nesiarchus* have stronger, better developed pelvic girdles with one spine and from three to four and one to five soft rays, respectively. *Eupleurogrammus* and *Tentoriceps* have a reduced scale-like element and no soft rays. *Benthodesmus* bears a scale-like element and a single soft ray. *Assurger*, *Evoxymetopon*, and the species of *Lepidopus* analyzed in this study have a scale-like element and two soft rays. *Lepturacanthus* and *Trichiurus* lack the pelvic girdle and fin elements.

**Character 41.** The position of the basipterygium relative to the pectoral girdle has been used as a taxonomic character for the identification of some trichiurid taxa (Nakamura and Parin, 1993). *Eupleurogrammus* and *Tentoriceps* are characterized by an abdominal basipterygium that is located posteriorly, well past the pectoral girdle, including the tip of the ventral postcleithrum. The outgroup taxa analyzed in this study are characterized by having a basipterygium that is located under the pectoral girdle. *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* have a basipterygium that is located completely or partly under the pectoral girdle (including the ventral postcleithrum). The basipterygium of adult *Aphanopus* is extremely reduced and located under the coracoid, anterior to the actinosts. The pelvic girdle of *Benthodesmus* is also reduced in size, and its position is variable among species. Nakamura and Parin (1993) used the position of the base of the pelvic-fin rays with respect to the pectoral-fin rays as a character for the identification of the different species of *Benthodesmus*. In the cleared and stained specimens of the species of *Benthodesmus* analyzed in this study, the basipterygium is always located under the pectoral girdle anterior to the ventral postcleithrum. *Assurger*, *Evoxymetopon*, and *Lepidopus* have a basipterygium in which the posterior process is partially or completely located posterior to a vertical | from the ventral tip of the ventral postcleithrum. However, in *Assurger*, *Evoxymetopon*, *Lepidopus*, and those species of *Benthodesmus* not available for this study, in which the base of the pelvic-fin rays is posterior to the pectoral-fin base, the articular facet of the basipterygium is always anterior to the tip of the ventral postcleithrum.

**Character 42.** In all the outgroups the central part of the basipterygium is dorsally inclined and extends anteriorly between the cleithrum and coracoid bones. Stiassny and Moore (1992) described this condition among percomorphs and noted that the central part of the pelvic girdle attaches to the cleithrum or coracoid by ligaments. They also concluded that among the acanthomorphs, this condition can be considered as apomorphic, with the pleiomorphic condition represented by a pelvic girdle that is parallel to the ventral body wall. All the

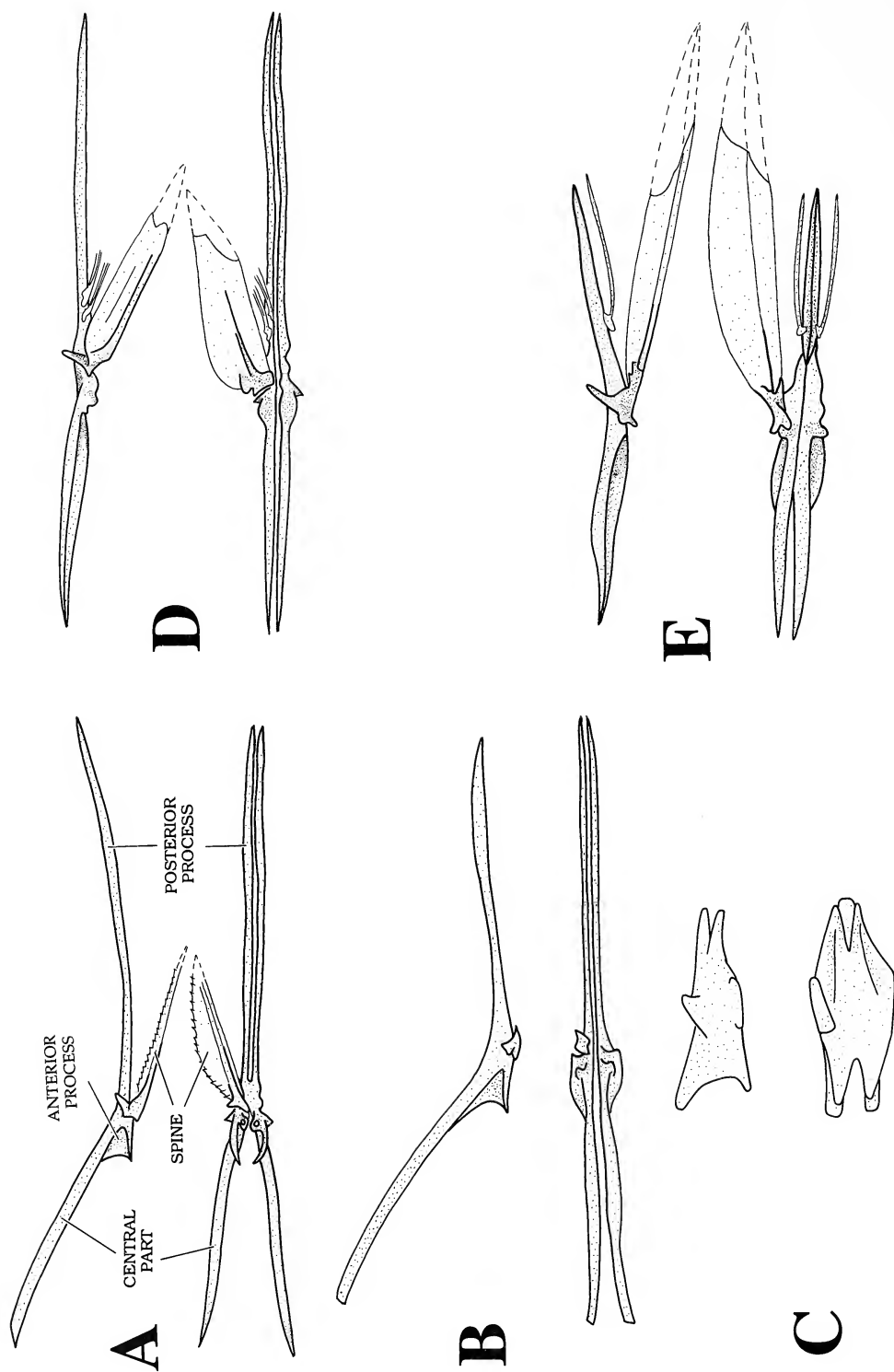


Figure 20. A–E. Lateral and ventral views (top and bottom, respectively) of the pelvic girdle: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus carbo*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

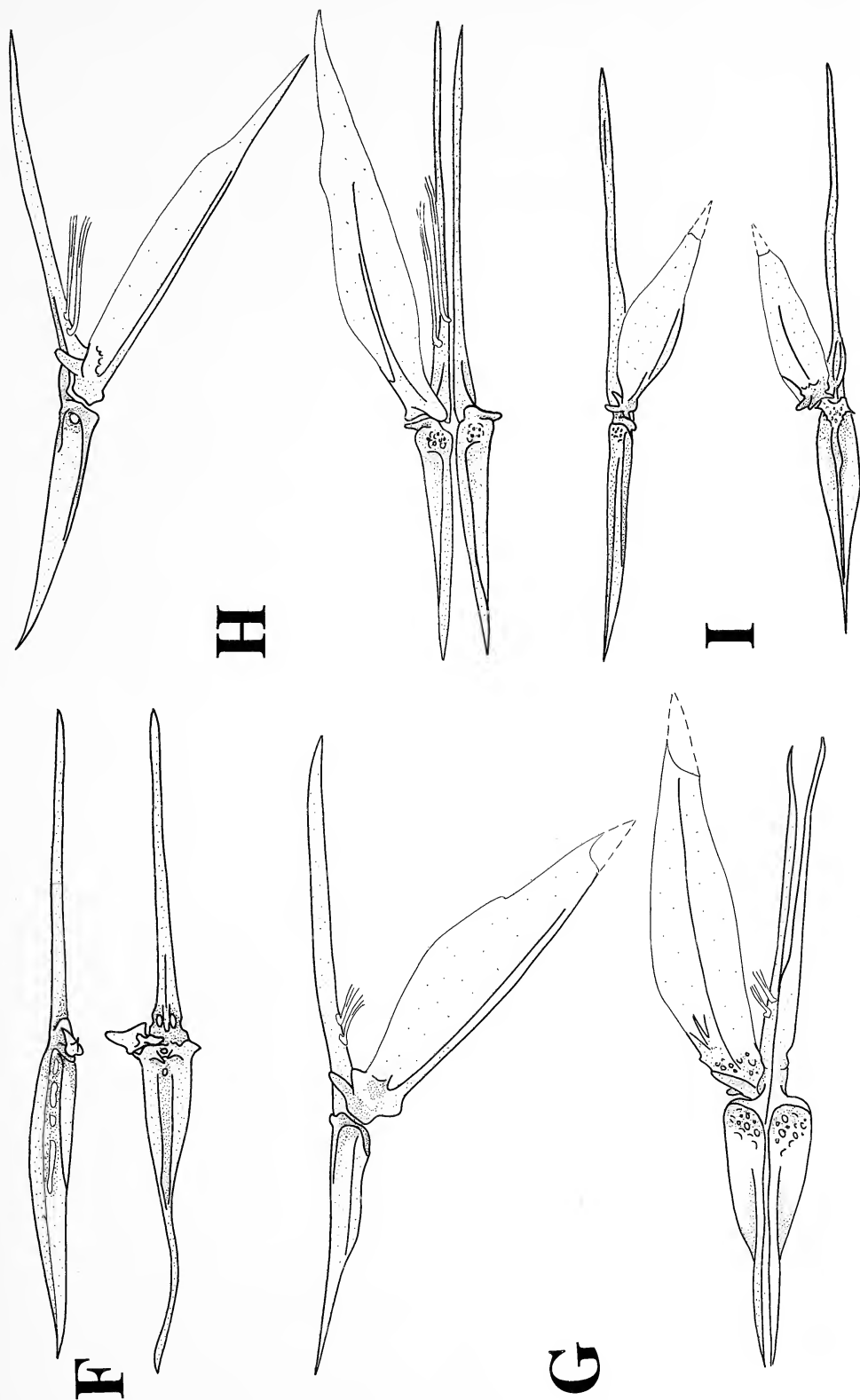


Figure 20. F-I. Lateral and ventral views (top and bottom, respectively) of the pelvic girdle: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Tentoriceps cristatus*.

trichiurids, except *Lepturacanthus* and *Trichiurus*, are characterized by having a basipterygium that is parallel or nearly parallel to the central body wall. The central part of the basipterygium in *Aphanopus*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* may be slightly inclined dorsally. However, the condition in these genera is not comparable to that present in the outgroups, in which the central part is extremely inclined and extends between the cleithrum and coracoid.

**Character 43.** *Eupleurogrammus* and *Tentoriceps* are characterized by having a basipterygium that is completely fused along its longitudinal axis. In *Benthodesmus*, the posterior process appears to be fused, whereas the central part is not. The reduced basipterygium of *Aphanopus* bears a central part that appears as two unfused processes. In contrast, *Assurger*, *Evoxymetopon*, *Lepidopus*, and the outgroups have a basipterygium that is not fused along its entire longitudinal axis.

## AXIAL SKELETON

### Vertebral Column

In the outgroups and the trichiurids, except *Tentoriceps*, the first rib is present on the third precaudal centrum (Fig. 21). *Tentoriceps* is the only taxon analyzed in which the first rib is on the second precaudal centrum. The trichiurids, except some of the specimens of *Lepidopus fitchi*, are characterized by the presence of ribs in all the rest of the precaudal centra. In the outgroups, some posterior precaudal centra bear haemal ribs that articulate laterally with a fully formed haemal arch. I found no evidence of haemal ribs in the posterior precaudal centra of the trichiurids, except in *Lepidopus fitchi*, in which the last two to four precaudal centra bear haemal ribs. However, in some specimens of *Lepidopus fitchi*, the last haemal ribs may be fused at their tips.

The neural prezygapophyses are well developed in the outgroups and the trichiurids. Those in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* are larger in size. In contrast, the neural postzygapophyses are smaller than the prezygapophyses. The haemal pre- and postzygapophyses are well developed in the caudal centra of all the outgroups and trichiurids. In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the haemal pre- and postzygapophyses are more vertically directed when compared with the rest of the taxa analyzed.

Lateral apophyses (extending on the frontal plane of the vertebral column) are present in the posterior-most precaudal centra and most of the caudal centra of the trichiurids. In the trichiurids with a caudal fin, the last caudal centrum bearing a lateral apophysis is that which still maintains an articulation with a dorsal or anal pterygiophore, or both. The proximal shafts of a few of the last anal and dorsal pterygiophores have lost their direct articulation with the corresponding neural and haemal spines.

The specimens of *Benthodesmus tenuis* analyzed in this study have a few posterior caudal vertebrae that lack lateral apophyses, although they still maintain an articulation with the corresponding dorsal and anal pterygiophores. The last centrum bearing an articulation with the corresponding pterygiophores has lateral apophyses.

Those trichiurids lacking a caudal fin (i.e., *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*) also have lateral apophyses. The lateral apophyses are better developed along the anterior half of their respective centra. As one proceeds posteriorly, the length of the lateral apophyses increases, and the length is gradually reduced again in the posterior caudal vertebrae. The last lateral apophysis is on the last centrum maintaining an articulation with the dorsal and anal pterygiophores. In the posterior caudal centra, the lateral apophyses extend anteriorly onto the preceding vertebral element. These lateral apophyses are more elongate in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* than in any of the other taxa analyzed. In *Eupleurogrammus*, the lateral apophyses become more vertically oriented as one proceeds posteriorly. As the lateral apophyses change orientation, the haemal prezygapophyses become reduced in size and appear to be replaced in position by the vertically oriented lateral apophyses. The outgroups, except *Gempylus*, lack or have extremely reduced lateral apophyses. *Gempylus* bears reduced lateral apophyses that do not extend past the anterior margin of their corresponding centra, as in the trichiurids.

**Character 44.** A characteristic of the trichiurids is the extreme elongation of their bodies. According to Nakamura and Parin (1993), the total number of vertebrae range from 57 to 64 in *Diplospinus*, 48 to 55 in *Gempylus*, 34 to 36 in *Nesiarchus*, 60 to 67 in *Paradiplospinus*, and 84 to 198 in the trichiurids. Collette et al. (1984: character 29) and Johnson (1986: character 16) utilized vertebral counts as a multistate character series. Johnson (1986) warned of the arbitrariness involved in categorizing the states of a meristic character. I agree with the conclusions of Carpenter et al. (1995) and consider their groupings among all the scombroids as a better representation of the distribution of vertebral numbers. Following the categorization of Carpenter et al. (1995) for all scombroids (with a slight modification to account for meristic data from this study and the literature), I consider the following character states with respect to the total number of vertebrae: 30 to 55 as state 0 among the gempylids (including *Gempylus* and *Nesiarchus*); 57 to 67 as state 1 among the gempylids (including *Diplospinus* and *Paradiplospinus*); 84 to 198 as state 2 for the trichiurids. Although this multistate character results in the assignment of an equivocal state at the outgroup node, I consider the condition present in the basal gempylids (i.e., gempylids minus *Diplospinus* and *Paradiplospinus*) as plesiomorphic.

**Character 45.** The first neural spine of all the

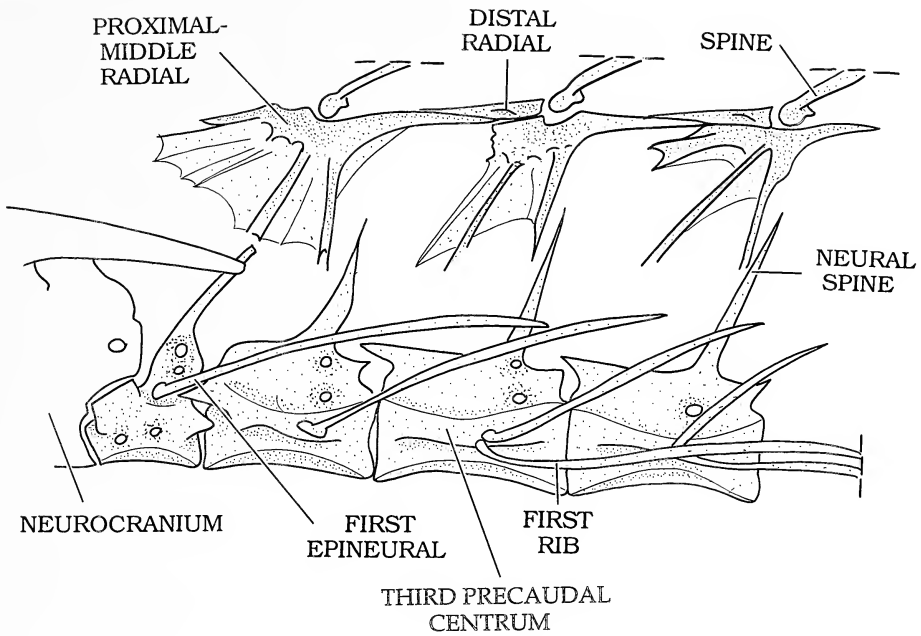
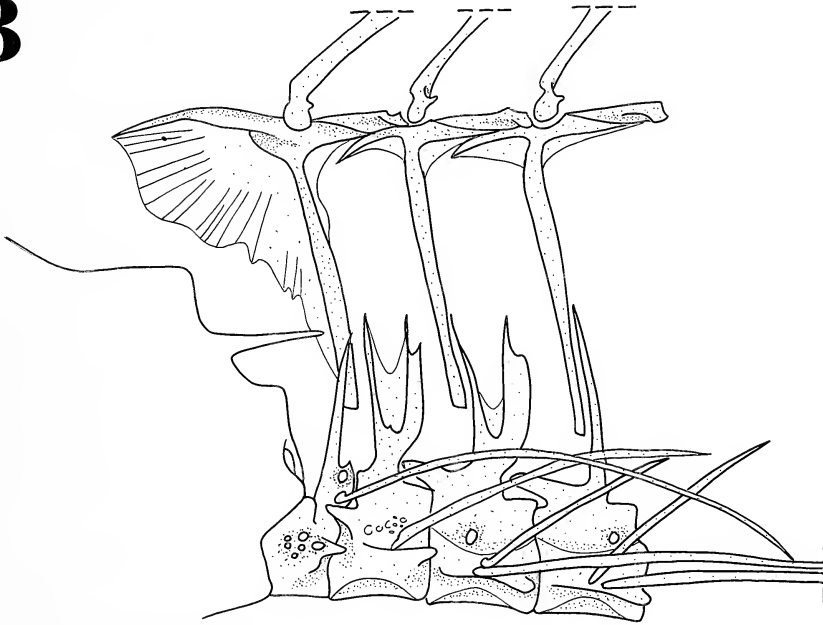
**A****B**

Figure 21. Left view of the anterior elements of the axial skeleton: (A) *Benthodesmus tenuis*; (B) *Trichiurus lepturus*.

trichiurids analyzed is distally bifurcate, and the proximal-middle radial of the first dorsal pterygiophore partially fits between its tips. The condition has been described in *Trichiurus* (Fig. 21B) by Potthoff et al. (1986). The outgroups, except *Gem-*

*pylus*, have a first neural spine that is not bifurcate at its tip. In the specimen of *Gempylus* analyzed in this study, the first vertebral element bears an extremely reduced, distally bifurcate neural spine. However, the condition in *Gempylus* is not com-

parable to that of the trichiurids. The unfused tips might be part of the neural arch, which is never completely closed during their ontogeny. The proximal-middle radial of the first dorsal pterygiophore does not fit between the unfused tips of the first neural spine.

**Character 46.** In *Lepturacanthus* and *Trichiurus*, the neural spines of centra two and three are expanded and plate-like with their anterior and posterior margins well ossified and bearing pointed tips that give the neural spines a forked shape (Fig. 21B). *Assurger*, *Eupleurogrammus*, and *Tentoriceps* share the same condition, but the expanded neural spines are on centra two to four, two to five, and two to six, respectively. All of the neural spines in the outgroups and in the trichiurids *Aphanopus* and *Benthodesmus* are simple and not expanded (Fig. 21A). Most of the specimens of *Evoxymetopon*, *Lepidopus altifrons*, *L. caudatus*, and *L. fitchi* analyzed bear slightly expanded anterior neural spines (not including the first centrum), but they are not distally forked as in *Assurger*, *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*.

### Intermuscular Bones

The intermusculars are segmental, serially homologous ossifications or ligaments in the myosepta of teleosts (Patterson and Johnson, 1995) that can be divided into myorhabdoi, epipleurals, epineurals, and epicentrals. Myorhabdoi, which occur only in a few teleosts, are not present in the trichiurids. Patterson and Johnson (1995) noted that epipleurals are absent in all acanthomorphs, except *Polymixia* Lowe 1838, *Velifer* Temminck and Schlegel 1850, and holocentrids. Epineurals appear as a series of bones or ligaments that develops in a rostrocaudal direction from the occipital region back. In the plesiomorphic condition, epineurals develop as outgrowths of the neural arches. In derived teleosts, epineurals have lost the ossified continuity with their respective neural arch and retain only a ligamentous attachment (Patterson and Johnson, 1995).

Epineurals are present in all the outgroups and the trichiurids, ranging from three to seven and articulating directly with the first three to seven vertebrae (Fig. 21). The first epineural originates on the neural arch of the first vertebral element, whereas the others originate farther ventrally on the head of the rib or the parapophyses. The distal margin of the anterior epineurals is forked in *Tentoriceps* and simple and pointed in other trichiurids and outgroups. However, *Evoxymetopon* and *Lepidopus* bear slightly expanded epineurals with a well-ossified central axis that supports two lateral thin plates.

In addition to the series of three to seven epineurals that articulate directly with the vertebrae, the outgroups are characterized by the continuation of the ossified epineural series farther back into the caudal region. *Nesiarchus* bears what appear to be

unattached epineurals from vertebrae 6 to 17 (the vertebral numbers are in reference to the position of the proximal tip of the epineural with respect to the vertebrae). These epineurals are simple, rod-like ossifications, with the exception of the epineurals on vertebrae 9 and 10, which are slightly forked proximally. In *Paradiplospinus*, the attached epineurals on vertebrae 4 to 6 are forked proximally. The anteromedial branch attaches to the corresponding centrum, whereas the anteroventral branch extends next to the preceding centrum. Dorsal to the seventh attached epineural there is a free, rod-like epineural similar in orientation and shape to the anteroventral branch and distal portion of the preceding epineurals. Farther posteriorly, *Paradiplospinus* bears simple, unattached, rod-like epineurals from vertebrae 8 to 59. I consider these apparently unattached epineurals as homologous with the anteroventral branches and distal portions of those anterior epineurals that are proximally forked. In *Diplospinus*, the unattached epineurals extend between vertebrae 6 and 54, and the attached epineurals of vertebrae 3 to 6 are forked. *Gempylus* bears three attached epineurals that articulate directly with the first three vertebrae (the first articulates at the base of the neural arch). The first two are simple and rod-like, but the third is forked proximally (i.e., the anteromedial branch attaches to the corresponding centrum and the anteroventral branch extends next to centrum 2). *Gempylus* is characterized by having the first unattached epineural originating anterior to the attached epineural of the first vertebra and medial to the supratemporal. The second epineural of *Gempylus* is also unattached; it is parallel to the distal portion of the first attached epineural, with its proximal tip lying above centrum 2. The next element of the series is represented by the anteroventral branch and distal portion of the forked epineural attached to centrum 3. Posterior to these few elements the rest of the epineurals are unattached, simple, and rod-like, with the series extending caudally to centrum 45. Although *Diplospinus*, *Nesiarchus*, and *Paradiplospinus* have no unattached epineurals originating anterior to centra 3 to 7, a series of ligaments parallel to the ossified, unattached epineurals extends anteriorly to these centra.

The epicentrals of teleosts develop in a rostrocaudal direction, lie in the horizontal septum, and are almost always simple rods (Patterson and Johnson, 1995). *Diplospinus*, *Gempylus*, and *Paradiplospinus* have a series of intermuscular bones that extend into the hypaxial musculature. These bones are simple, rod-like ossifications, and they are in reverse orientation to their unattached epineural counterparts. Their proximal tips appear to be unattached and lie laterally to their corresponding centrum. I consider this series of intermusculars as epicentrals. The proximal tips of the epicentrals originate next to centra 4 to 54 in *Diplospinus*, 3 to 45 in *Gempylus*, and 6 to 59 in *Paradiplospinus*. Although both of the epicentral series and most of



the epineurals appear to be unattached, it is possible that they have a ligamentous connection with their corresponding centra. The proximal tips of the unattached intermuscular bones in the outgroups are extremely thin, and I could not determine the presence of a ligamentous attachment at their proximal tips. Furthermore, the vertebral ranges described above are based on a single or a few representative specimens of each genus. Variation in these ranges was observed in those taxa for which more than one specimen was available. In this section, only the upper and lower limits of these ranges are presented. Thus, these meristics should not be taken as an absolute description of the distribution of intermusculars in these fishes.

**Character 47.** Presence or absence of unattached, ossified epineurals and epicentrals is considered as a multistate character. *Diplospinus*, *Gempylus*, and *Paradiplospinus* are characterized by the presence of unattached epineural and epicentral series that extend into the caudal region. *Nesiarchus* has a series of unattached epineurals that extends into the caudal region but lacks an epicentral series. Trichiurids bear a few attached epineurals, but they lack the series of unattached epineurals and epicentrals.

## Dorsal Fins

Tucker (1953) indicated that the presence of a continuous dorsal fin in most trichiurids clearly sets them apart from *Aphanopus*, *Benthodesmus*, the gempylids, and other scombroids.

**Character 48.** *Aphanopus* and *Benthodesmus* have a notch on the dorsal-fin membrane that separates the two dorsal fins, whereas the rest of the trichiurids have a continuous dorsal-fin membrane. All gempylids have a well-developed notch that separates the soft and spinous portions of the dorsal fin.

**Character 49.** In the gempylids the spinous dorsal fin bears from 19 to 39 spines and its base is longer than that of the soft dorsal. Most trichiurids have a spinous dorsal fin with a base that is shorter than the soft dorsal. Within the trichiurids, *Aphanopus* has a spinous dorsal fin that bears from 38 to 45 spines and is only slightly shorter than the soft-dorsal portion. *Assurger* and *Benthodesmus* are both characterized by a spinous dorsal fin that bears 31 to 46 spines and is less than half of the length of the soft-dorsal portion. A further derived condition, where the spinous dorsal fin is extremely short with only three to 10 spines, could be hypothesized for all trichiurids, except *Aphanopus*, *Assurger*, and *Benthodesmus*. Nakamura and Parin (1993: 70) indicated that *Aphanopus* and *Benthodesmus* have from 38 to 45 and 31 to 46 dorsal-fin spines, respectively. They also reported that *Assurger* only has "a few weak anterior spines hardly differing from the soft rays." However, upon close examination of radiographs and cleared and stained specimens of *Assurger* I found that its dor-

sal fin is composed of 34 to 35 spinous rays. These rays are true spines in that they are unsegmented, median elements with a closed base bearing a central foramen. In contrast, the soft rays are usually segmented, bilaterally divided, and branched at their tips. The spinous rays can also be identified in the trichiurids and outgroups by the type of articulation with their respective pterygiophores. The bases of the spinous rays do not embrace the distal radial (extra distal "x" radial of Johnson, 1986: character 30).

**Character 50.** Johnson (1986) noted that the morphology and development of pterygiophores of the soft-dorsal and anal fins in the trichiurids is similar to that of spinous pterygiophores. The pterygiophores supporting spinous-dorsal rays in the gempylids and the trichiurids are composed of proximal-middle and distal radials, which articulate by extensive overlapping (Johnson, 1986: character 21). These proximal-middle and distal radials have a concave dorsal face. In *Gempylus* the proximal-middle radials are extremely concave dorsally and bear well-developed pointed corners in their middle portions. Furthermore, Johnson (1986: character 22) indicated that in the gempylids, the posterior facet of the spinous distal radials is convex and acts as an articular condyle for the concave ventral margin of the closed bases of the dorsal spines. This condition is also shared by the spinous-dorsal elements of the trichiurids.

Johnson (1986: character 30) noted that the bases of the soft rays in the dorsal and anal fins of trichiurids embrace an extra distal "x" element that develops, as a separate ossification, posterior to its corresponding distal radial. The pterygiophores of the soft-dorsal and anal fins in the outgroups utilized in this study also have a separate radial that is embraced by the bases of the soft rays. This element is similar in shape to the "x" radial described by Johnson (1986), which is embraced by the open bases of the soft rays of the trichiurids (Fig. 22). The "x" element in the trichiurid soft rays bears an anteroventrally projecting pedestal (anterodorsally in the anal-fin pterygiophores) that ends in a cartilaginous knob that articulates with the concave articular facet of the preceding distal radial. The "x" radial also bears two laterally directed wings posteriorly. In trichiurids, the "x" element is a single ossification. In the outgroups, the distal radial, which is embraced by the open base of the corresponding soft ray, is not ossified along its medial axis, but the posterolateral wings and the lateral faces of the anterior pedestal are ossified. Johnson (1986) considered the possibility that the "x" element, embraced by the bases of the soft rays in the trichiurids, is a neomorph. The ontogenetic data of Gago (1997) indicate that the extra distal radial of Johnson (1986) is not a neomorph. Ontogenetic series of the outgroup genera show that the trichiurids and gempylids share a similar pattern of development of their dorsal fin pterygiophores. The presence of only two radials (proximal-middle and dis-

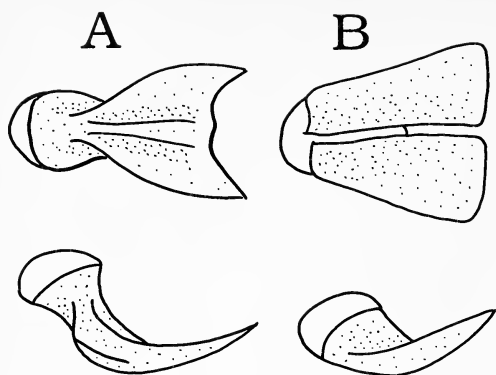


Figure 22. Ventral and lateral views (top and bottom, respectively; cartilage is not stippled) of the anal-fin 'x' radial of Johnson (1986) in adult: (A) *Trichiurus lepturus*, 288 mm TL; (B) *Paradiplospinus antarcticus*, 278 mm SL.

tal) supporting the soft rays of the dorsal fin in gempylids is the result of the fusion of the proximal and middle radials during development. In the trichiurids, the proximal and middle radials do not fuse during development and the adult retains three separate radials. Thus, the extra distal radial of Johnson (1986) appears to be homologous to the distal radial of other scombroids.

Günther (1860) and James (1960) reported hyperostosis of some of the dorsal proximal-middle radials in some specimens of *Lepidopus caudatus* and *Trichiurus lepturus*. James (1960) indicated that of the four species of trichiurids occurring in Indian waters (i.e., *Eupleurogrammus glossodon*, *E. muticus* (Gray 1831), *Lepturacanthus savala*, and *T. lepturus*) this condition was only present in *T. lepturus*. Radiographs of the holotype of *Evoxymetopon taeniatus* also show hyperostosis of some of the dorsal-fin proximal-middle radials. Smith-Vaniz et al. (1995) only listed the presence of hyperostosis in one species of trichiurid. To this list I add the report of hyperostosis on the dorsal-fin pterygiophores of *L. caudatus* and the new record of this condition in the holotype of *E. taeniatus*. The first dorsal pterygiophore of all the outgroups and the trichiurids bears a supernumerary spine and a second spine that articulates with the posterior facet of the distal radial.

**Character 51.** Johnson (1986: character 20) reported an extreme plate-like expansion of the proximal shaft of the first proximal-middle radial in the trichiurids (Fig. 21) and gempylids, except *Lepidocybium* and *Ruvettus*, which bear only a moderate expansion. In all trichiurids, except *Aphanopus* and *Benthodesmus*, this plate-like expansion of the first dorsal pterygiophore extends anteriorly above the occipital region of the neurocranium. The outgroups plus *Aphanopus* and *Benthodesmus* are characterized by a first proximal-middle radial

that does not extend onto the occipital region of the neurocranium.

In *Benthodesmus*, several of the anterior proximal-middle radials following the first pterygiophore also bear a plate-like extension on the anterior and posterior margins of the proximal shaft. The posterior margin of the plate-like extension is well ossified and, in conjunction with the obliquely oriented proximal shaft, gives the bone the appearance of an inverted "V." The tubular shaft bears a cartilaginous tip and lies free in the corresponding interneural space, whereas the posterior margin of the plate-like extension articulates with the neural spine of the subsequent vertebral element. As one proceeds posteriorly, the plate-like ossifications become smaller and the tubular margin shifts gradually and posteriorly until it comes in contact with the neural spine of the subsequent vertebral element.

All trichiurids, except *Aphanopus* and *Benthodesmus*, have a first dorsal proximal-middle radial with an elongate proximal shaft that fits primarily in the second interneural space. However, the anterior plate-like extension of the proximal shaft extends onto the occipital region and passes between the bifurcate tip of the first neural spine. *Aphanopus* and *Benthodesmus* have a shorter proximal shaft on the first dorsal proximal-middle radial that does not extend very far into the second interneural space. The anterior plate-like extension of the proximal-middle shaft in these two genera partially fits between the bifurcate tip of the first neural spine. *Diplospinus* and *Paradiplospinus* also have a proximal shaft on the first dorsal pterygiophore, which sits above the first and second interneural spaces, but the first neural spine is not bifurcate. The first neural spine of *Nesiarchus* is fused. The proximal shaft of the first dorsal pterygiophore is long in both *Gempylus* and *Nesiarchus*. In *Nesiarchus* it fits primarily in the second interneural space, but in *Gempylus* it extends above both the first and the second interneural spaces.

**Character 52.** In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, a plate-like ossification at the anteroventral corner between the proximal and distal portions of the proximal radials bears a small foramen. This foramen is absent or extremely reduced in the proximal radials of the other trichiurids and the outgroups.

## Anal Fin

The morphology of the anal-fin pterygiophores in the outgroups and most of the trichiurids is identical to that described for the dorsal-fin pterygiophores.

**Character 53.** The first anal pterygiophore in the outgroups bears two well-developed supernumerary spines (Fig. 23A, B). *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* bear two supernumerary spinous elements on the first anal pterygiophore (Fig. 23C–E, G, H). The first

supernumerary spine in these taxa is extremely reduced in size. Nakamura and Parin (1993) and Senta (1975) described the presence of two spines in the anal fin of *Tentoriceps*. However, in all the cleared and stained and alcohol-preserved specimens of *Tentoriceps* analyzed, I only found a single scale-like supernumerary element (Fig. 23J). *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* also have a single supernumerary element on the first anal pterygiophore. In the outgroups, the third fin-ray element associated with the first anal pterygiophore appears spinous in nature. The base of this element is completely or almost completely fused, forming a central foramen that accepts the posterior tip of the distal radial in *Gempylus* and *Nesiarchus*. However, this fin-ray element is bilaterally divided. *Diplospinus* and *Paradiplospinus* also have a third fin-ray element that is bilaterally divided, but the distal radial of the first anal pterygiophore does not pass through the central foramen. The distal radial of the first anal pterygiophore, which is in close association to the third fin-ray element, appears as a single ossification. The third fin-ray element of the first anal pterygiophore in the trichiurids is extremely reduced in size. In some specimens only one or two extremely reduced scale-like elements remain, and they appear to be remnants of a soft ray.

The two supernumerary spines of the first anal pterygiophore in *Gempylus* and *Nesiarchus* are well developed and rounded in cross section, except at their base, which embraces the articular facet of the first proximal-middle radial. The first supernumerary spine is longer than the second in *Nesiarchus*, whereas the rest of the outgroups have a longer second supernumerary spine. The supernumerary spines of the first anal pterygiophore of *Diplospinus* and *Paradiplospinus* are well developed, but V-shaped in cross section and bearing lateral wings. The first supernumerary spine of *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* is extremely reduced. The second supernumerary spine of *Aphanopus* is elongate, triangular in ventral view, and slightly V-shaped in cross section. The supernumerary elements of the first anal pterygiophore in *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* are modified and scale-like. The second supernumerary element is variable in shape, but it appears cardiform, or triangular, in ventral view, with well-developed lateral wings and V-shaped cross section.

The single scale-like supernumerary element of the first anal pterygiophore in *Tentoriceps* is similar to the second supernumerary elements of *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*. In *Eupleurogrammus*, the single supernumerary element is scale-like and bears lateral wings, but it is extremely reduced in size (Fig. 23F). The single supernumerary element in *Lepturacanthus* and *Trichiurus* is spinous in appearance (Fig. 23I, K) but triangular in cross section. This spine is much longer in *Lepturacanthus* than in *Trichiurus*, and this

feature was used by Nakamura and Parin (1993) as a character to differentiate these two genera.

The morphology of the posterior supernumerary element of the first anal-fin pterygiophore could be treated as a multistate character. However, the condition at the outgroup node is equivocal and the character is variable and difficult to categorize objectively. This potential multistate character must await a study that includes the gempylids and trichiurids together.

*Benthodesmus* is unique in that the first anal pterygiophore is abdominal in position, being located under the precaudal vertebrae. In all the outgroups and the rest of the trichiurids, the first anal pterygiophore articulates with the haemal spine of the first (or one of the first) caudal vertebrae.

The first anal pterygiophore of all the trichiurids, except *Benthodesmus*, and of the outgroups bears an elongate proximal shaft on the proximal-middle radial that articulates with its corresponding haemal spine. *Benthodesmus elongatus* and *B. simonyi* lack a proximal shaft on the first pterygiophore. However, the specimen of *B. tenuis* analyzed in this study has two poorly ossified proximal shafts that do not articulate with the vertebral column. The presence or absence of a proximal shaft in the first anal pterygiophore might prove to be a phylogenetically informative character within the genus *Benthodesmus*. However, its incorporation into a phylogenetic analysis must await the inclusion of most or all of the species of this genus in future studies. All of the trichiurids and the outgroups, except *Gempylus*, have a short anterior process on the first anal pterygiophore. *Gempylus* is unique in that the anterior process is extremely elongate and is almost equal in length to the proximal shaft.

Radiographs of the holotype of *Evoxymetopon taeniatum* show hyperostosis of some of the anal-fin proximal-middle radials.

**Character 54.** All the outgroups and the trichiurids *Aphanopus* and *Benthodesmus* have true soft rays (i.e., bilaterally divided, segmented, and distally branched) throughout the whole length of the anal fin (Fig. 24A, B). In *Assurger*, *Lepidopus*, and *Evoxymetopon*, most of the anal-fin rays are extremely reduced; only the last few rays are external, can be identified as true soft rays, and are connected by a membrane. In *Aphanopus* and some species of *Benthodesmus*, the anal fin is composed of true external soft rays that are united by a membrane along its entire length. However, one must be cautious in the interpretation of this character because its condition appears to be dependent on the size of the specimens. In this study, the cleared and stained specimens of *Lepidopus* have well-developed soft rays throughout the anal fin but only the posterior ones are connected by a membrane. Larger dry-skeletal preparations of this taxon show an extreme reduction of these anterior fin rays. In *Lepturacanthus* and *Trichiurus*, the anal-fin soft rays are reduced to spinule-like processes that are not branched or segmented (Fig. 24E). These spinules

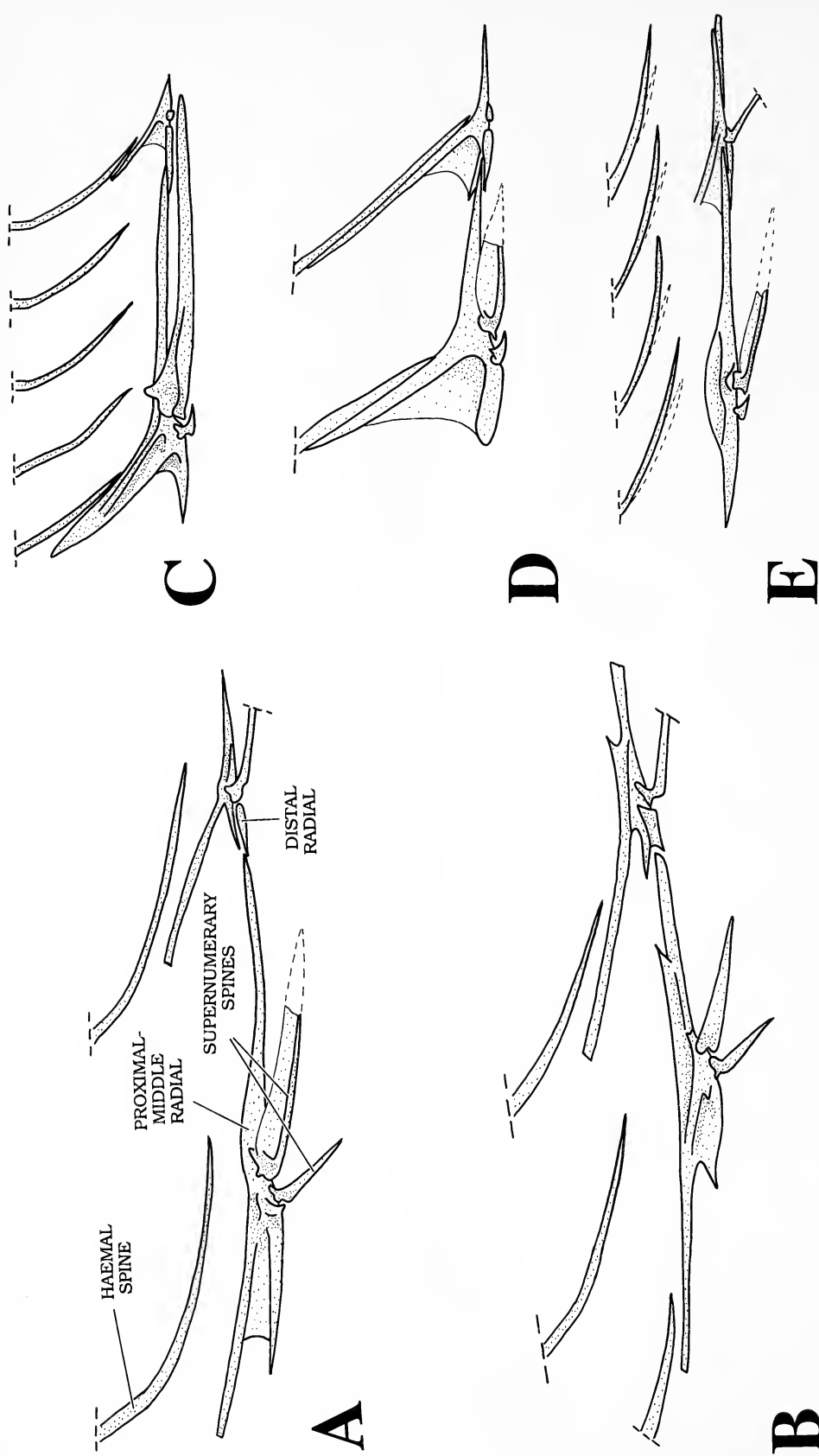


Figure 23. A–E. Left view of the first and second anal-fin pterygiophores: (A) *Benthodesmus elongatus*; (B) *Benthodesmus elongatus*; (C) *Benthodesmus elongatus*; (D) *Benthodesmus elongatus*; (E) *Benthodesmus elongatus*.

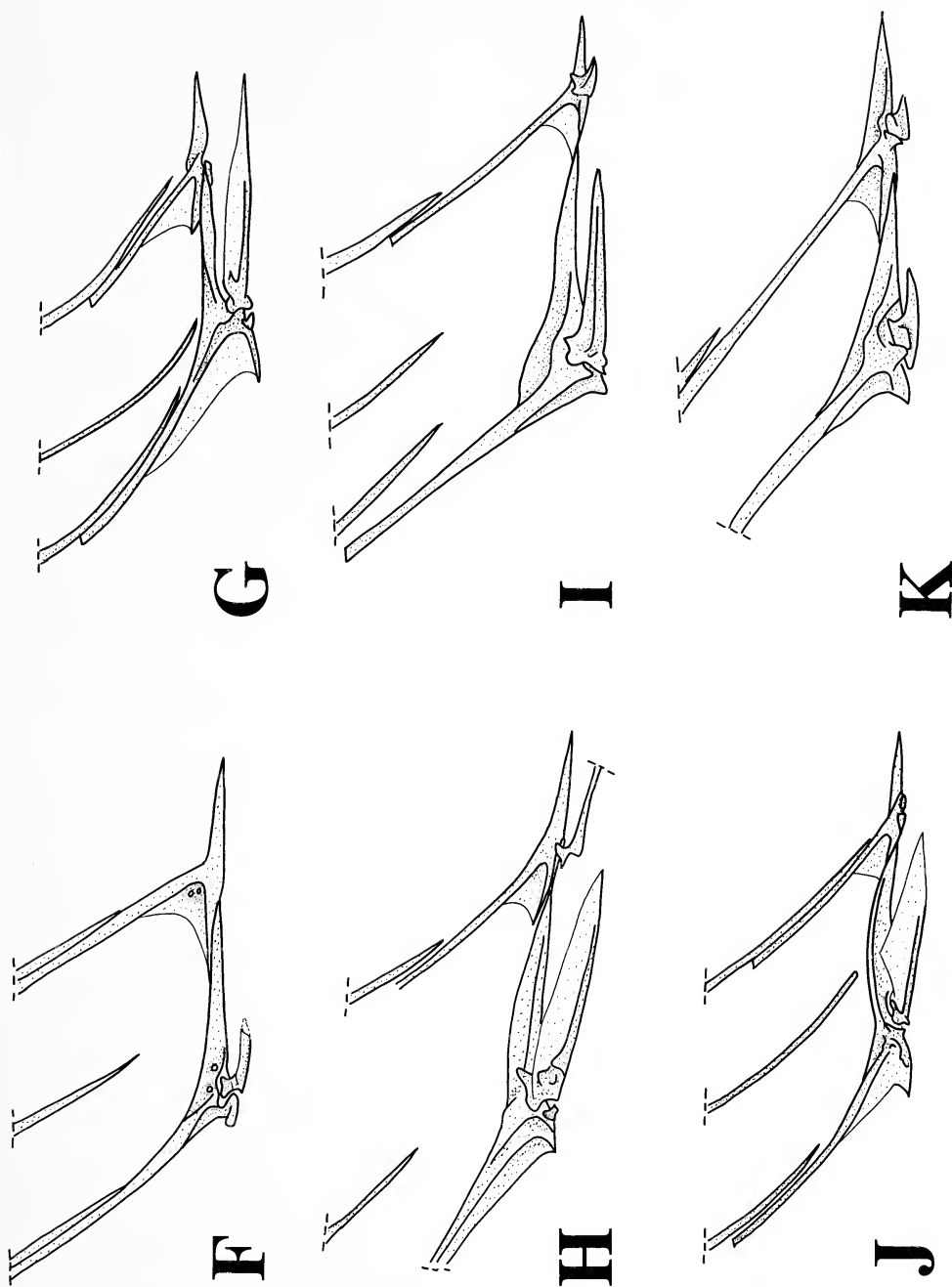


Figure 23. F-K. Left view of the first and second anal-fin pterygiophores: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatum*; (H) *Lepidopus fitchii*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

are V-shaped in cross section and resemble the morphology of the supernumerary spine of the first anal pterygiophore.

*Tentoriceps* shares the same condition as *Lepturacanthus* and *Trichiurus*, but the rays are reduced to minuscule scale-like elements that do not penetrate the skin externally (Fig. 24D). *Eupleurogrammus* shows another derived condition in which the rays barely penetrate the skin and appear as small fused knobs on the proximal-middle radials (Fig. 24C).

**Character 55.** The anal-fin pterygiophores of the outgroups are characterized by the presence of proximal-middle and distal radials (Fig. 24A). Trichiurids, except *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, have an anal fin in which the pterygiophores of the soft ray portion are composed of proximal, middle, and distal radials (proximal-middle and extra distal of Johnson, 1986; Fig. 24B). *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus* are characterized by the fusion of the radials as a single unit (Fig. 24C–D).

## CAUDAL COMPLEX

The caudal complex is composed of a series of caudal rays and supporting bones (Fig. 25).

**Character 56.** All the gempylids are characterized by the presence of a well-developed caudal complex. In some of the trichiurids, the caudal fin complex has become reduced or completely lost (Fig. 26). Senta (1975) briefly described the presence of an extremely reduced internal caudal complex in *Tentoriceps*. The posterior tip of the body in *Tentoriceps* is more rounded in appearance than those of *Lepturacanthus* and *Trichiurus*, which bear extremely pointed caudal tips. Internally, *Tentoriceps* bears two rudimentary hypural plates on the last vertebral element. From 6 to 14 rudimentary rays are also present in the cleared and stained specimens of *Tentoriceps* analyzed in this study. These rays barely penetrate the skin and articulate mainly on the margins of the reduced hypural plate and the dorsal surface of the last vertebral element. Adults of *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* are characterized by the complete absence of a caudal complex.

**Character 57.** All outgroups and those trichiurids with a well-developed caudal skeleton bear an ultimate centrum that has undergone flexion and forms a urostyle. In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the last vertebral centrum has not undergone flexion. In *Lepturacanthus* and *Trichiurus*, the posterior tip of the body is pointed, and the last vertebral element bears an extremely reduced neural process and a haemal spine that is branched distally in some specimens. The last vertebral element of *Eupleurogrammus* also bears an extremely reduced neural process. However, the haemal spine of this last verte-

bral element is spatulate and supports the more rounded tail of this genus.

The following descriptions refer only to those trichiurids and outgroups that bear a well-developed caudal complex, unless noted otherwise.

## Caudal-fin Rays

The caudal rays are divided into principal and procurent rays. The principal caudal rays are usually branched and more elongate and articulate with the upper and lower hypural plates, including the parhypural (Dunn, 1983). The procurent rays are usually unbranched and articulate with the neural or haemal elements of the preural centra. Collette et al. (1984) tabulated the meristic differences of caudal fin rays among the scombroids. All scombroids bear a 9+8 pattern of principal caudal rays on the dorsal and ventral hypural plates, respectively. However, a slight meristic difference appears in the numbers of procurent rays among the major scombroid groups. Trichiurids are characterized by having 6 or 7 dorsal and ventral procurent rays. All gempylids, except *Diplospinus* and *Paradiplospinus*, have between 8 and 11 procurent rays dorsally and ventrally. *Diplospinus* and *Paradiplospinus* are similar to the trichiurids in that they bear 4 or 5 and 5 or 6 procurent rays dorsally and ventrally, respectively. Scombrids have between 10 and 17 dorsal and 10 and 18 ventral procurent rays, whereas billfishes bear between 8 and 13 and 11 and 13, respectively. Although there is a reduction in the number of procurent rays in the trichiurids, the character is not used in the analysis because of the subjectivity in the determination of possible character states. Collette and Chao (1975) noted that in trichiurids and gempylids the bases of the caudal-fin rays extend only partly onto the hypural plate. In contrast, scombrids are characterized by having caudal-fin ray bases that cover the hypural plates almost completely.

## Epurals

The epurals are median bones located between the neural spine of preural centrum 2 and the upper hypural plate.

**Character 58.** All trichiurids have a single epural. *Diplospinus* and *Paradiplospinus* are characterized by the presence of two epurals, whereas *Gempylus* and *Nesiarchus* have three. Russo (1983) noted that all gempylids, except *Diplospinus* and *Paradiplospinus*, have three epurals. Although the condition for this character in this study appears to be equivocal at the outgroup node, I consider the plesiomorphic condition to be that present in most gempylids (i.e., presence of three epurals).

## Uroneurals

Uroneurals are paired bones located anterodorsally above the urostyle. The uroneurals represent the modified neural arches of the first preural and ural centra.

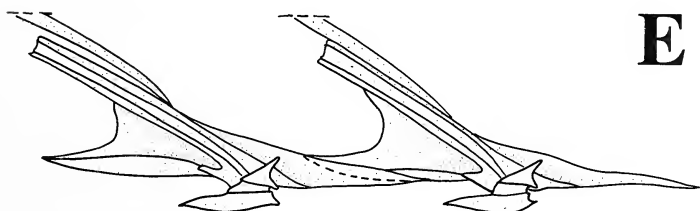
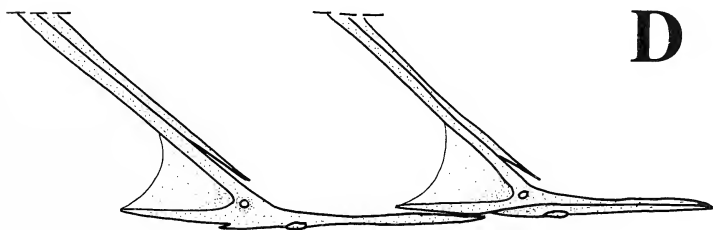
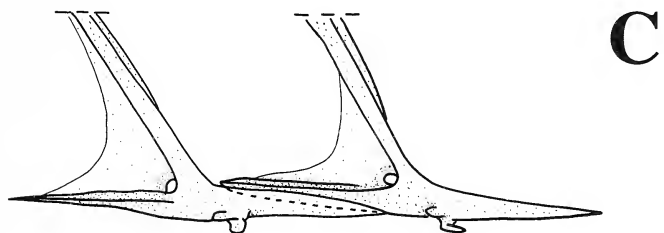
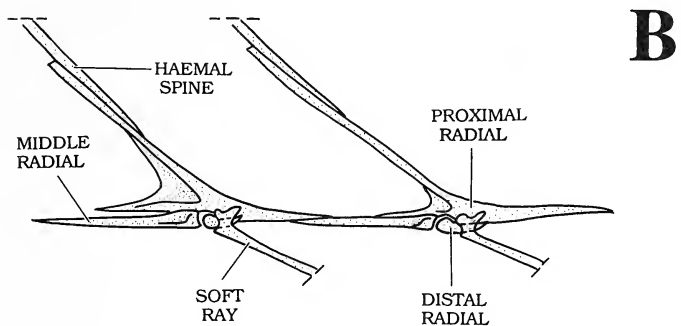
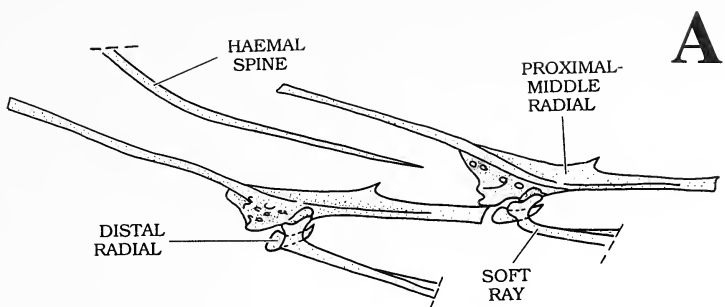


Figure 24. Left lateral view of two anal-fin pterygiophores and soft rays: (A) *Paradiplospinus antarcticus*; (B) *Aphanopus carbo*; (C) *Eupleurogrammus glossodon*; (D) *Tentoriceps cristatus*; (E) *Trichiurus lepturus*.

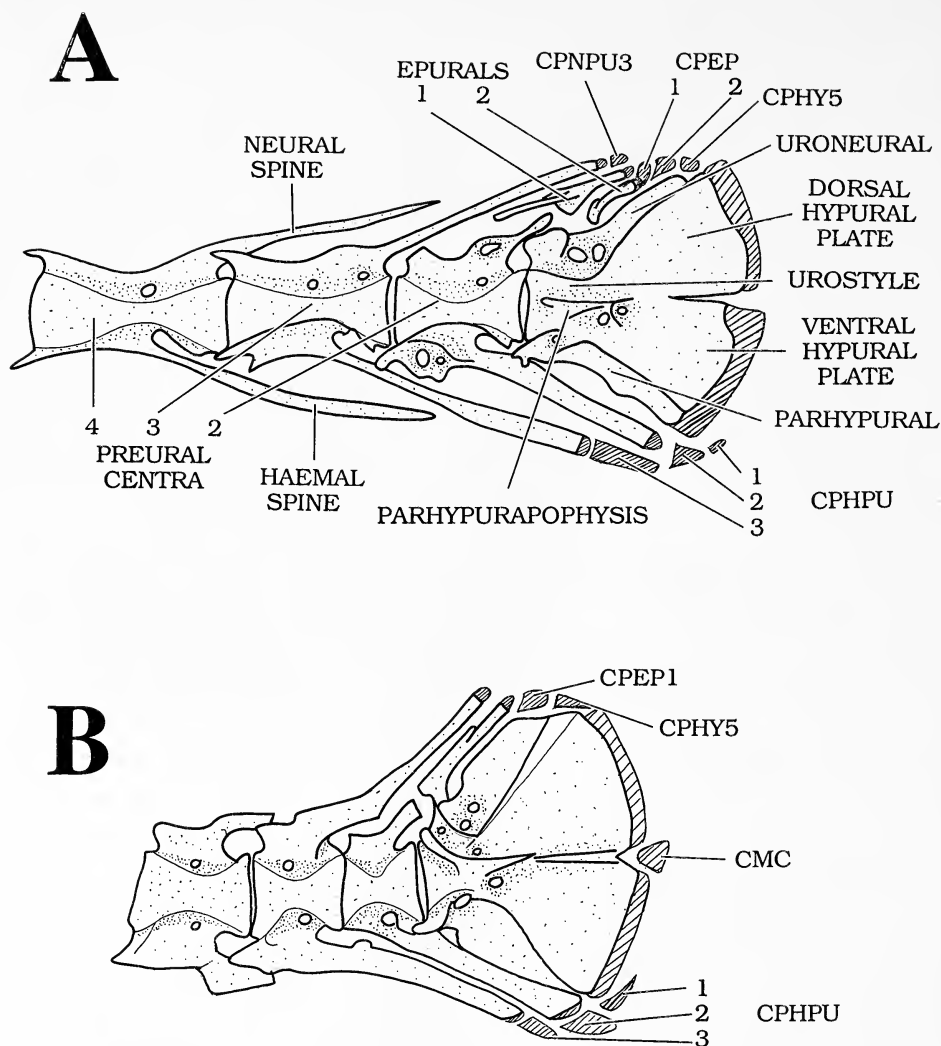


Figure 25. Left lateral view of the caudal-fin skeleton (fin rays not included; cartilaginous elements striped; CPNPU3, postneural spine cartilage of preural centrum 3; CPEP, postepural cartilages; CPHY5, posthypural cartilage of hypural 5; CMC, median caudal cartilage; CPHPU, parhypural and haemal spine cartilages of preural centra): (A) *Paradiplospinus antarcticus*; (B) *Assurger anzac*.

All trichiurids and the outgroups *Diplospinus*, *Gempylus*, and *Paradiplospinus* have a single uroneural. *Nesiarchus* has two uroneurals. Russo (1983) considered the fusion of the uroneurals with the urostyle in *Diplospinus*, *Gempylus*, and *Paradiplospinus* to be a synapomorphy uniting these three genera. Fujita (1990) reported that the uroneural of *Diplospinus* is fused to the urostyle and the upper hypural plate but concluded that the urostyle of *Gempylus* is autogenous. In this study, I also note that the uroneurals of *Paradiplospinus* and all the trichiurids with a well-developed caudal fin complex are fused, except in *Aphanopus* and *Benthodesmus*. In these two trichiurids, the uroneural is closely associated with the urostyle, but a joint between these two bones is visible. The degree

of fusion of the uroneurals to the urostyle and upper hypural is excluded from this analysis because the condition appears to be quite variable and dependent on the size and degree of ossification of the specimens and is difficult to interpret.

### Preural Centra

The preural centra discussed in this study include the three posterior-most vertebral elements, excluding the urostyle. They bear well-developed haemal and neural arches and spines. These elements are numbered from posterior to anterior, starting anteriorly to the urostyle, as preural centra 2, 3, and 4. In the trichiurids and outgroups, preural centra 2 and 3 bear well-developed haemal spines that



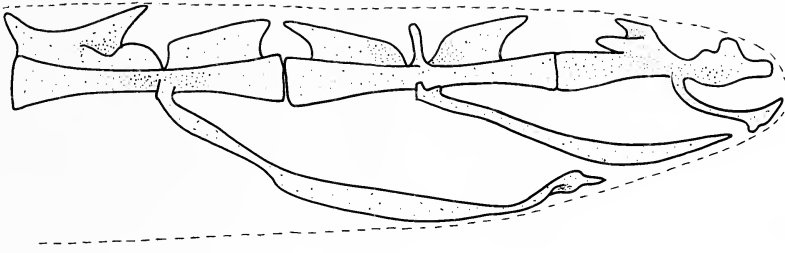
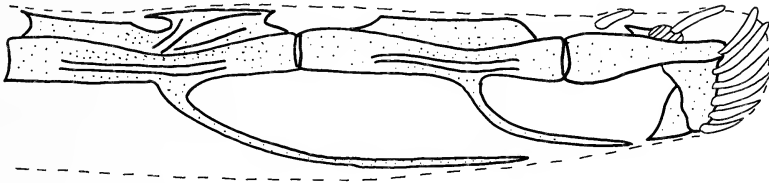
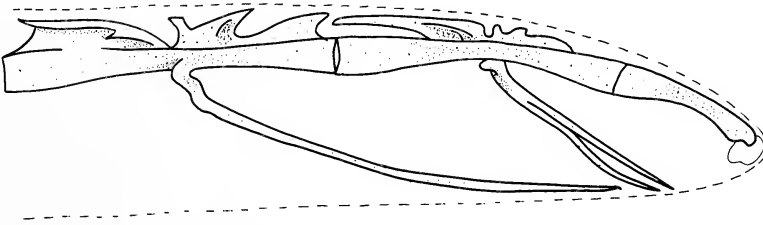
**A****B****C**

Figure 26. Left lateral view of the caudal tip (cartilaginous elements striped): (A) *Eupleurogrammus glossodon*; (B) *Tentoriceps cristatus*; (C) *Trichiurus lepturus*.

support the ventral procurent rays. In addition, preural centrum 3 of the trichiurids bears a well-developed neural spine that supports some of the dorsal procurent rays.

In trichiurids, the haemal spines of preural vertebrae 2 and 3 are fused to their respective centra. The haemal spines of preural centra 2 and 3 in the outgroups are usually autogenous. However, in a large specimen of *Paradiplospinus*, the haemal spine of the preural centrum 3 appeared to be fused. In his phylogenetic analysis of the gempylids, Russo (1983) noted that all gempylids, except *Dip-*

*lospinus* and *Paradiplospinus*, bear preural centra with fused haemal spines. He considered the presence of an autogenous haemal spine on preural centrum 2 to be a synapomorphy uniting these two genera. The degree of fusion of the haemal spines to their respective preural centra varies with size, is dependent on the degree of ossification of the specimens, and is difficult to interpret. In scombroids preural centrum 2 lacks a neural spine (Russo, 1983).

*Character 59.* In trichiurids, preural centrum 4 is characterized by the presence of shortened haemal

and neural spines which do not extend well past the anterior margin of preural centrum 3. The outgroups are characterized by the presence of haemal and neural spines on preural centrum 4 that are long and extend past, or as far as, the posterior margin of preural centrum 3.

### Urostyle

The urostyle supports the parhypural and the dorsal and ventral hypural plates posteriorly and the uroneural anterodorsally. The morphology of the urostyle is similar among the taxa analyzed in this study.

### Parhypural

The parhypural is a median bone located ventral to the urostyle and anteroventral to the ventral hypural plate. The parhypural is considered to be the modified haemal spine of the first preural centrum. It bears the last haemal arch that is traversed by the dorsal aorta. The parhypural bears a longitudinal lateral shelf or parhypurapophysis. Fujita (1990) noted that the parhypural is autogenous in all the gempylid taxa that he analyzed, except *Diplospinus*, where the parhypural is fused to the urostyle and the ventral hypural plate. *Gempylus* and *Nesiarchus* share the condition described by Fujita (1990) for the rest of the gempylids. Russo (1983) indicated that the parhypural of *Gempylus* is closely associated with the ventral hypural plate, but a distinct joint can be seen between them. Fujita (1990: table 2-20) indicated that *Benthodesmus elongatus pacificus* Parin and Becker 1970 (= *B. pacificus*) is characterized by a parhypural that is completely fused to the ventral hypural plate. However, in his illustrations, Fujita (1990: fig. 522) depicted a clear border between the parhypural and the ventral hypural plate. All of the specimens of *Diplospinus* and the trichiurids analyzed in this study share the presence of a fused parhypural. A small specimen of *Paradiplospinus* was characterized by the presence of an autogenous parhypural, whereas larger specimens had fused parhypurals. Russo (1983) also indicated that a joint is present distally between the parhypural and the ventral hypural plate of *Paradiplospinus*. The degree of fusion between the parhypural and the ventral hypural plate is variable among the gempylids and dependent on the degree of ossification of the specimens.

### Hypurals

The hypurals are a series of five median bones that are subtriangular in shape and articulate or are fused to the posterior margin of the urostyle. The hypurals are fused into two or more units or plates that support the bases of the principal caudal-fin rays.

**Character 60.** Russo (1983) considered the pattern of fusion among the hypurals as two charac-

ters. In his character 79, Russo (1983) concluded that the presence of separate third, fourth, and fifth hypurals represents the plesiomorphic condition; the fusions of the third and fourth or the third, fourth, and fifth represent the apomorphic conditions. Furthermore, in his character 81, Russo (1983) considered the separation of the first and second hypurals as the plesiomorphic condition and their fusion as the apomorphic condition. All trichiurids, plus the outgroups *Diplospinus* and *Paradiplospinus*, have a ventral and a dorsal hypural plate formed by the fusion of the first and second and the third, fourth, and fifth hypurals, respectively. In *Gempylus*, the dorsal and ventral hypural plates are formed by the fusions of the first and second and the third and fourth hypurals, respectively. The fifth hypural of *Gempylus* is closely associated with the fourth hypural and the urostyle, but a distinct joint is present between these bones. In *Nesiarchus*, all hypurals are separate. The degree of fusion of these elements is dependent on the size of the specimens. Although this character should be interpreted with caution, I include it in the analysis as a single multistate character that combines the conditions of the ventral and dorsal hypural plates described by Russo (1983). The condition of this character at the outgroup node is equivocal. However, I agree with Russo's (1983) analysis and consider the plesiomorphic condition to be that in which all the hypurals are free (i.e., the hypural plates formula is I + II + III + IV + V). The apomorphic conditions are the presence of three hypural plates (i.e., I-II + II-IV + V) or two hypural plates (i.e., I-II + III-IV-V).

**Character 61.** The ventral and dorsal hypural plates of the trichiurids and the gempylids *Diplospinus* and *Paradiplospinus* are fused longitudinally, except distally at their corners. Thus, the posterior margin of the hypural plates forms a notch (hypural notch of Russo, 1983). Russo (1983: character 80) concluded that the presence of a small hypural notch represents a synapomorphy uniting *Diplospinus* and *Paradiplospinus*. The trichiurids share this condition. The plesiomorphic condition is that present in the rest of the gempylids, which bear a large hypural notch.

### Cartilaginous Elements

Fujita (1990) described the cartilaginous elements of the caudal fin complex of several scombroids, including the trichiurid *Benthodesmus elongatus pacificus* (= *B. pacificus*) and the gempylids *Diplospinus multistriatus*, *Nealotus tripes* Johnson 1865, *Neopinnula orientalis* (Gilchrist and von Bonde 1924), *Nesiarchus nasutus*, *Promethichthys prometheus* (Cuvier in Cuvier and Valenciennes 1832), and *Ruvettus pretiosus* Cocco 1829.

All trichiurids and outgroups bear a single posthypural cartilage at the posterior tip of the fifth hypural (CPHY5 of Fujita, 1990). Trichiurids and the outgroups, except *Diplospinus* and *Paradiplo-*

*spinus*, have a single post-epural cartilaginous element (CPEP of Fujita, 1990). In trichiurids this post-epural cartilaginous element is associated with the single epural bone of these taxa (CPEP1). In contrast, the single post-epural element of the outgroups, excluding *Diplospinus* and *Paradiplospinus*, is associated with the third epural bone of these taxa (CPEP3). *Diplospinus* and *Paradiplospinus* are characterized by the presence of two separate post-epural cartilages (CPEP1 and 2 of Fujita, 1990) associated with the two epurals in their caudal skeleton. A cleared and stained specimen of *Paradiplospinus antarcticus* in this study shows a single post-epural cartilage. However, upon close examination through transmitted light, one can discern the presence of two darker blue cartilaginous centers within this single unit.

All of the trichiurids bear three posthaemal spine cartilaginous elements distally on the parhypural and the haemal spines of preural centra 2 and 3 (CPHPU1, 2 and 3 of Fujita, 1990). *Diplospinus*, *Gempylus*, and *Paradiplospinus* share this condition with the trichiurids. Fujita (1990) noted that *Nesiarchus* and all of the other gempylids, except *Diplospinus*, plus the three species of scombrids in his study have two posthaemal spine cartilages.

**Character 62.** All of the trichiurids with a well-developed caudal fin have a median caudal cartilage (CMC of Fujita, 1990). This single cartilaginous block lies slightly posterior to the hypural notch formed by the upper and lower hypural plates. All the outgroups lack this element.

**Character 63.** All of the outgroups bear a cartilaginous postneural spine element on the third preural vertebra (CPNPU3 of Fujita, 1990). The third postneural spine cartilage is absent in all trichiurids.

## OTOLITH MORPHOLOGY

Otolith features are depicted in Figure 27. The medial face of the sagittae is characterized by the presence of a longitudinal groove, the sulcus, which is usually divided into an anterior ostium and a posterior cauda. The ostium usually opens anteriorly through the excisura, which may or may not be bordered by a rostrum and an antirostrum. If present, a postcaudal trough marks the opening of the cauda. The dorsal and ventral borders of the sulcus are delimited by longitudinal ridges called the cristae superior and inferior, respectively.

The outgroup genera *Gempylus* and *Nesiarchus* (Fig. 28B, C) have very similar otolith morphologies. The sagittae have extremely elongate rostra and well-defined antirostra; an extremely shallow sulcus that opens both posteriorly and anteriorly; reduced, nonoverhanging cristae superior and inferior. The only difference between the sagittae of these two genera seems to be the presence of a notch in the posterior margin of the otolith and a shorter antirostrum in *Nesiarchus nasutus*. However, the variability of these characters cannot be

evaluated since only a single drawing of the otolith of *Nesiarchus* was available for comparison.

*Diplospinus*, *Paradiplospinus*, and all the trichiurids analyzed in this study, except *Lepidopus fitchi* (Fig. 28I), have sagittae with a sulcus that lacks a postcaudal trough. On the other hand, the sagittae of *Gempylus* and *Nesiarchus* show a very shallow sulcus that is open posteriorly. Other scombroids analyzed (e.g., basal gempylids and billfishes) have sagittae with a wide postcaudal trough or a sulcus with a wide, fan-shaped posterior margin (e.g., some scombrids). The latter group, even though they have a continuous posterior margin, could still be considered as open because of the extreme fan shape of the posterior margin of the cauda. Frost (1928) described the sagittal otoliths of *Lepidopus caudatus* as having a narrow postcaudal trough. A description and drawing of a sagitta of *L. caudatus* by Demestre et al. (1993) does not show a postcaudal trough. The 20 sagittae of this species analyzed in this study do not have a postcaudal trough (Fig. 28H). If the sagittae of some specimens of *L. caudatus* have a postcaudal trough, it may be very uncommon. Fitch and Gotshall (1972) included a photograph of a sagitta of *Lepidopus xantusi* Goode and Bean 1895 (= *L. fitchi*) that clearly shows a posterior opening of the sulcus. The same condition was found in most of the 42 sagittae of this species analyzed.

Anderson and Cailliet (1975) noted that the otolith morphology of their specimen of *Benthodesmus elongatus pacificus* (= *B. pacificus*) differs from that described by Fitch and Gotshall (1972) in the presence of a reduced antirostrum and a more rounded ventral surface with the greatest height occurring along the middle third of the longitudinal axis. Although they acknowledge that the specimens had been preserved in formalin prior to examination of the sagittae, the morphology is clearly distinct. In Anderson and Cailliet (1975; fig. 2) it appears that the sulcus extends along the whole medial face and opens both posteriorly and anteriorly. The well-developed sulcus and the elongate rostrum are in contrast with the sagitta of *B. pacificus* analyzed in this study (Fig. 28G).

Reduced ornamentation of the ventral margins of the otoliths is characteristic of *Diplospinus*, *Gempylus*, *Paradiplospinus*, and all the trichiurids in this study, except *Lepidopus*, *Lepturacanthus*, and *Trichiurus*. *Diplospinus* seems to have some slight ornamentation on the ventral margin, but its condition is not comparable to the strongly serrate and irregular ventral margins that characterize *Nesiarchus*, *Lepidopus*, *Lepturacanthus*, *Trichiurus*, and most scombroids. However, the degree of ornamentation seems to be quite variable within species. For example, large sagittae of *Gempylus* appear to have little ornamentation, whereas smaller sagittae are heavily ornamented.

*Diplospinus*, *Paradiplospinus*, and all the trichiurids have sagittae with reduced ornamentation on their dorsal margins. All other scombroid genera

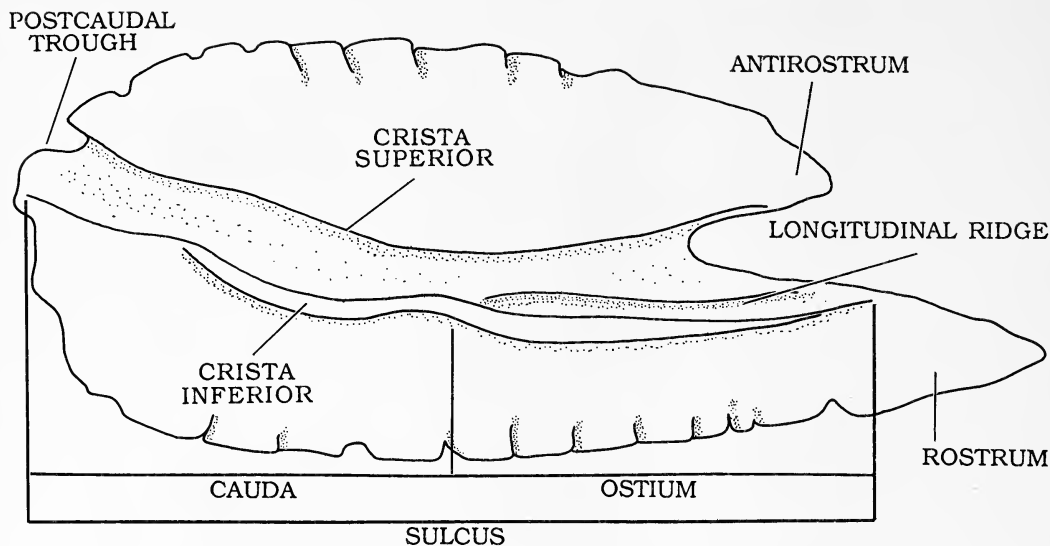


Figure 27. Generalized diagram of the medial face of a left sagitta from a hypothetical trichiurid.

analyzed have sagittae with strong ornamentation in the form of irregular, serrate dorsal margins. Some of the otoliths of *Diplospinus* and *Paradiplospinus* have a slightly ornamented dorsal margin. However, this is not comparable to the plesiomorphic condition present in *Gempylus* and *Nesiarchus*. Again, the ornamentation appears to be variable through ontogeny.

A possible autapomorphy for the genus *Assurger* is the presence of a tapering posterior end that turns abruptly downward forming a posteroventral dome (Fig. 28F), which is absent or reduced in the other genera studied. However, this possible character is not included in the data matrix because its variability could not be determined since only three otoliths (i.e., two individuals) of *Assurger* were available.

**Character 64.** *Diplospinus* and *Paradiplospinus* (Fig. 28A, D), plus the trichiurids *Aphanopus* and *Benthodesmus* (Fig. 28E, G), have poorly developed rostra and antirostra. Fitch and Gotshall (1972) described the sagittae of *Aphanopus* as lacking a rostrum. *Gempylus* and *Nesiarchus*, the rest of the trichiurids, and the other scombroid genera analyzed in this study have well-developed rostra and antirostra. Although the condition for this character at the outgroup node of this study is equivocal, the presence of well-developed rostra and antirostra is considered to be the ancestral condition since it is present in the rest of the scombroids analyzed outside of the trichiurids and the outgroups *Diplospinus* and *Paradiplospinus*. This character, however, is variable and should be interpreted with caution. *Gempylus* and *Nesiarchus* have an extremely elongate rostrum, whereas *Assurger*, *Lepidopus*, *Lepturacanthus*, and *Trichiurus*

possess a well-developed rostrum and antirostrum that is not nearly as elongate.

**Character 65.** The presence of overhanging cristae inferior and superior characterizes the genera *Aphanopus*, *Assurger*, *Lepidopus*, *Lepturacanthus*, and *Trichiurus*. All the other trichiurids and outgroups lack the presence of overhanging cristae.

**Character 66.** *Lepturacanthus* and *Trichiurus* (Fig. 28J, K) share the presence of a longitudinal ridge on the ostium. The longitudinal division of the ostium by a ridge was already noted by Frost (1928) in the sagittae of *Trichiurus*. The otoliths of *Lepturacanthus* have not been previously described. The otolith morphology of *Lepturacanthus* is extremely similar to that of *Trichiurus*. The rest of the trichiurids and outgroups lack a longitudinal ridge on the ostium.

## DISCUSSION

Analysis of the data matrix supports some of the previously proposed hypotheses of relationships within the trichiurid fishes. Among these hypotheses are: the monophyly of the trichiurids; the monophyly of *Diplospinus* and *Paradiplospinus* and their sister group relationship to the trichiurids; the close relationships of the trichiurids *Lepturacanthus* and *Trichiurus*; and the basal position within the cutlassfishes of *Aphanopus* and *Benthodesmus*.

Johnson (1986) proposed a monophyletic Trichiurinae (trichiurids of this study) based on nine synapomorphies. The present study includes four of these nine synapomorphies and increases the support for his hypothesis by adding 17 more (Fig. 4).

The sister group relationship of *Diplospinus*-*Paradiplospinus* to the trichiurids (Fig. 4) agrees

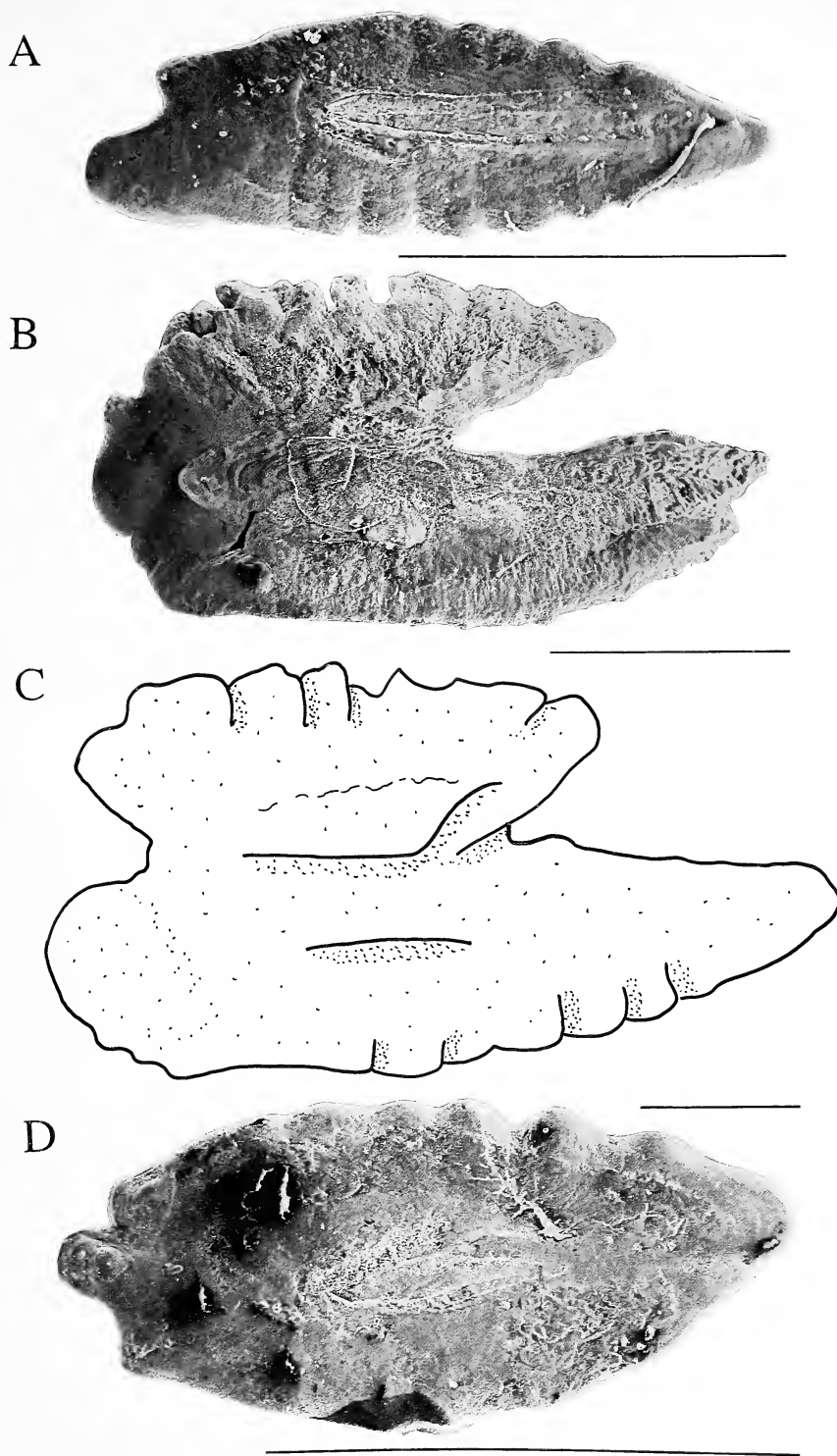
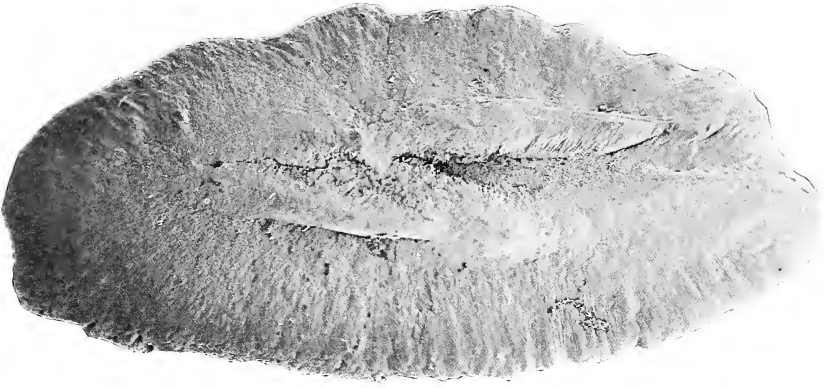
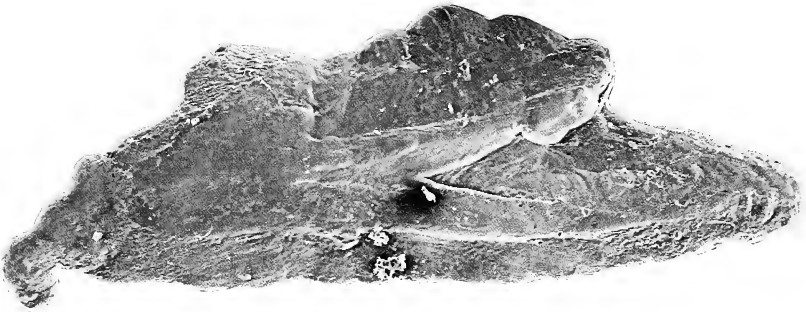


Figure 28. A–D. Electron microscopy photographs and line drawing (scale bar = 2 mm) of the medial face of the left sagittae of: (A) *Diplospinus multistriatus*; (B) *Gempylus serpens*; (C) *Nesiarchus nasutus* (provided by Dr. D. Nolf); (D) *Paradiplospinus antarcticus*.

E



F



G

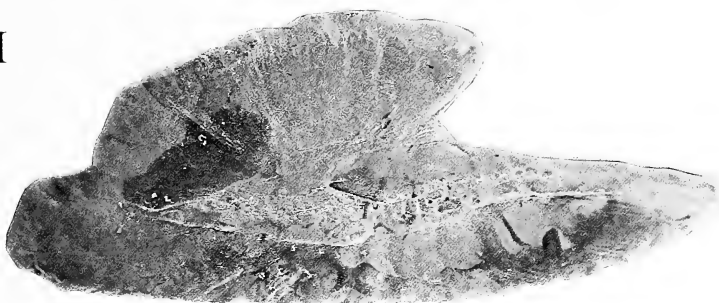


Figure 28. E–G. Electron microscopy photographs and line drawing (scale bar = 2 mm) of the medial face of the left sagittae of: (E) *Aphanopus arigato*; (F) *Assurger anzac*; (G) *Benthodesmus pacificus*.

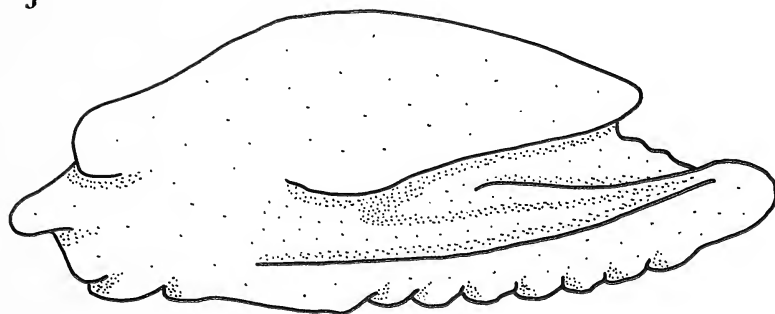
H



I



J



K

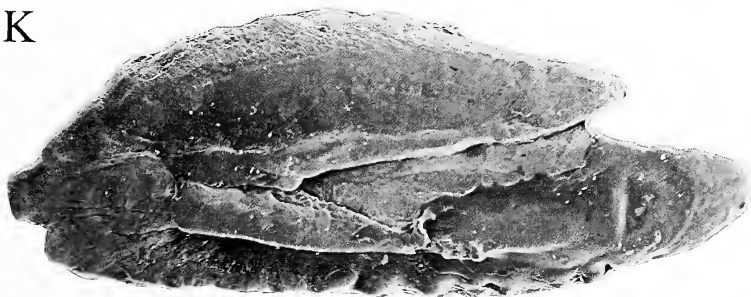


Figure 28. H-K. Electron microscopy photographs and line drawing (scale bar = 2 mm) of the medial face of the left sagittae of: (H) *Lepidopus caudatus*; (I) *Lepidopus fitchi*; (J) *Lepturacanthus savala*; (K) *Trichiurus lepturus*.



with the conclusion of Parin and Becker (1972), who also considered these gempylid genera as the closest relatives of the trichiurids. Previous to the work of Parin and Becker (1972), most authors included *Diplospinus* and *Paradiplospinus* within the Trichiuridae. Recently, Carpenter et al. (1995) presented the results of several analyses of relationships among the scombroids based on morphological characters. They analyzed a revised version of the data matrix of Johnson (1986), a combined data set from Collette et al. (1984) and Johnson (1986), and a data set in which the coding of one of Johnson's (1986) characters was changed. In all of their analyses, the clade including *Diplospinus* and *Paradiplospinus* appeared as the sister group of the trichiurids.

*Diplospinus* and *Paradiplospinus* are so similar in their osteology that they have been considered a single genus (Russo, 1983). In addition, Fitch and Gotshall (1972) questioned the validity of *Paradiplospinus*, indicating that the small differences in the sagittae of these two genera seem to be specific rather than generic in magnitude. However, in this study, one feature defines the species *P. antarcticus*: a posteriorly directed basibranchial attachment on the urohyal. According to Russo's (1983) hypothesis of gempylid relationships, this basibranchial attachment appears to have been lost once at the ancestral node separating *Lepidocybium* from remaining gempylids, to be regained independently in *Epinnula*, *Thyrsitoides*, and *Thyrsitops*. In addition, the distinct condition of the pelvic girdle, in which the external elements are absent and the basipterygium is well developed, also distinguishes this genus from the closely related *Diplospinus*.

The loss of external elements of the pelvic girdle has occurred twice independently within the trichiurids: in *Aphanopus* and the clade *Lepturacanthus-Trichiurus*. This conclusion is supported by the ontogenetic data of Gago (1997), which also showed that larvae of *Aphanopus* bear a well-developed pelvic girdle with external elements. The condition in *Aphanopus* is unique because the basipterygium is extremely reduced and consists of only a small ossification under the pectoral girdle. *Lepturacanthus* and *Trichiurus* lack all elements of the pelvic girdle. Remaining trichiurids have reduced pelvic girdles, but they still retain the external fin elements. Among the other gempylids, not analyzed in this study, *Promethichthys*, *Rexichthys* Parin and Astakhov 1987, and some species of *Rexea* have also lost the external pelvic-girdle elements (Nakamura and Parin, 1993). Following the hypothesis of gempylid relationships of Russo (1983), this loss of external pelvic-girdle elements appears to have occurred independently at least three times. However, Russo (1983) did not describe the pelvic girdle of gempylids. Thus, I have no evidence about the degree of reduction of the basipterygium among these genera.

In this study, monophyly of *Lepturacanthus* and

*Trichiurus* is defined by six synapomorphies, including two homoplasies (Fig. 4). Tucker (1956) included these two genera within the subfamily Trichiurinae Swainson 1839. In his tree, the Trichiurinae appears as emerging at the same node with his subfamily Lepidopodinae and a monophyletic group including *Aphanopus* and *Benthodesmus*. Furthermore, he questioned whether the subfamily Trichiurinae appeared as a descendant of his *Nesiarchus-Diplospinus* bridge or if it had an earlier divergence within the Gempylidae. Tucker (1956) indicated that, if further examination of the palatine of the gempylid *Thyrsitoides marleyi* Fowler 1929 indicated the presence of a villiform band of teeth, it could be considered as evidence for an earlier offshoot of the Trichiurinae. Matsubara and Iwai (1958) indicated the absence of teeth in *Mimasea* (= *Thyrsitoides*), whereas Russo (1983) described the presence of a single row of teeth on the ventral margin of the palatine of this species. Matsubara and Iwai (1958: 33) concluded that, because the presence of a number of small teeth on the palatine "is rather variable by the species, it appears likely that the palatine teeth are not so important [a] characteristic in considering the gempylid-trichiurid relationship," as assumed by Tucker (1956). Although Russo (1983) indicated that replacement teeth were present dorsomedially to the ventral row of teeth in his specimens of *Thyrsitoides marleyi*, the condition is not comparable to that in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*. The specimens of these three genera analyzed in this study are characterized by the presence of a villiform band of small teeth that covers most of the length of the palatine.

Tucker (1956) also mentioned the presence of a concave free margin of the subopercle as a character that is present not only in *Lepturacanthus* and *Trichiurus* but also in some gempylids such as *Epinnula* and *Neopinnula*. Russo (1983) concluded that the apparent concave condition of the subopercle in the gempylids *Nealotus*, *Promethichthys*, *Rexea*, and *Ruwettus* is not comparable to that of the trichiurids. Furthermore, he noted that *Epinnula* and *Neopinnula* have a subopercle with a convex posteroventral margin.

The presence of a postorbital ossification appears as a homoplastic character (character 9, Appendix). Although the condition of the postorbital ossification in *Lepturacanthus* and *Trichiurus* (i.e., large, thick, and triangular) is treated as being homologous to that of the other trichiurids possessing a postorbital ossification (i.e., poorly ossified, thin, and irregular in shape), it is possible that the two are not homologous and that the ossification of *Lepturacanthus* and *Trichiurus* represents a unique, derived condition.

Complete loss of the pelvic girdle appears to have occurred only once within the trichiurids. Although absence of the basipterygium (character 39, Appen-



dix) is included in the analysis, five other synapomorphies support the single loss of all pelvic elements at the node uniting *Lepturacanthus* and *Trichiurus* (Fig. 4).

*Eupleurogrammus* appears as the sister group to *Lepturacanthus* and *Trichiurus*, and the monophyly of these three genera is supported by nine synapomorphies including five homoplasies (Fig. 4). Gill (1863) included *Eupleurogrammus* and *Trichiurus* in the subfamily Lepturinae. His genus *Trichiurus* included *T. savala* Cuvier 1829 (= *Lepturacanthus savala*). Goode and Bean (1895) had already noted the similarity of *Eupleurogrammus* to *Trichiurus* by calling it "a Chinese form" of the latter genus and including both in their own family Trichiuridae. Tucker (1956) excluded *Eupleurogrammus* from the subfamily Lepturinae of Gill (1863). He considered that the presence of a median lateral line, ethmofrontal elevation, pelvic fins, a rounded opercle, and a uniserial row of palatine teeth represents evidence of the close relationship of *Eupleurogrammus* to the lepidopodines and thus its exclusion from the Trichiurinae. My observations differ from those of Tucker (1956) because I found that *Eupleurogrammus* shares with *Lepturacanthus* and *Trichiurus* the presence of a villiform band of teeth covering most of the length of the palatine. Furthermore, the degree of elevation of the frontal ridges on the ethmoidal region appears to be a continuous character among the trichiurid genera *Assurger*, *Evoxymetopon*, *Tentoriceps*, and some species of *Lepidopus*. Although *Eupleurogrammus* is characterized by a frontal bone that is elevated in the ethmoidal region, the condition is different from that present in *Assurger*, *Evoxymetopon*, *Tentoriceps*, and some species of *Lepidopus* (character 23, Appendix). Thus, the original composition of the subfamily Trichiurinae (=Lepturinae of Gill, 1863), including *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, is supported as a monophyletic group.

Loss of the caudal fin appears to have occurred once within the trichiurids. Monophyly of the four genera that lack a caudal fin (*Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*) is supported by 13 synapomorphies (excluding loss of the caudal fin elements and lack of flexion in the ultimate centrum, characters 56 and 57, respectively, Appendix), of which only two are homoplasies (Fig. 4). However, some authors have questioned the validity of using the presence and absence of a caudal skeleton as a phylogenetically informative character among the trichiurids. Starks (1911) questioned the use of the presence of a caudal fin as a character to define the family Lepidopidae of Goode and Bean (1895), which included *Aphanopus*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*. Tucker (1956) placed *Tentoriceps* and *Eupleurogrammus* into two different groups separate from *Lepturacanthus* and *Trichiurus*, which also lack a caudal fin. Further support for the monophyly of

the four ecaudate genera comes from the apparent gradual reduction of the caudal skeleton in *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, in that phyletic order. *Tentoriceps* bears some reduced internal elements on the ventral and dorsal margins of the unflexed ultimate centrum. *Eupleurogrammus* bears a well-developed distally expanded haemal spine on the ultimate centrum, whereas *Lepturacanthus* and *Trichiurus* have a thin, pointed haemal spine. Ontogenetic data (Gago, 1997) show that larvae of *Trichiurus* and *Lepturacanthus* bear one or two small cartilaginous plates ventrally at the ultimate centrum. They also have a few short ray-like elements that barely penetrate the skin. This larval condition resembles the reduced caudal skeleton of adult *Tentoriceps*.

*Aphanopus* appears as the sister group to the rest of the trichiurids (Fig. 4). Parin and Becker (1972) considered *Aphanopus* as the earliest diverging branch within the trichiurids. Tucker (1956) included *Aphanopus*, *Benthodesmus*, and *Diplospinus* within the subfamily Aphanopodinae. Tucker (1956; fig. 23) placed *Aphanopus* as an earlier offshoot of the branch leading to *Benthodesmus*, and *Diplospinus* as a branch that diverges before an apparent trichotomy at the base of his three trichiurid subfamilies.

The subfamilies Aphanopodinae and Lepidopodinae of Tucker (1956) appear as paraphyletic groups in the most parsimonious trees obtained in this study. Tucker's (1956) subfamily Aphanopodinae included *Aphanopus* and *Benthodesmus*, and his subfamily Lepidopodinae included *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps*. In the most parsimonious trees obtained in this study, *Aphanopus*, *Benthodesmus*, *Lepidopus caudatus*-*L. fitchi*, *L. altifrons*-*Evoxymetopon*, *Assurger*, and *Tentoriceps* appear sequentially and in that phyletic order as sister groups to the monophyletic Trichiurinae of Swainson (1839), which includes *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* (Fig. 4).

No autapomorphies were found that define the genus *Lepidopus* based on the three species available for this study. Some of the data indicate *Lepidopus* to be paraphyletic. All of the three most parsimonious trees obtained separate *L. caudatus* and *L. fitchi* from *L. altifrons*. In these three trees *L. altifrons* appears forming a monophyletic group with *Evoxymetopon* or a trichotomy with *Evoxymetopon* and a clade that includes *Assurger*, *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*.

Three homoplastic characters support node V and the separation of *Lepidopus altifrons* and *Evoxymetopon* from *L. caudatus* and *L. fitchi* (Fig. 4). These three characters are all related to the elevation of the ethmofrontal region (characters 21, 23, and 26; Appendix). No evidence is presented here for the independence of these characters, and it is possible that these three characters are not in-

dependent of each other. Furthermore, as indicated earlier, the degree of elevation of the ethmofrontal region and the convexity of the interorbital space appears to be gradual between *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Tentoriceps*, and *Lepidopus*.

Monophyly of the clade *Evoxymetopon-Lepidopus altifrons* is supported in two of the three most parsimonious trees (Fig. 5). However, support for this clade is weak. Only a single character reversal (character 36) supports the monophyly of these two genera. If character 36 is assumed to have evolved independently within the *L. caudatus-L. fitchi* clade (node IVa) and above node V (Fig. 5A), then no support is offered for the monophyly of *Evoxymetopon* and *L. altifrons*.

The first published description of a specimen of *Lepidopus altifrons* is that of Tucker (1957) who identified it as *Evoxymetopon taeniatus*. Parin and Collette (1993; Collette, personal communication) also found that most of the specimens in the USNM and MCZ collections previously identified as *E. taeniatus* were actually specimens of their new species *L. altifrons*.

Parin and Collette (1993) noted that the placement of *Lepidopus altifrons* within the genus *Lepidopus* is arbitrary because it does not fit the diagnostic characters presented by Tucker (1956). Parin (personal communication) has indicated that the species within the genus *Lepidopus* could possibly be separated into different genera. The similarities between *L. altifrons* and *Evoxymetopon* spp. might prove to be evidence in support of such a hypothesis. However, in this study no attempt is made at revising the classification of the genus *Lepidopus*. A revision of the genus *Lepidopus* should await the availability of more specimens of all the *Lepidopus* species for inclusion in an analysis of relationships.

In two of the three most parsimonious trees obtained in this study, *Lepidopus caudatus* and *L. fitchi* appear as a monophyletic group. Support for the monophyly of *L. caudatus-L. fitchi* is based only on the independent acquisition of the derived condition of character 36 (Fig. 5A).

Rosenblatt and Wilson (1987) described the eastern Pacific material previously referred to as *Lepidopus xantusi* as the new species *L. fitchi*. They considered *L. fitchi* not to be conspecific with the original holotype of *L. xantusi* from Cabo San Lucas. They determined that *L. xantusi* represents a synonym of the western Pacific-eastern Atlantic species *L. caudatus*. Such a conclusion places the holotype of *L. xantusi* as the only specimen of *L. caudatus* from the eastern Pacific. Furthermore, their meristic analyses of the number of vertebrae and anal and dorsal-fin rays for the species of *Lepidopus* shows that *L. fitchi* and *L. caudatus* have the lowest and highest ranges for these counts, respectively. The ranges and 95% confidence limits of the means of the meristic counts do not overlap. Even though four other species of *Lepidopus* oc-

cupy an intermediate position between *L. fitchi* and *L. caudatus*, there is no indication of a geographic morphocline. The otoliths of these two species offer more evidence of their morphological differentiation. In addition to the presence of a postcaudal trough, the sagittae of *L. fitchi* have longer, better-defined rostra and antirostra and an overall shape that is different from that of *L. caudatus*. However, this potential character was not included in the analysis because the definition of objective characters states with regard to the degree of extension of the rostrum and antirostrum is difficult.

Parin and Collette (1993) noted that the presence of a convex interorbital space and a sagittal crest that extends onto the ethmoidal region are characters that seem to change in a gradual manner in the series *Lepidopus manis* and *L. fitchi*, *L. caudatus* and *L. calcar*, *L. dubius*, and *L. altifrons*. *Assurger*, *Evoxymetopon*, and *Tentoriceps* could be added to this series as the more derived conditions. In this study, *Tentoriceps* is clearly separated from *Assurger*, *Evoxymetopon*, and *Lepidopus* by 15 synapomorphies that include it in a clade with the other three ecaudate trichiurid genera. *Assurger* is also separated from *Evoxymetopon* and *Lepidopus* and appears as the sister group to the ecaudate trichiurids (Fig. 4, node VI). However, node VI is only supported by a single synapomorphy: the anterior neural spines are distally expanded and forked.

Ontogenetic data (Gago, 1997) have provided evidence that supports several of the arguments of character evolution proposed in this study (Fig. 29). Monophyly of the trichiurids is strongly supported by both the adult and larval data. Furthermore, both data sets also support the monophyly and the same phyletic sequence of the four ecaudate trichiurid genera (*Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*). The adult data place *Aphanopus*, *Benthodesmus*, the *Lepidopus fitchi-L. caudatus* clade, the *Lepidopus altifrons-Evoxymetopon* clade, and *Assurger* as the sister groups, in that phyletic sequence, to the ecaudate trichiurids. The larval data (Gago, 1997) also support the position of *Aphanopus* as the most basal trichiurid, but the ontogenetic and adult characters are incompatible with respect to the phyletic placement of *Assurger*, *Benthodesmus*, and *Lepidopus*.

Johnson (1993) noted that specialized larval characters and the patterns of chondrification and ossification in ontogenetic series can be helpful in phylogenetic studies by providing evidence for monophyly and intrarelationships in studies at the family level and below, and by testing hypotheses of homology in adult characters.

In the larval data (Fig. 29), *Assurger* appears as the sister group to the clade that includes *Benthodesmus* and *Lepidopus*. In contrast, in the adult phylogeny (Fig. 4), *Assurger* appears as the sister group of the ecaudate trichiurids, and *Benthodesmus* appears as the sister group to all the trichiurids, except *Aphanopus*. Placement of *Benthodes-*



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## APPENDIX

### List of Characters

Characters are grouped together according to structural units or types (e.g., neurocranium). The numbers refer to the character number as shown in Table 1. Character states are within parentheses.

#### OPERCULAR SERIES

1. Posterior and ventral margins of opercle, subopercle, and interopercle. Complete; only the dorsal flap of the opercle and the posterior corner of the subopercle may be slightly splintered (0). Strongly splintered or fimbriate (1).
2. Lateral process on articular head of the opercle. Plate-like and covering most of the articular fossa of the bone (0). Elongate and flat in cross section (1). Elongate and round in cross section (2).
3. Fimbriations on posteroventral corner of the subopercle. Not much longer than the preceding ventral ones, giving a convex appearance to the ventral margin of the bone (0). Much more elongate than the preceding ventral ones, giving a slightly concave appearance to the ventral margin of the bone (1).
4. Articular process of subopercle. Extends dorsally at a right angle, articulating mainly with the anteroventral corner of the opercle (0). Extends anteriorly and articulates mainly with the posterodorsal corner of the interopercle (1).
5. Posterodorsal margin of preopercle. Convex (0). Concave (1).

#### CIRCUMORBITAL SERIES

6. Circumorbital series. Complete (0). Incomplete with a short gap between the first infraorbital elements and

the postorbitals (1). Extremely reduced; only the lachrymal and jugal are present (2).

7. Shape of ventral wing of lachrymal. Ovoid; fimbriations in the anterior and posterior margins of the ventral wing are not perpendicular to the dorsal, longitudinal, lateral-line canal (0). Quadrilateral; fimbriations in the anterior and posterior margins of the ventral wing are nearly perpendicular to the dorsal, longitudinal, lateral-line canal (1).
8. Posterodorsal plate of lachrymal. Short; ends before or above the posterior pore of the longitudinal, dorsal lateral-line canal (0). Elongate; extends past the posterior pore of the longitudinal, dorsal lateral-line canal ending above the jugal (1).
9. Postorbital ossification. Absent (0). Reduced and thin (1). Large and thick (2).

#### JAWS

10. Dentary and premaxillary fangs and serial teeth. Smooth (0). Serrate (1).

#### SUSPENSORIUM

11. Posterodorsal process of quadrate. Long; extends well past the ventral margin of the metapterygoid (0). Short; does not extend well past the ventral margin of the metapterygoid (1).
12. Posteromedial arm of ectopterygoid. Does not reach the metapterygoid (0). Reaches the metapterygoid (1).
13. Well-developed condyle posterior to anteromedial



shelf of palatine. Absent (0). Present and visible in lateral view (1).

14. Teeth on ventral margin of palatine. Large and few; a single row covering only a very small portion of the ventral margin of the bone (0). Small and numerous; in several rows covering most of the ventral margin of the bone (1).

## HYOID COMPLEX

15. Anterodorsal corner of ceratohyal. Not pointed; does not extend anteriorly (0). Pointed; extends anteriorly abutting the dorsal margin of the dorsal hypohyal (1).
16. Shape of posteroventral processes of glossohyal in ventral view. Neither triangular nor quadrilateral; do not have their lateral corners pointing posteriorly (0). Wing-like, with corners pointed posteriorly (1). Quadrilateral (2). Triangular (3).

## BRANCHIAL COMPLEX

17. Shape of articular head of first basibranchial. Tapers to a point; not knob-like (0). Knob-like, but not bearing dorsolateral processes (1). Knob-like and bearing dorsolateral processes (2).
18. Laterally pointed processes on second basibranchial. Absent (0). Present (1).
19. Shape of fourth ceratobranchial. Straight (0). Sigmoidal (1).

## NEUROCRANIUM

### Ethmoidal Region

20. Anterior tip of nasal. Straight (0). Curved; giving the bone a concave lateral margin in dorsal view (1).
21. Dorsal ridges on ethmoid. Absent or reduced; do not extend well above the nasals in lateral view (0). Present; extend well above the nasals in lateral view (1).
22. Connection of supraorbital and infraorbital lateral-line canals. Supraorbital lateral-line canal connects with the infraorbital canal through a dorsally or laterally directed pore (0). Lateral bony tubular extension of supraorbital lateral-line canal to orbital rim (1).
23. Elevation of frontal ridges on ethmoidal region. Not elevated (0). Elevated; laterally convex (1). Extremely elevated; appear as laterally flat sheets (2).

### Orbital Region

24. Sclerotics. Present (0). Absent (1).

### Otic Region

25. Supraoccipital crest. Reduced; runs close to and parallel to the epiotic ridges; dorsal profile of the neurocranium is flat in lateral view (0). Dorsally expanded; runs higher and not parallel to the epiotic ridges; dorsal profile of the neurocranium is not flat in lateral view (1).
26. Highest point of supraoccipital crest. Posterior to the orbits (0). Above the orbits (1).
27. Pterotic. Ends before the posterior margin of the neurocranium (0). Ends well past the posterior margin of the neurocranium (1).
28. Intercalar. Visible dorsally (0). Not visible dorsally (1).
29. Exoccipital ridge. Reaches the vagus foramen (0). Does not reach the vagus foramen (1).

## PECTORAL GIRDLE

30. Length of dorsal articular process of posttemporal. Short; ends before or slightly past the anterior margin of the supratemporal (0). More than twice the length of the supratemporal (1).
31. Posteroventral process of posttemporal. Absent (0). Reduced, flat in cross section; comes in contact or close association with the articular head of the supracleithrum (1). Long, round in cross section; does not come in contact or close association with the articular head of the supracleithrum (2).
32. Anteroventral process of posttemporal. Originates on the posterior corner of the bone (0). Shares a common origin with the posteroventral process; close to or on the anterior half of the canal-bearing portion of the bone (1). Separate from the posteroventral process; originates close to or on the anterior half of the canal-bearing portion of the bone (2).
33. Posterodorsal corner of posttemporal. Not expanded (0). Expanded (1).
34. Articular head of the supracleithrum. Posteriorly expanded; bears a completely enclosed canal that transmits the lateral line to the posttemporal (0). Posteriorly expanded; bears an open canal or shelf connecting the lateral line to the posttemporal (1). Not expanded; lacks a canal (2).
35. Lateral process on articular head of supracleithrum. Absent (0). Present (1).
36. Anteroventral process on articular head of supracleithrum. Absent (0). Present (1).
37. Posteroventral plate on coracoid. Absent; ventral margin of coracoid is flat; its posterior corner ending before the fourth radial (0). Present; ventral margin is round; its posterior corner ending past the fourth radial (1).
38. Length of pectoral-fin rays. Posterior fin rays are longer (0). Anterior fin rays are longer (1).

## PELVIC GIRDLE

39. Basipterygium. Present (0). Absent (1).
40. External spinous elements of pelvic fin. Spine-like (0). Scale-like (1).
41. Position of basipterygium. Thoracic; articular facet is anterior to distal tip of ventral postcleithrum (0). Abdominal; articular facet is posterior to distal tip of ventral postcleithrum (1).
42. Central part of basipterygium. Dorsally inclined (0). Nearly parallel to the ventral body wall (1).
43. Central part of basipterygium. Bilaterally divided (0). Longitudinally fused (1).

## AXIAL SKELETON

### Vertebral Column

44. Total number of vertebrae. 30–55 (0). 57–67 (1). 84–198 (2).
  45. First neural spine. Not distally bifurcate (0). Distally bifurcate (1).
  46. Anterior neural spines. Not expanded or forked distally (0). Expanded and forked distally (1).
- Intermusculars
47. Series of unattached epineurals and epicentrals extending into caudal region. Both present (0). Only the epineural series present (1). Both absent (2).



## Dorsal and Anal Fins

48. Notch in the fin membrane separating the spinous and soft portions of the dorsal fin. Present (0). Absent (1).
49. Spinous portion of the dorsal fin. XIX–XXXIX spines; its base is longer than that of the soft portion (0). XXXVIII–XLV spines; its length is only slightly shorter than length of soft portion (1). XXXI–XLVI spines; its base is less than half of the length of the soft portion but not extremely short (2). Only III–X spines; its base is extremely short compared to the base of the soft portion (3).
50. Number of radials in soft dorsal-fin pterygiophores. 2; proximal-middle and distal (0). 3; proximal, middle, and distal (1).
51. Proximal-middle radial of first dorsal pterygiophore. Does not extend above occiput (0). Extends above occiput (1).
52. Foramen at anteroventral corner between the proximal and distal portions of the dorsal-fin proximal radials. Absent (0). Present (1).
53. Number of supernumerary elements on first anal-fin pterygiophore. Two (0). One (1).
54. Anal-fin soft rays. Well-developed soft rays throughout the whole length of the anal fin (0). Well-developed soft rays only in the posterior portion of the anal fin (1). Modified as small spinule-like elements (2). Reduced to small scale-like ossifications that do not penetrate the epithelium (3). Modified into small fused knobs that barely penetrate the epithelium (4).
55. Anal-fin pterygiophores. Two (proximal-middle and

distal) or three (proximal, middle, and distal) radials present (0). The proximal, middle, and distal radials are fused with each other and appear as a single unit (1).

## CAUDAL COMPLEX

56. Caudal complex. Well developed (0). Reduced to a few small internal elements (1). Absent (2).
57. Ultimate centrum. Flexed and forming a urostyle (0). Not flexed (1).
58. Number of epurals. Three (0). Two (1). One (2).
59. Haemal and neural spines of preural centrum 4. Long; extends past or as far as the posterior margin of the preural centrum 3 (0). Short; does not extend well past the anterior margin of the preural centrum 3 (1).
60. Hypural plates formula. I + II + III + IV + V (0). I–II + III–IV + V (1). I–II + III–IV–V (2).
61. Hypural notch. Large (0). Small (1).
62. CMC cartilage. Absent (0). Present (1).
63. CPNPU3 cartilage. Present (0). Absent (1).

## OTOLITHS

64. Excisura. Delimited by a well-developed rostrum and antirostrum (0). Delimited by a reduced rostrum and antirostrum (1).
65. Cristae superior and inferior. Reduced (0). Well developed and overhanging (1).
66. Longitudinal ridge on the ostium. Absent (0). Present (1).







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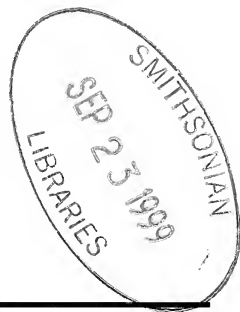
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# CONTRIBUTIONS IN SCIENCE

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NEW FANWORM SPECIES (POLYCHAETA: SABELLIDAE:  
FABRICIINAE) FROM PHUKET, THAILAND, WITH  
COMMENTS ON *FABRICIOLA FLAMMULA* ROUSE  
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KIRK FITZHUGH

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# NEW FANWORM SPECIES (POLYCHAETA: SABELLIDAE: FABRICIINAE) FROM PHUKET, THAILAND, WITH COMMENTS ON *FABRICIOLA FLAMMULA* ROUSE AND *FABRICIOLA CRI* ROUSE

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KIRK FITZHUGH<sup>1</sup>

**ABSTRACT.** Two new fanworm species in the genera *Fabriciola* Friedrich and *Pseudoaugeneriella* Fitzhugh are described from Panwa Bay, Phuket, Thailand. *Fabriciola phuketensis* n. sp. is similar to *Fabriciola* sp. cf. *F. berkeleyi* Banse, *F. mediaseta* Fitzhugh, *F. rubra* Fitzhugh, *F. flammula* Rouse, and *F. cri* Rouse in having a low anterior peristomial ring collar, red peristomial and pygidial eyes, and abdominal neuropodial pinhead setae. The new species is distinguished from *F. mediaseta* and *F. rubra* by the absence of thoracic broadly hooded flagellate setae and differs from *Fabriciola* sp. cf. *F. berkeleyi*, *F. flammula*, and *F. cri* in that it lacks crown and trunk pigmentation; it differs in collar construction as well. *Fabriciola flammula* and *F. cri* were originally described as having broadly hooded flagellate setae. Examination of paratype material reveals that all inferior thoracic notosetae are narrowly hooded; descriptions of the species are appropriately emended. The total number of described *Fabriciola* species is increased to 16. *Pseudoaugeneriella brevirama* n. sp. is the second species described in the genus and differs from *P. unirama* Fitzhugh in having vascularized ventral filamentous appendages that are no more than half the length of the branchial crown. Appendages in *P. unirama* are almost the same length as the crown. The monophyly of *Pseudoaugeneriella* is discussed, and cladistic relationships among *Fabriciola* species are presented.

## INTRODUCTION

The present account describes a new species of *Fabriciola* Friedrich, 1939, and a new species of *Pseudoaugeneriella* Fitzhugh, 1998, from the intertidal zone at Phuket Island, Thailand. Recognition of the diversity of *Fabriciola* has especially increased during the past several years. Including the species described here, there have been seven *Fabriciola* species described since 1990 (Fitzhugh, 1990a, 1992a, 1998; Rouse, 1993, 1996), giving a total of 16 species. In the process of comparing the *Fabriciola* described here to similar species, I found that the descriptions of *F. flammula* Rouse, 1993, and *F. cri* Rouse, 1996, must be emended with respect to the type of thoracic notosetae in each.

*Pseudoaugeneriella* was originally described from a single species, *P. unirama* Fitzhugh, 1998, from Okinawa Island, Japan. Fitzhugh (1998) noted that the genus resembles *Augeneriella* Banse, 1957, in that both have an anterior peristomial ring collar only developed ventrally as a wide lobe, well-developed triangular dorsal lips, and vascularized ventral filamentous appendages. The difference between the two genera is that the filamentous appendages in *Pseudoaugeneriella* are unbranched, whereas fully formed filaments in *Augeneriella* are

branched to some extent. Fitzhugh (1998; see also Fitzhugh, 1990b) pointed out, however, that filaments in *Augeneriella* are initially unbranched, with branching developing as animals grow. Based on a cladistic analysis of Fabriciinae taxa, Fitzhugh (1998) found the presence of unbranched vascularized filaments to be plesiomorphic for the subfamily, such that it is not possible to include *P. unirama* in *Augeneriella*. Justification for the placement of a second species in *Pseudoaugeneriella* as well as monophyly of the genus are provided by an update of the cladistic analysis of fabriciina genera and species performed by Fitzhugh (1998).

## SYSTEMATICS

Family Sabellidae Latrielle, 1825

Subfamily Fabriciinae, Rioja, 1923

*Fabriciola* Friedrich, 1939

*Fabriciola phuketensis* n. sp.

Figures 1–2

**MATERIAL EXAMINED.** Indian Ocean, Andaman Sea, Thailand, Phuket Island. Holotype: LACM-AHF 1896, Panwa Bay, just north (about 100 m) of Phuket Marine Biological Center pier, scraping of low mat of detritus and algae from shale rock, midintertidal zone, collection made at low tide, depth 0 m, 18 August 1997, coll. K. Fitzhugh. Paratypes: LACM-AHF 1897, 11 specimens (10 complete, 1 missing crown), same locality as holotype. Paratypes: LACM-AHF 1898, 11 specimens (2 complete,

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9 lacking crown), same locality as holotype, scrapings off dead, branching, *Acropora*-like coral, midintertidal zone, collection made at low tide, depth 0 m, 18 August 1997, coll. K. Fitzhugh.

**ETYMOLOGY.** The specific epithet refers to the occurrence of the species at Phuket Island.

**DESCRIPTION.** Holotype a complete male with 8 thoracic and 3 abdominal setigers; branchial crown length, 0.45 mm; remainder of body, 1.70 mm long; maximum width, 0.12 mm (Fig. 1A). Body slender, nearly uniform in width except for slight tapering posteriorly. Branchial crown with 3 pairs of radioles, distal ends filamentous, same width as pinnules. Branchial or "radiolar" skeleton (*sensu* Rouse 1993) not observed. Radioles each with 3 pairs of pinnules, all terminating at about same height as ends of radioles. Dorsal lips erect, triangular, rounded distally, and distinct from dorsal-most radioles; low, distally rounded, ventral liplike process present at base of proximal-most pinnule of ventral-most radioles (Fig. 1B). Nonvascularized ventral filamentous appendages present, slightly shorter than total length of radioles, surfaces smooth, about same width as pinnules (Figs. 1B, 2B–C). Dorsal margins of branchial lobes not fused to one another. Branchial hearts present. Anterior margin of anterior peristomial ring as low membranous collar (Fig. 2), with distal margin smooth all around; middorsum completely separated by narrow gap; collar height uniform. Collar of even thickness throughout, about same length as posterior peristomial ring. Annulation between collar and posterior peristomial ring only present ventrally. Anterior peristomial ring, including collar, about same length as posterior ring. Middorsal medial lobe just dorsal to mouth almost same height as collar. Pair of round, red eyes in posterior peristomial ring. Setiger 1 about same length as posterior peristomial ring, distinctly wider than long; setigers 2–6 each successively longer, with setigers 4–8 longer than they are wide. Setiger 9 about same length as 1, with setigers 10–11 each slightly shorter than setiger 9. Pygidium about same length as setiger 11, posterior margin slightly tapered, rounded. Some paratype specimens exhibit greater longitudinal contraction, with most thoracic setigers about as long as they are wide. Pair of round, bright red pygidial eyes. Superior thoracic notosetae elongate, narrowly hooded, 3–4 per fascicle. Inferior thoracic notosetae in setigers 2–8 also narrowly hooded but shorter, 1 per fascicle. Abdominal neuropodia of setigers 9–11 with very elongate, narrowly hooded setae, 1–2 per fascicle, and 2 pin-head setae per fascicle. Thoracic uncini acicular, main fang slender; teeth above main fang slender and slightly decreased in size away from fang; hood not observed; 4–5 uncini per fascicle in single rows (6–7 in some paratypes). Abdominal uncini with 5–6 rows of teeth in profile, 3–5 teeth per row; manubrium over 2 times longer than dentate region, slightly expanded proximally (Fig.

1C); uncini in setigers 9–11 number 13, 12, and 10, respectively. Anus midventral, along anterior margin of pygidium. Males with spermiogenesis occurring in setigers 4–8, oocytes in females in setiger 4. Preserved specimens white, no pigmentation on crown or body wall. Tubes composed of fine, flocculent detrital material, total tube width about 2 times greater than body width. Brooding of young not observed.

**REMARKS.** This species falls within the *Fabriciola* species complex defined by the presence of abdominal neuropodial pin-head setae (*sensu* Ben-Eliahu, 1975), which includes *F. mediaseta* Fitzhugh, 1990 (Aldabra Atoll, western Indian Ocean), *Fabriciola* sp. cf. *F. berkeleyi* Banse, 1956 (*sensu* Fitzhugh, 1992a; California), *F. flammula* Rouse, 1993 (Belize), *F. cri* Rouse, 1996 (Papua New Guinea), and *F. rubra* Fitzhugh, 1998 (Okinawa Island). *Fabriciola mediaseta* and *F. rubra* have broadly hooded, flagellate setae in thoracic notopodia, whereas inferior notosetae in *F. phuketensis*, *Fabriciola* sp. cf. *F. berkeleyi*, *F. flammula*, and *F. cri* have elongate narrowly hooded setae. The body of *F. phuketensis* lacks pigmentation, whereas *Fabriciola* sp. cf. *F. berkeleyi* and *F. cri* have peristomial and branchial crown pigmentation, respectively. The posterior margin of the middorsal collar gap in *F. flammula* (Rouse, 1993: figs. 1–2) and *F. cri* (Rouse, 1996: figs. 1–2) is noticeably expanded, whereas the gap in *F. phuketensis* is uniformly narrow (Fig. 2A).

Rouse (1993, 1996) allied *F. flammula* and *F. cri* with *F. mediaseta* on the basis of the fact that the 3 species have inferior, notopodial, broadly hooded, flagellate setae (*sensu* Fitzhugh, 1990a: fig. 6C; see also Fitzhugh, 1998: fig. 1B) in some thoracic setigers. Rouse (1993: fig. 3; 1996: fig. 3) described these species as having these setae in setigers 2–8 and 2–6, respectively. After examining paratypes of *F. flammula* and *F. cri*, I find that these species do not have broadly hooded, flagellate setae. I completely concur with Rouse (1996) that in *F. cri*, there are qualitative differences in hood shape in some setigers, and, as much as possible, these differences should be reported. Comparatively, however, I regard the setae in *F. cri* to come closest to the condition of elongate narrowly hooded as opposed to flagellate. In the latter condition, there is a marked disjunction between the hood and distal continuation of the shaft. The setae in *F. flammula*, *F. cri*, and *F. phuketensis* show a smooth transition between hood and distal shaft. Emendations to *F. flammula* and *F. cri* are provided in order to reflect these changes.

#### *Fabriciola flammula* Rouse, 1993, Emended

*Fabriciola flammula* Rouse, 1993: 250–253, figs. 1–10, 48.

**MATERIAL EXAMINED.** Caribbean Sea, Belize, Carrie Bow Cay. Paratypes: LACM-AHF 1630, 3 specimens,



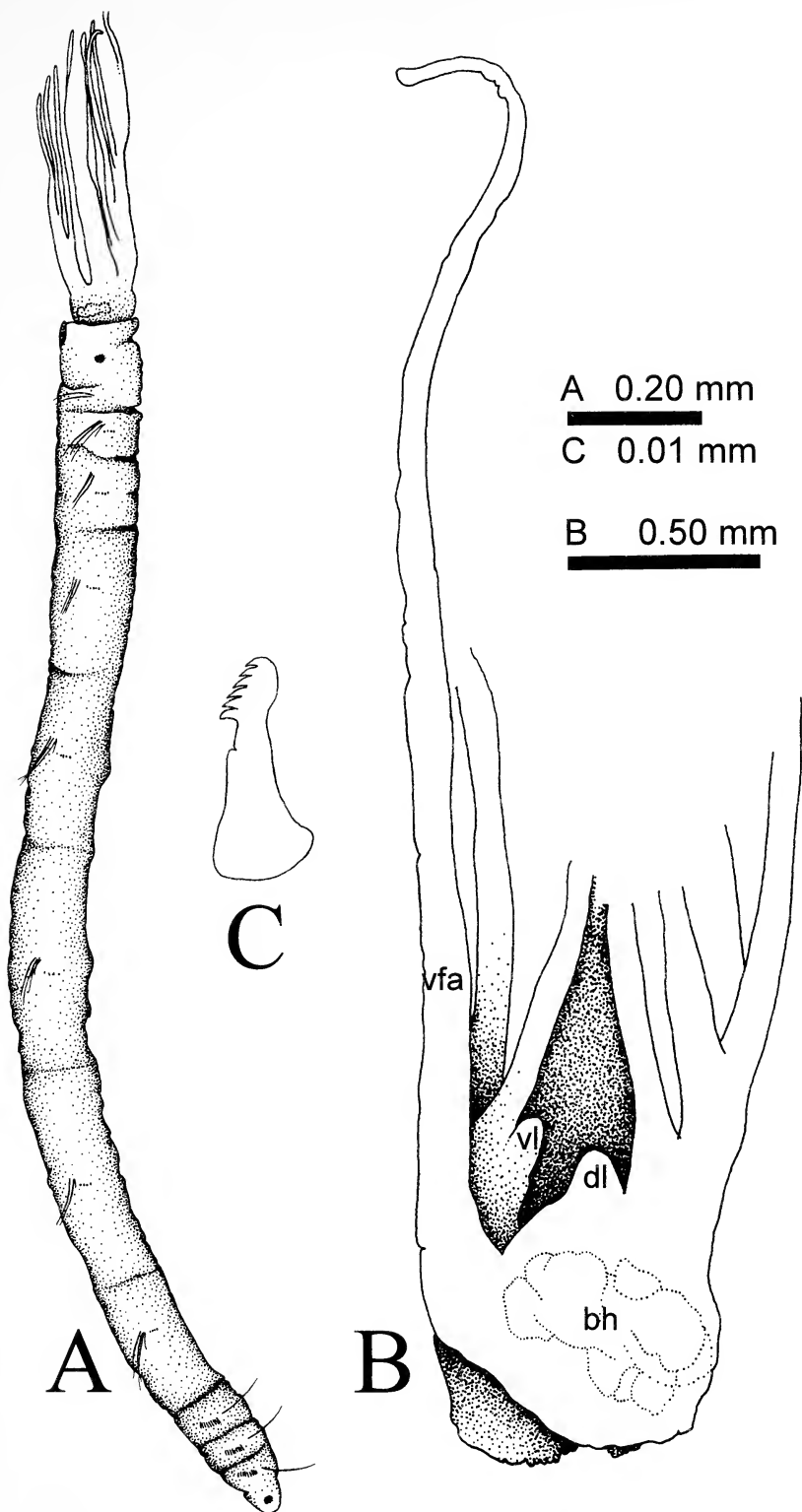


Figure 1. *Fabriciola phuketensis* n. sp. A, entire animal, lateral view (holotype, LACM-AHF 1896); B, right half of branchial crown, inner view (paratype, LACM-AHF 1897); C, abdominal uncinus from setiger 9 (paratype, LACM-AHF 1897). Abbreviations: bh, branchial heart; dl, dorsal lip; vfa, ventral filamentous appendage; vl, ventral liplike process.

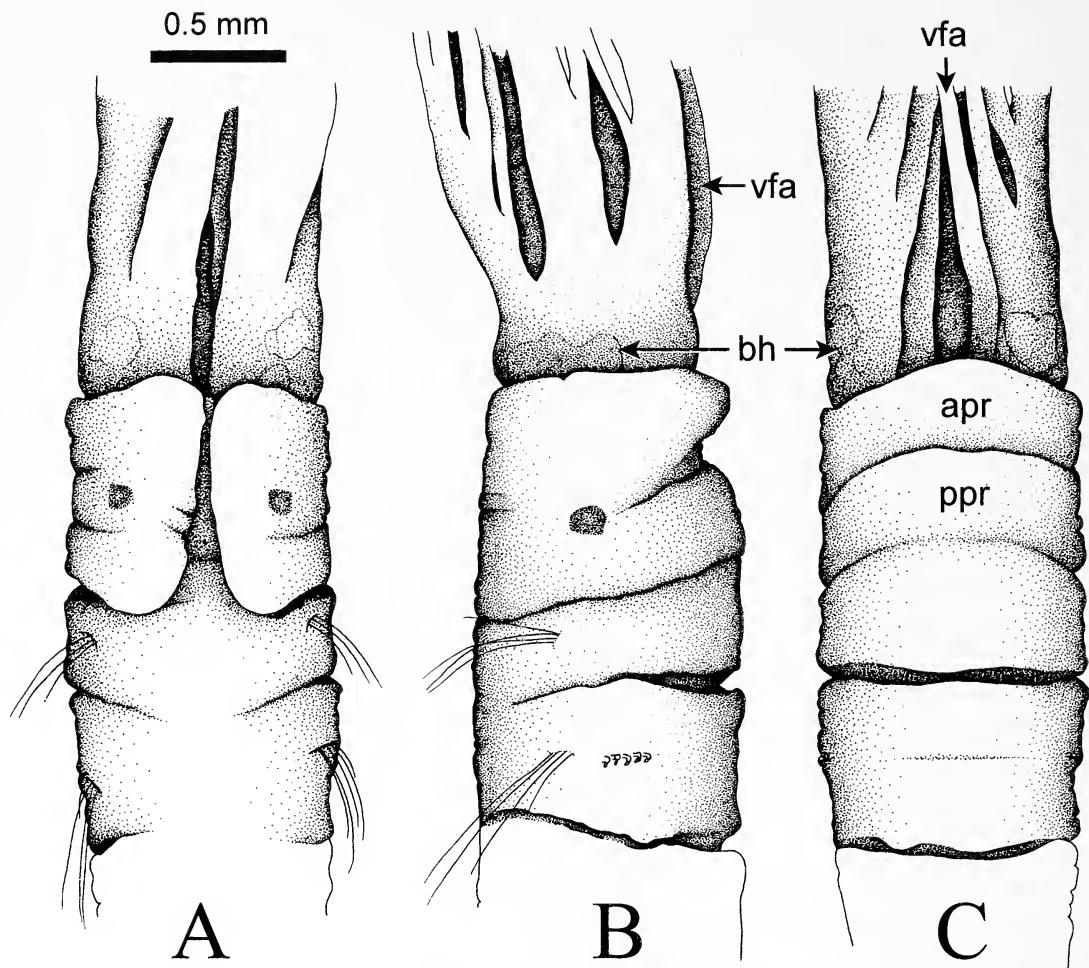


Figure 2. *Fabriciola phuketensis* n. sp. A–C, dorsal, lateral (right side), and ventral views of anterior end, respectively (holotype, LACM-AHF 1896). Abbreviations: apr, anterior peristomial ring; bh, branchial heart; ppr, posterior peristomial ring; vfa, ventral filamentous appendage.

south side of leeward jetty, algal turf on boulders and *Strombus* shells, sta. F400, 22 May 1991, coll. G. Rouse.

**REMARKS.** Rouse (1993: 252) described inferior thoracic notosetae in setigers 2–8 as broadly hooded, flagellate. All inferior thoracic notosetae are elongate, with narrow hoods, as seen in most other *Fabriciola* species. It should be noted, however, that the hoods of inferior notosetae in setiger 1 of most *Fabriciola* are narrower than those seen in subsequent setigers.

Rouse (1993: 251) stated that ventral lips are absent. At the base of each proximalmost pinnule of the ventral radioles, there is a distinct, distally rounded swelling, similar to that described here in *F. phuketensis* (Fig. 1B) and several other *Fabriciola* (e.g., Fitzhugh, 1990a: fig. 1E for *F. baltica* Friedrich, 1939; Fitzhugh, 1998: fig. 2B for *F. rubra*) as a “ventral lip-like process.”

#### *Fabriciola cri* Rouse, 1996, Emended

*Fabriciola cri* Rouse, 1996: 1765–1768, figs. 1–12, 39, 42–43.

**MATERIAL EXAMINED.** Pacific Ocean, Papua New Guinea, Madang Province. Paratypes: LACM-AHF 1798, 10 specimens, from log lying in mangroves opposite Riwo village, sta. F645, 23 August 1993, coll. G. Rouse, K. Fauchald, L.A. Ward, and P. Scott.

**REMARKS.** Rouse (1996: 1767, fig. 3) described inferior thoracic notosetae in setigers 2–6 as broadly hooded, flagellate. I consider these setae to be elongate, narrowly hooded, as seen in most other *Fabriciola* species. As I noted in the remarks on *F. phuketensis*, however, I agree with Rouse’s assessment that the hoods of inferior setae in setigers 2–6 are somewhat broader than those seen in setigers 1 and 7–8.

Rouse (1993: 251) stated that ventral lips are absent. The bases of the proximal-most pinnules of the ventral radioles do show some slight swelling, but this is not pronounced and does not impart the appearance of the "ventral lip-like process" described above in *F. phuketensis* (Fig. 1B) or several other *Fabriciola* species (e.g., Fitzhugh, 1990a: fig. 1E for *F. baltica*; Fitzhugh, 1998: fig. 2B for *F. rubra*).

REVISED KEY TO *FABRICIOLA* SPECIES

The following key is modified from Fitzhugh (1998). As with that key, this one does not include *F. spongicola* (Southern, 1921) or *F. pacifica* (Annenkova, 1934), as material is unavailable and original descriptions are too incomplete. *Fabriciola tonerella* Banse, 1959, is included based on the original description.

- 1a. Two abdominal setigers . . . *F. minuta* Rouse
- b. Three abdominal setigers . . . . . 2
- 2a. Pygidial eyes present . . . . . 3
- b. Pygidial eyes absent . . . . . *F. parvus* Rouse
- 3a. Abdominal neuropodial pin-head setae present, peristomial and pygidial eyes range from red to brown . . . . . 4
- b. Pin-head setae absent, eyes black to light brown . . . . . 9
- 4a. Thoracic notopodia with inferior flagellate setae in setigers 3–7 . . . . . 5
- b. Flagellate setae absent . . . . . 6
- 5a. Peristomial and pygidial eyes bright red . . . . . *F. rubra* Fitzhugh
- b. Peristomial and pygidial eyes faint red . . . . . *F. mediaseta* Fitzhugh
- 6a. Peristomial and pygidial eyes bright red . . . . . 7
- b. Peristomial and pygidial eyes reddish-brown . . . . . *Fabriciola* sp. cf. *F. berkeleyi* Banse
- 7a. Body without pigmentation . . . . . 8
- b. Base of branchial crown with black pigment . . . . . *F. cri* Rouse
- 8a. Posterior margin of middorsal gap in peristomial collar distinctly expanded . . . . . *F. flammula* Rouse
- b. Middorsal collar gap narrow along entire length . . . . . *F. phuketensis* n. sp.
- 9a. Anterior peristomial ring collar relatively even in height all around . . . . . 10
- b. Collar higher ventrally . . . . . 11
- 10a. Middorsal gap in collar very wide . . . . . *F. ghardaqa* Banse
- b. Collar gap narrow . . . . . *F. berkeleyi* Banse
- 11a. Thoracic uncini few in number, 2–3 per fascicle . . . . . 12
- b. Thoracic uncini more numerous, 5–8 per fascicle . . . . . 13
- 12a. Dorsal and lateral margins of anterior peristomial ring collar relatively high . . . . . *F. baltica* Friedrich
- b. Dorsal and lateral margins of collar very low . . . . . *F. liguronis* Rouse
- 13a. Branchial crown comprises 1/5 to 1/8 of total body length . . . *F. brevibranchiata* Fitzhugh
- b. Branchial crown longer . . *F. tonerella* Banse

*Pseudoaugeneriella* Fitzhugh, 1998

*Pseudoaugeneriella brevirama* n. sp.

Figures 3–4

**MATERIAL EXAMINED.** Indian Ocean, Andaman Sea, Thailand, Phuket Island. Holotype: LACM-AHF 1899, detrital scrapings off dead, branching, *Acropora*-like coral, midhintertidal zone, collection made at low tide, depth 0 m, 18 August 1997, coll. K. Fitzhugh. Paratypes: LACM-AHF 1900, 17 specimens (1 complete, 16 missing posterior end), same locality as holotype, scraping of low mat of detritus and algae from shale rock, midintertidal zone, collection made at low tide, depth 0 m, 18 August 1997, coll. K. Fitzhugh.

**ETYMOLOGY.** The specific epithet refers to the short, vascularized, ventral filamentous appendages of the crown.

**DESCRIPTION.** Holotype complete with 8 thoracic and 3 abdominal setigers; branchial crown length, 0.4 mm; remainder of body, 1.3 mm long; maximum width, 0.15 mm. Body slender, slightly tapering anteriorly and posteriorly (Fig. 3A). Branchial crown with 3 pairs of radioles, distal ends filamentous, same width as pinnules. Radioles each with 4–5 pairs of pinnules, terminating at or slightly below distal ends of radioles. Dorsal lips erect but low, broadly rounded distally, distinct from radioles; low, distally rounded, ventral liplike processes present at bases of proximalmost pinnules of ventral radioles (Fig. 3B). Vascularized ventral filamentous appendages present, about one-half the total length of radioles, surfaces slightly to very wrinkled, about one-third wider than pinnules; interior of each filament occupied by large blood vessel (Figs. 3A–B, 4B–C). Dorsal margins of branchial lobes not fused to one another. Branchial hearts present. Anterior margin of anterior peristomial ring is a low ridge dorsally and laterally (Figs. 3A, 4A–B). Collar developed ventrally as low, triangular lobe; wide basally, tapering distally to broadly rounded margin (Fig. 4C). Annulation between anterior and posterior peristomial rings visible ventrally. Middorsal medial lobe just dorsal to mouth low, triangular. Pair of reniform (dorsal view) or rounded (lateral) black eyes in anterior half of posterior peristomial ring. Posterior peristomial ring is four to five times longer than anterior ring. Setiger 1 slightly shorter than posterior peristomial ring, distinctly wider than it is long; remaining setigers slightly longer but all wider than they are long. Setiger 9 slightly shorter than 8; setigers 10–11 each about one-half the length of 9. Pygidium about the same length as setiger 11, posterior margin slightly tapered, rounded. Pair of round, black pygidial eyes. Superior thoracic notosetae elongate, narrowly hooded, 3 per fascicle. Inferior thoracic notosetae in setigers 2 and 7–8 also narrowly hooded but shorter, 1–2 per fascicle; setigers 3–6 each with 2 pseudospatulate setae (Fig. 3C). Abdominal neuropodia of setigers 9–11 with very elongate, narrowly hooded setae, 2–3 per fascicle. Thoracic uncini acicular, main fang slender; single large tooth slightly offset over main fang, followed by a series of smaller teeth;

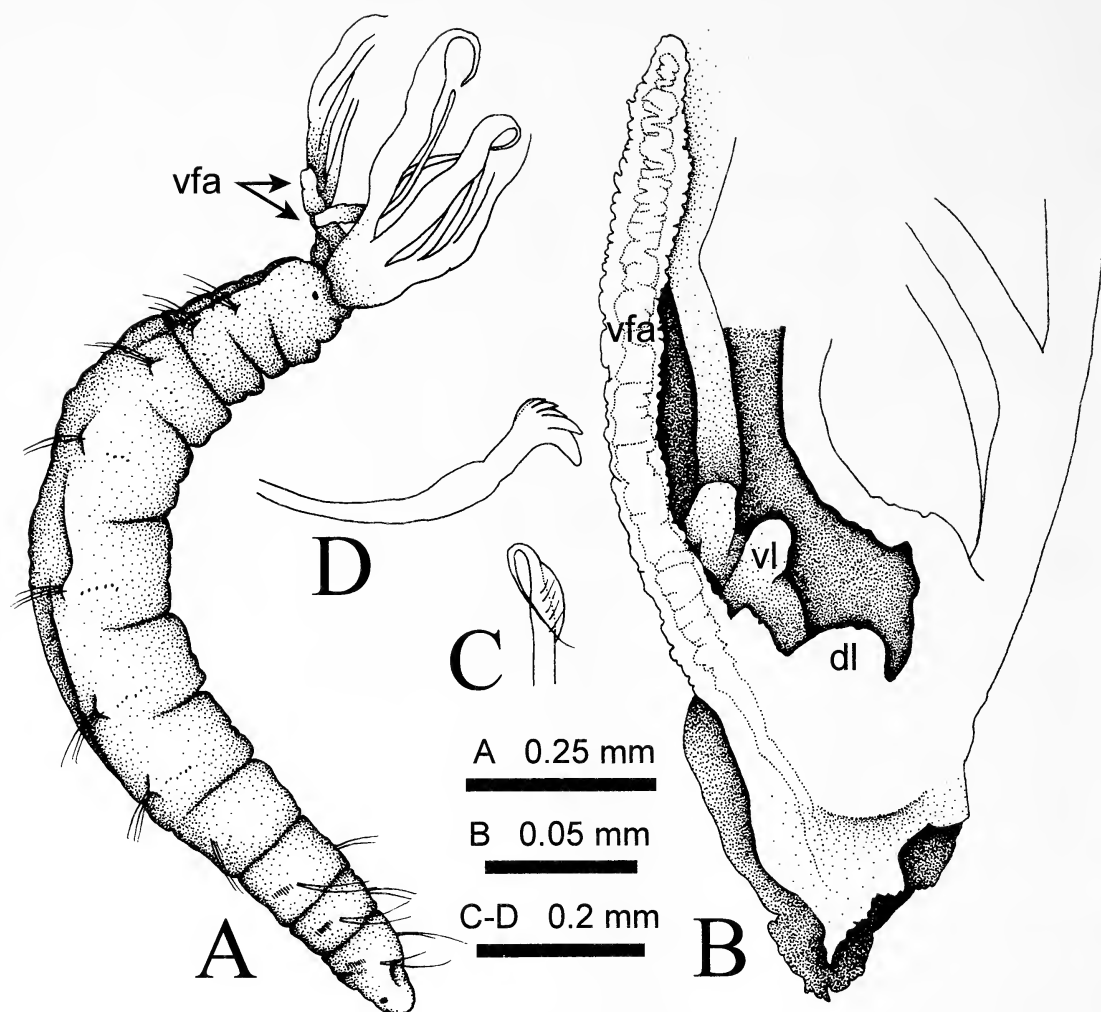


Figure 3. *Pseudoaugeneriella brevirama* n. sp. A, entire animal, lateral view (holotype, LACM-AHF 1899); B, right half of branchial crown, inner view, entire crown length is 0.62 mm, ventral filamentous appendage length is 0.27 mm (paratype, LACM-AHF 1900); C, inferior thoracic notopodial pseudospatulate seta from setiger 3 (paratype, LACM-AHF 1900); D, thoracic uncinus from setiger 3 (paratype, LACM-AHF 1900). Abbreviations: dl, dorsal lip; vfa, ventral filamentous appendage; vl, ventral liplike process.

hood present (Fig. 3D); 4–7 uncini per fascicle in straight or irregular single rows. Abdominal uncini with 7–8 rows of teeth in profile, 3–4 teeth per row; manubrium about 1.5 times longer than dentate region, slightly expanded proximally; uncini in setigers 9–11 number 17, 16, and 11, respectively. Anus midventral, along anterior margin of pygidium. Occurrence of oocytes or sperm could not be determined. Branchial crown unpigmented in all specimens. Dark to light brown pigment present in most specimens (absent in holotype) in dorsum of posterior peristomial ring and present dorsally, laterally, and ventrally in setigers 2 or 3; remainder of body cream colored. Specimens in loose tubes com-

posed of detritus and mucus. No brooding of young observed.

**REMARKS.** *Pseudoaugeneriella brevirama* is nearly identical to *P. unirama*, known only from Okinawa Island. Both species have inferior thoracic pseudospatulate setae in setigers 3–6 and abdominal uncini with manubria that are about 1.5 times longer than the dentate region. The only difference between the two species lies in the length of the ventral filamentous appendages. The appendages extend to nearly the distal end of the crown in *P. unirama* (Fitzhugh, 1998: fig. 10B), whereas in *P. brevirama*, appendages are one-half the length of the crown.

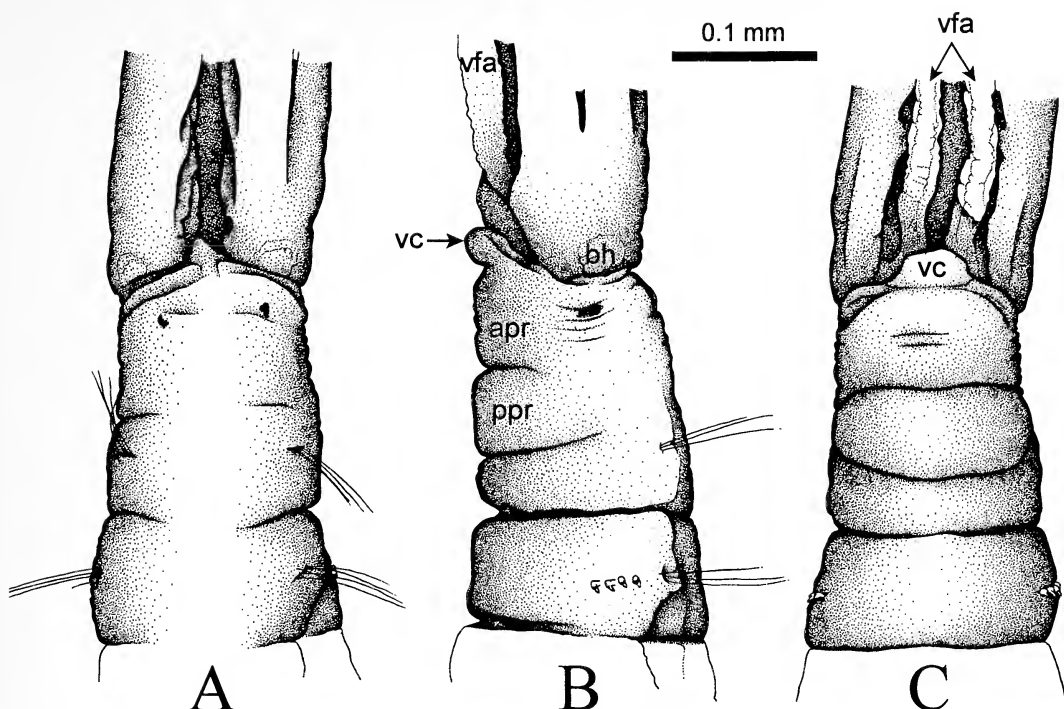


Figure 4. *Pseudoaugeneriella brevirama* n. sp. A–C, dorsal, lateral (left side), and ventral views of anterior end, respectively (paratype, LACM-AHF 1900). Abbreviations: apr, anterior peristomial ring; bh, branchial heart; ppr, posterior peristomial ring; vc, ventral lobe extension of anterior peristomial ring; vfa, ventral filamentous appendage.

The holotype of *P. brevirama* is one of the smaller specimens in the type series. One of the largest specimens, which is complete except for the abdomen, has a crown length of 0.53 mm and a thorax length of 1.20 mm.

#### THE STATUS OF PSEUDOAugENERIELLA

The description of the monotypic *Pseudoaugeneriella* by Fitzhugh (1998) was basically developed out of necessity as a means of accommodating a species that could not be placed in *Augeneriella*. With the discovery of a species nearly identical to *P. unirama*, the question of the monophyly of *Pseudoaugeneriella* must be addressed. This is especially critical since there are no features unique to *Pseudoaugeneriella* that are not also found in at least some other Fabriciinae taxa. The most recent cladistic analysis of relationships among Fabriciinae taxa was that of Fitzhugh (1998), which provided the basis for recognizing *Pseudoaugeneriella*. The data from that study were used to perform a cladistic analysis here, with the inclusion of *P. brevirama* and *Fabriciella phuketensis*.

A total of 21 characters were used (Appendix I), comprising a total of 40 apomorphic states, these being the same ones used by Fitzhugh (1998) in an analysis of relationships among Fabriciinae genera and species. In that analysis, Fitzhugh (1998) con-

ducted two separate analyses, taking into consideration different outgroup conditions for the dentition in thoracic uncini (character 11), and the following states were treated as plesiomorphic in the respective analyses: state 1, teeth gradually decrease in size away from the main fang; and state 2, large tooth slightly offset from midline, followed by a series of smaller teeth. Separate analyses were also performed in the present study. Taxa included 58 fabriciina species among 13 genera. The recognition of *Fabriciella berkeleyi* and *Fabriciella* sp. cf. *berkeleyi* as different species and thus their inclusion as separate entities in the analysis here was justified by Fitzhugh (1992a: 71). Character state assignments for species (Appendix II) are the same as those used by Fitzhugh (1998), except in the cases of *F. flammula* and *F. cri*, which have been recoded with only narrowly hooded inferior thoracic notosetae [state 13(0)] in accordance with the emendations discussed above. Cladograms were constructed using the program Hennig86 (Farris, 1988), with the heuristic command options "mhennig\*" and "bb\*." Character state distributions among trees were examined using the Tree Gardener program (Ramos, 1997).

Both analyses produced over 1,071 trees (maximum held in computer memory), each with a length of 65 steps, a consistency index (ci) of 0.63, and a retention index (ri) of 0.89. The consensus trees for both analyses (Figs. 5–6) are similar to those found by

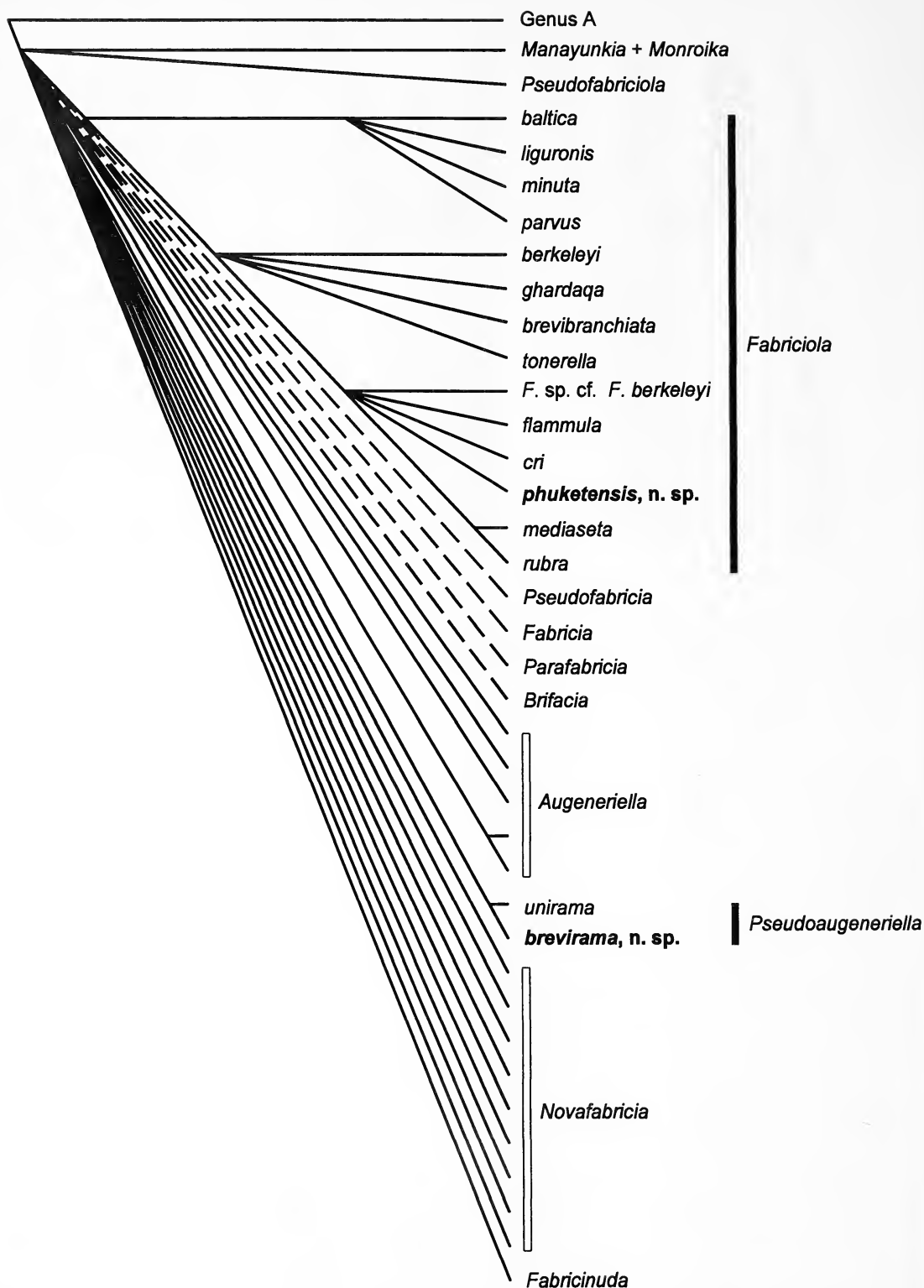


Figure 5. Strict consensus cladogram based on 1,071 cladograms from analysis with character 11 (thoracic uncini dentition) coded as state 1 (teeth gradually decrease in size away from main fang) for the outgroup. Monotypic genera are indicated by dashed branches; species are shown for *Fabriciola* and *Pseudoaugeneriella*; nonmonophyletic genera are indicated by white bars.

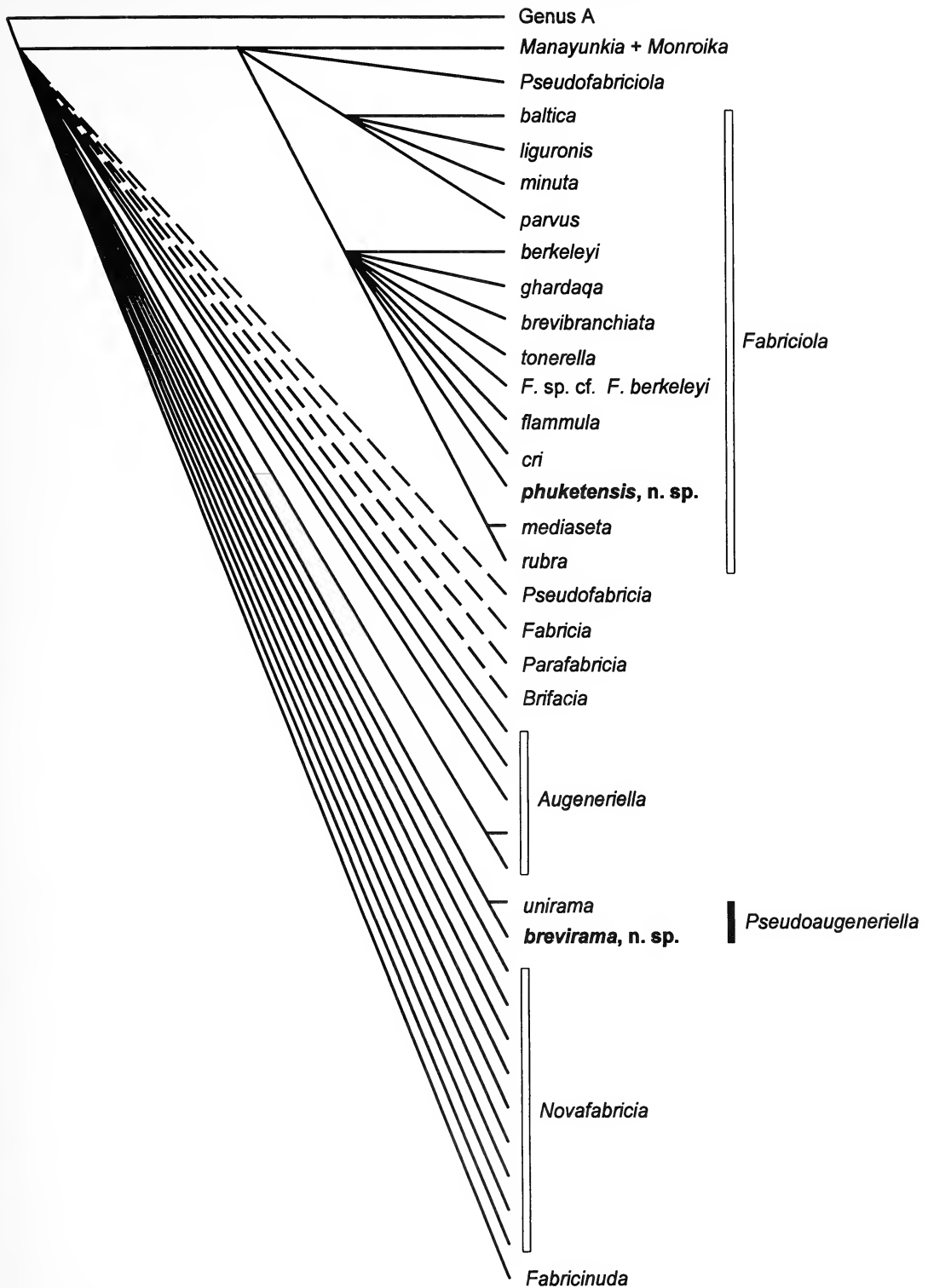


Figure 6. Strict consensus cladogram based on 1,071 cladograms from analysis with character 11 (thoracic uncini dentition) coded as state 2 (large tooth above main fang followed by series of smaller teeth) for the outgroup. Monotypic genera are indicated by dashed branches; species are shown for *Fabriciola* and *Pseudoaugeneriella*; nonmonophyletic genera are indicated by white bars.

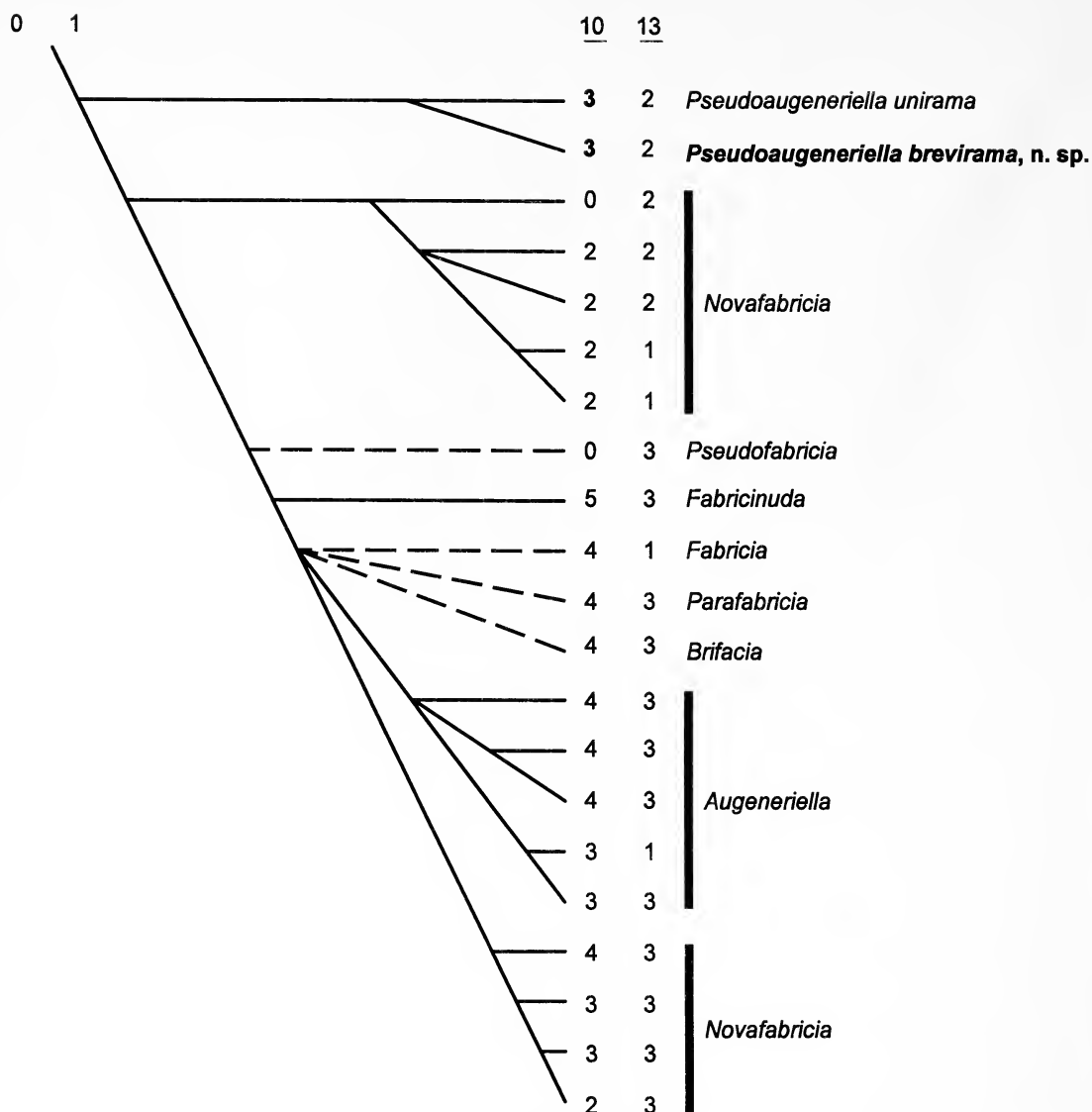


Figure 7. Portion of a single minimum-length tree showing the relationship of *Pseudoaugeneriella* to other genera. Monotypic genera are indicated by dashed branches; species-level relationships are shown for *Novafabricia* and *Augeneriella*. The distribution of states for characters 10 (thoracic pseudospatulate setae) and 13 (manubrium length in abdominal uncini) is shown for terminal taxa. Note that the presence of pseudospatulate setae in setigers 3–6 [10(3)] is a synapomorphy for *Pseudoaugeneriella* (cf. Fig. 8).

Fitzhugh (1998: figs. 18, 28), indicating the presence of topologies in which *Augeneriella* and *Novafabricia* Fitzhugh, 1990, are not monophyletic. As well, the consensus tree for the analysis with state 11(2) plesiomorphic (Fig. 6) also allows for the possibility that *Fabriciola* may not be monophyletic (see also Fitzhugh, 1998: figs. 28, 31). Relationships among *Fabriciola* species will be addressed in the next section.

In all trees produced in both analyses, *Pseudoaugeneriella* is monophyletic, with *P. unirama* and *P. brevirama* as sister taxa (e.g., Figs. 7–8). In all topologies, *Pseudoaugeneriella* is sister group to a

clade that contains at least *Augeneriella*; *Novafabricia*; *Parafabricia* Fitzhugh, 1992; *Brifacia* Fitzhugh, 1998; *Fabricia* Blainville, 1828; and *Fabricinuda* Fitzhugh, 1990. The lack of resolution in the consensus tree is the result of movements of *Pseudofabricia* Cantone, 1972, within and outside this clade (see Fitzhugh, 1998).

The *Pseudoaugeneriella* clade is defined by either state 10(3)-(distribution of inferior thoracic pseudospatulate setae; Fig. 7) or 13(2)-(length of the manubrium of abdominal uncini; Fig. 8), depending on the topology. The two species of *Pseudoau-*



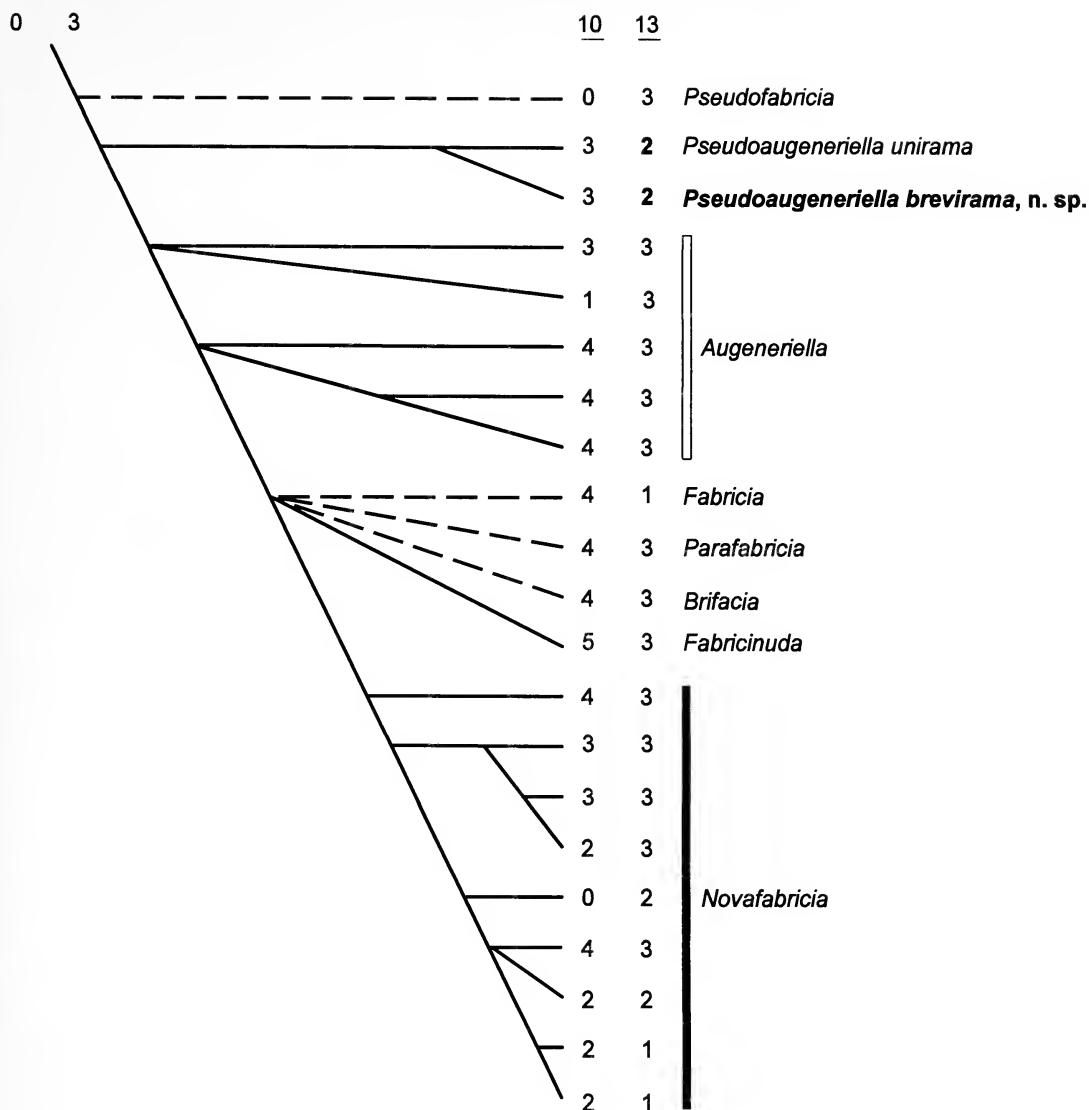


Figure 8. Portion of a single minimum-length tree showing the relationship of *Pseudoaugeneriella* to other genera. Monotypic genera are indicated by dashed branches; paraphyletic *Augeneriella* is indicated by a white bar; species-level relationships are shown for *Novafabricia* and *Augeneriella*. The distribution of states for characters 10 (thoracic pseudospatulate setae) and 13 (manubrium length in abdominal uncini) is shown for terminal taxa. Note that the presence of a manubrium 1.5 times longer than the dentate region in abdominal uncini [13(2)] is a synapomorphy for the genus (cf. Fig. 7).

*generiella* have pseudospatulate setae in setigers 3–6 [10(3)] and have a manubrium length 1.5 times longer than the dentate region in abdominal uncini [13(2)]. Other taxa with pseudospatulate setae limited to setigers 3–6 include two *Augeneriella* species (*A. hummelincki* Banse, 1957; *A. pectinata* Fitzhugh, 1990) and two *Novafabricia* species [*N. chilensis* (Hartmann-Schröder, 1962); *N. labrus* Fitzhugh, 1998]. Additional taxa with a manubrium length like that of *Pseudoaugeneriella* include several species in *Pseudofabriciella* Fitzhugh (*P. californica* Fitzhugh, 1991; *P. peduncula* Fitzhugh,

1996; *P. sofia* Fitzhugh, 1996) and *Novafabricia* (*N. tenuiseta* Fitzhugh, 1990; *N. triangularis* Fitzhugh, 1990; *N. exiguus* Fitzhugh, 1998). The *Pseudoaugeneriella* clade can be defined by pseudospatulates in setigers 3–6 only in those topologies in which *Augeneriella* is not the most plesiomorphic taxon in the clade that is most closely related to *Pseudoaugeneriella* (Fig. 7). Manubrium length is a synapomorphy for *Pseudoaugeneriella* in those topologies in which *Novafabricia* is not the most plesiomorphic taxon in the clade that is most closely related to *Pseudoaugeneriella* (Fig. 8).

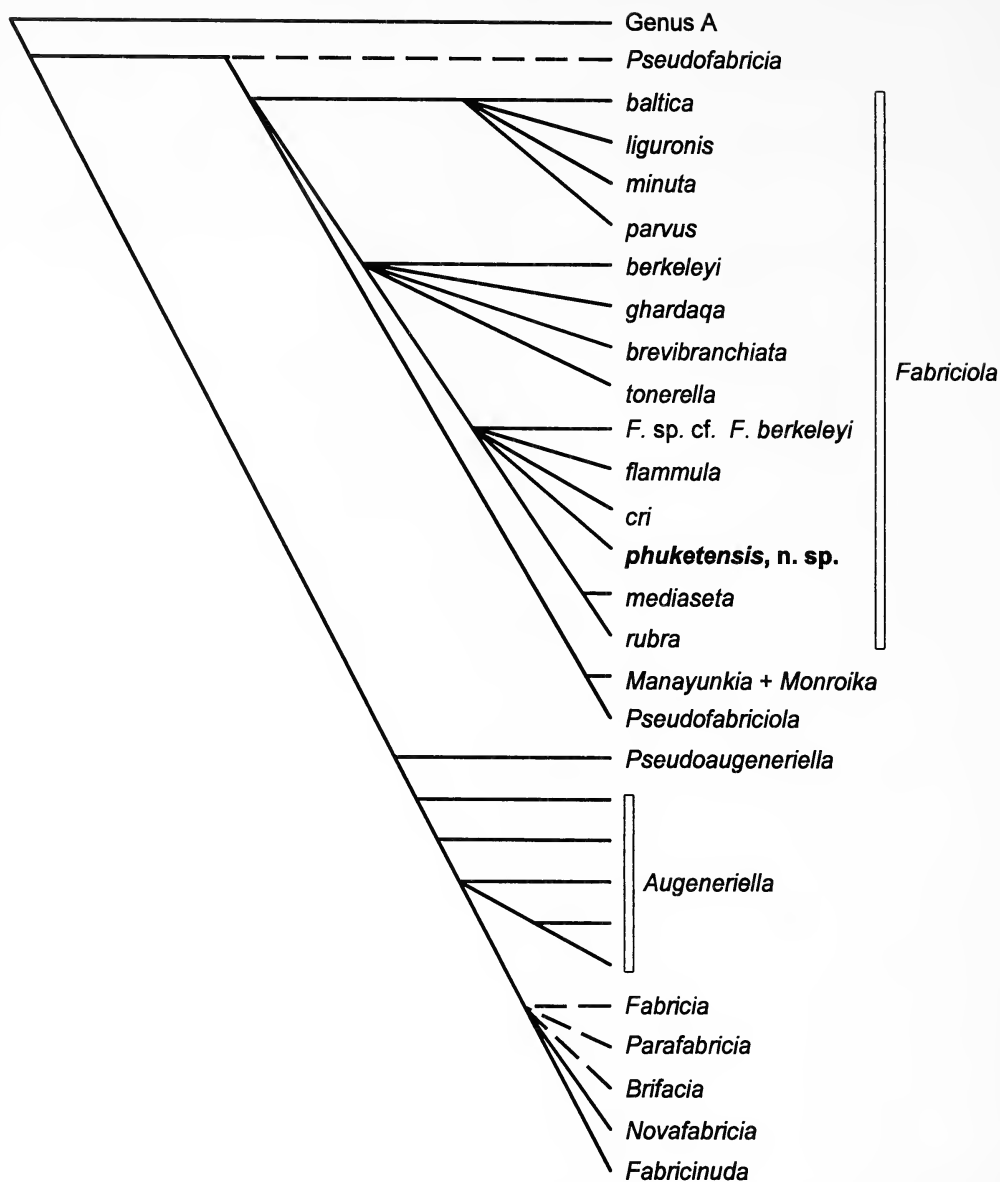


Figure 9. Single cladogram showing the placement of *Pseudofabricia* as sister group to *Fabriciola*, *Manayunkia*, *Monroika*, and *Pseudofabriciola*. Note that this arrangement results in *Fabriciola* being paraphyletic, since nonvascularized filamentous appendages [1(1)] are present both in *Pseudofabricia* and *Fabriciola*, and are thus plesiomorphic for the clade. Monotypic genera are indicated by dashed branches; paraphyletic genera are indicated by white bars; species-level relationships are only shown for *Fabriciola* and *Augeneriella*.

Fitzhugh (1998) noted that the increase in Fabriciinae species and genera has not been followed by a similar increase in character data, which has led to greater topological instability in relationships as well as ambiguity in the monophyly of some genera (e.g., *Augeneriella* and *Novafabricia*). Unfortunately, while the definition of *Pseudoaugeneriella* has not changed from that provided by Fitzhugh (1998), the addition of a second species leaves the issue of monophyly still unresolved.

#### CLADISTIC RELATIONSHIPS AMONG FABRICIOLA SPECIES

The present cladistic analyses of fabriciina genera and species show relationships among *Fabriciola* similar to those described by Fitzhugh (1998: figs. 18, 28, 31). *Fabriciola* is monophyletic in all trees in the analysis with state 11(1) as plesiomorphic (Fig. 5), whereas some topologies in the analysis with state 11(2) as plesiomorphic allow for *Fabri-*

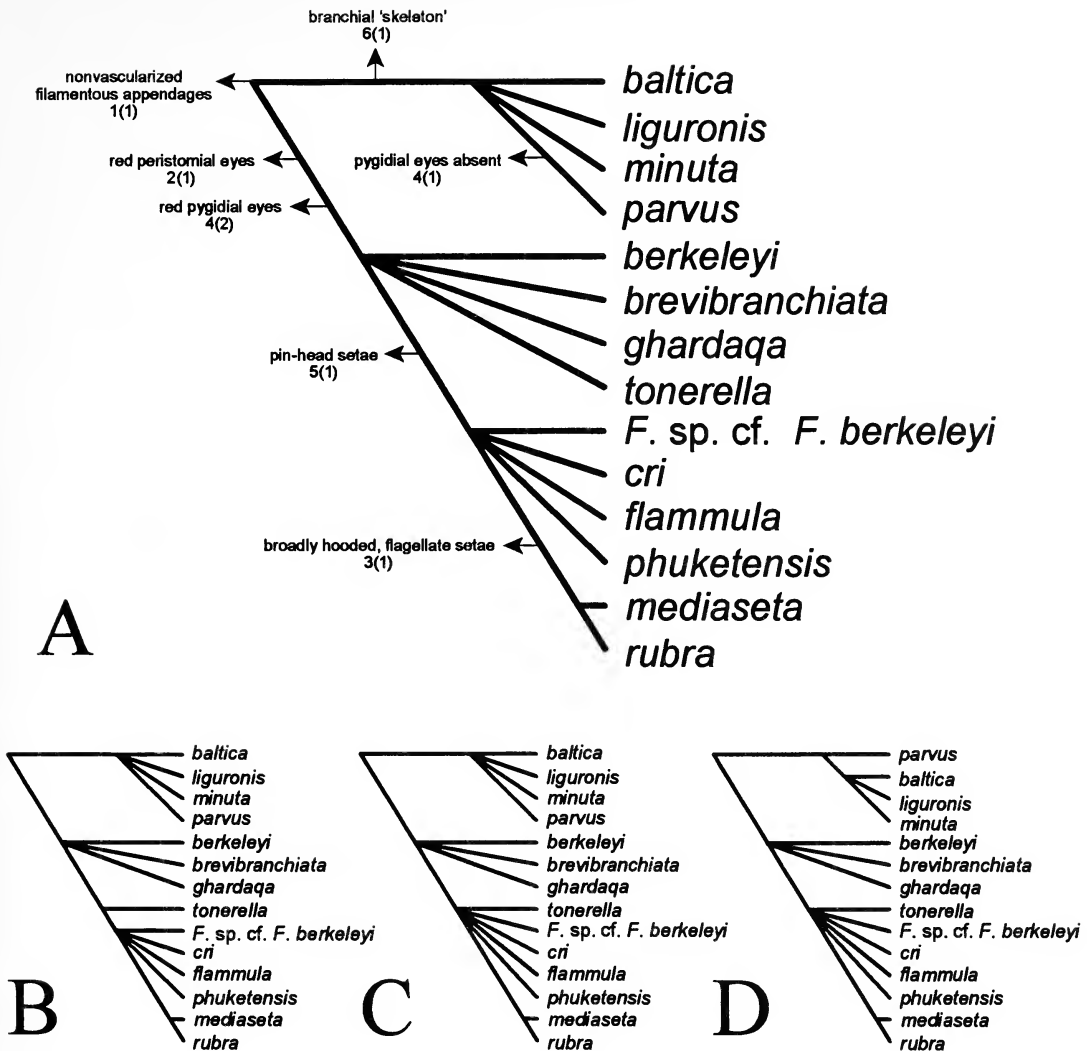


Figure 10. A–C, relationships among *Fabriciolo* species derived from data in Appendix IV. Character state changes are shown in A and are the same in all trees. D, relationships among *Fabriciolo* species derived from data in Appendix IV, except that the absence of pygidial eyes [4(1)] is plesiomorphic. Relationships produced by this change are the same as in A–C, except that *F. parvus* is plesiomorphic to the clade that includes *F. baltica*, *F. liguronis*, and *F. minuta*.

*ciola* to be paraphyletic relative to *Manayunkia* Leidy, 1859; *Monroika* Hartman, 1951; and *Pseudofabriciolo* (Figs. 6, 9). These instances of paraphyly in *Fabriciolo* are due to the placement of *Pseudofabriciolo* as sister group to *Fabriciolo*, *Manayunkia*, *Monroika*, and *Pseudofabriciolo*, such that nonvascularized ventral filamentous appendages [1(1)] are plesiomorphic for this clade (Fig. 9). Given the extensive instability in the placement of *Pseudofabriciolo* (see Fitzhugh, 1998), I consider the possibility that *Fabriciolo* may be paraphyletic to be an anomalous situation resulting from the lack of character data sufficient to resolve the placement of *Pseudofabriciolo*.

Current relationship patterns among *Fabriciolo* species were examined in a separate cladistic anal-

ysis using a subset of the characters from the above analyses [i.e., six characters with a total of seven apomorphic states (Appendix III), as well as the 14 species (Appendix IV)]. The outgroup condition for pygidial eyes (character 4) was coded as either absent [4(2)] or black eyes present [4(0)], which reflects the possible plesiomorphic conditions for *Fabriciolo* based on the earlier analyses. The exhaustive search command "ie\*" was used in Hennig86, and this command produced three trees (Fig. 10), regardless of the outgroup assignment for pygidial eyes, each of which had a length of 7 steps and a ci and ri of 1.00. The topologies produced are similar to those reported by Fitzhugh (1998: fig. 34). With black pygidial eyes coded as plesiomorphic (Fig. 10A–C), there are two major clades—(i) *F.*

*baltica*; *F. liguronis* Rouse, 1993; *F. minuta* Rouse, 1996; and *F. parvus* Rouse, 1993; and (ii) *F. berkeleyi*; *F. brevibranchiata* Fitzhugh, 1992; *F. ghardaqa* Banse, 1959; *F. tonerella* Banse, 1959; *Fabriciola* sp. cf. *F. berkeleyi*; *F. cri*; *F. flammula*; *F. phuketensis*; *F. mediaseta*; and *F. rubra*. The former clade is defined by the presence of a branchial "skeleton" [6(1)], the latter by the presence of red peristomial [2(1)] and pygidial eyes [4(2)]. The clade with red eyes also has an apomorphic clade of species which have abdominal pinhead setae [5(1)]. Differences between the trees is due to the movement of *F. tonerella* (cf. Fig. 10A–C), since the presence or absence of pinhead setae is unknown for that species. Topologies are the same when pygidial eyes are coded as absent for the plesiomorphic condition (e.g., Fig. 10D), except within the clade comprising *F. baltica*, *F. liguronis*, *F. minuta*, and *F. parvus*. Since pygidial eyes are absent in *F. parvus*, the presence of black eyes defines the more inclusive clade comprising *F. baltica*, *F. liguronis*, and *F. minuta*.

The only notable difference between the topologies obtained by Fitzhugh (1998: fig. 34) and those reported here (Fig. 10) is the separation of *F. cri* and *F. flammula* from the clade with *F. mediaseta* and *F. rubra*. Fitzhugh's (1998) analysis grouped these species by the presence of inferior thoracic flagellate setae, which were shown above to be absent in *F. cri* and *F. flammula*. It is possible that greater resolution could be obtained for *Fabriciola* relationships if peristomial collar construction were taken into consideration. For instance, in several cladistic analyses (Fitzhugh, 1991, 1992b, 1993) of relationships among Fabriciinae genera and species as well as among *Fabriciola* species (Fitzhugh, 1992a), collar height has been taken into consideration. Within *Fabriciola*, most species have a low membranous collar of even height all around. The ventral collar margin is, however, distinctly higher in *F. baltica*, *F. liguronis*, *F. minuta*, *F. parvus*, and *F. tonerella*. I have opted to not take this feature into consideration here, since there is complete ambiguity as to the plesiomorphic collar state among species of *Fabriciola*. Species of *Manayunkia* have a membranous collar with a higher ventral margin, but an exclusive sister group relationship with *Fabriciola* is not unambiguous (e.g., Figs. 5–6). *Pseudofabriciola*, too, has a membranous collar, but it is uniformly high all around. Remaining fabriciina genera have a collar condition unlike that seen in these three genera.

## ACKNOWLEDGMENTS

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**Appendix I. Characters and states used to determine cladistic relationships among Fabriciinae genera and species.**

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1. Ventral filamentous appendages: (0) absent; (1) nonvascularized, unbranched; (2) vascularized, unbranched; (3) vascularized, branched.
  2. Dorsal lips: (0) well-developed, triangular lobes, with dorsal margins well separated from proximalmost pinnules of dorsal radioles; (1) dorsal margins fused with proximalmost radioles to some extent, forming low to moderately narrow ridges; (2) absent.
  3. Position of branchial crown: (0) extends over entire anterior end; (1) shifted dorsally to some extent.
  4. Branchial lobe shape: (0) wide and short; (1) narrow and elongate, and/or with pedunclelike process.
  5. Anterior peristomial ring collar: (0) low ridge dorsally and laterally, ventrally as narrow lobe; (1) membranous, of varying height; (2) low ridge dorsally and laterally, ventrally as broad lobe; (3) low ridge all around.
  6. Middorsal collar surface: (0) separate; (1) entire and distinctly grooved; (2) entire and smooth.
  7. Middorsal collar margin: (0) separate; (1) entire; (2) notched or incised.
  8. Anterior peristomal ring dimensions: (0) wider than long; (1) longer than wide.
  9. Peristomal eyes: (0) red in live specimens, disappear in preservation; (1) red in live specimens, persist in preservation; (2) black, well developed, in live and preserved specimens; (3) black, poorly developed, in live and preserved specimens.
  10. Distribution of inferior thoracic pseudospatulate notosetae among setigers 2–8: (0) absent; (1) 2–5; (2) 3–5; (3) 3–6; (4) 3–7; (5) 3–8; (6) broadly hooded, flagellate in 3–7 or 2–8.
  11. Dentition above main fang of thoracic uncini: (0) series of uniformly small teeth; (1) teeth gradually decrease in size away from main fang; (2) large tooth slightly offset from midline, followed by series of smaller teeth.
  12. Dentition of abdominal uncini: (0) >1 row of teeth; (1) single row of teeth.
  13. Manubrium of abdominal uncini: (0) *Amphicorina*-like; (1) about two times longer than dentate region; (2) about 1.5 times longer than dentate region; (3) same length as dentate region.
  14. Pygidial eyes: (0) absent in live and preserved specimens; (1) black in live and preserved specimens; (2) red in live specimens, persist in preservation; (3) red in live specimens, disappear in preservation.
  15. Radioles: (0) 3 or more pairs; (1) 2 pairs.
  16. Body-wall spicules: (0) absent; (1) present.
  17. Branchial hearts: (0) absent; (1) present.
  18. Displaced pinnules: (0) absent; (1) present.
  19. Pinnule arrangement: (0) distinctly pectinate; (1) 2–4 pinnules at bases of branchial lobes.
  20. Abdominal neuropodial pinhead setae: (0) absent; (1) present.
  21. Branchial “skeleton”: (0) absent; (1) present.
-

Appendix II. Character-state matrix for Fabriciinae genera and species based on character states presented in Appendix I.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Outgroup	0	0	0	0	0	0	0	0	0	0	1/2	0	0	3	0	0	0	0	0	0	0	0
<i>Manayunkia aestuarina</i>	2	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1	0	1	0	1	0
<i>M. baicalensis</i>	2	0	0	0	1	0	0	0	2	0	1	0	1	0	1	0	1	1	0	0	0	0
<i>M. brasiliensis</i>	2	0	0	0	1	0	0	0	2	1	1	0	1	0	1	0	1	1	1	0	0	0
<i>M. polaris</i>	2	0	0	0	1	0	0	0	2	3	1	0	1	0	1	0	1	0	1	0	0	0
<i>M. speciosa</i>	2	0	0	0	1	0	0	0	2	0	1	0	1	0	1	0	1	1	0	0	0	0
<i>Monroika africana</i>	2	0	0	0	1	0	0	0	?	2	2	0	3	?	1	0	1	1	0	0	0	0
<i>Augeneriella dubia</i>	2	0	0	0	2	0	0	0	0	0	0	0	1	3	0	1	1	0	0	0	0	0
Genus A sp.	2	0	0	0	2	0	0	0	0	0	0	0	1	3	0	1	1	0	0	0	0	0
<i>Fabriciella baltica</i>	1	0	0	0	1	0	0	0	2	0	1	0	1	1	0	0	1	0	0	0	0	1
<i>F. berkeleyi</i>	1	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	1	0	0	0	0	0
<i>F. sp. cf. F. berkeleyi</i>	1	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	1	0	0	1	0	0
<i>F. brevibranchiata</i>	1	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	1	0	0	0	0	0
<i>F. cri</i>	1	0	0	0	1	0	0	0	1	6	1	0	1	2	0	0	1	0	0	1	0	0
<i>F. flammula</i>	1	0	0	0	1	0	0	0	1	6	1	0	1	2	0	0	1	0	0	1	0	0
<i>F. ghardaqa</i>	1	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	1	0	0	0	0	0
<i>F. liguronis</i>	1	0	0	0	1	0	0	0	2	0	1	0	1	1	0	0	1	0	0	0	0	1
<i>F. mediaseta</i>	1	0	0	0	1	0	0	0	1	6	1	0	1	2	0	0	1	0	0	1	0	0
<i>F. minuta</i>	1	0	0	0	1	0	0	0	2	0	1	0	1	1	0	0	1	1	0	0	0	1
<i>F. parvus</i>	1	0	0	0	1	0	0	0	2	0	1	0	1	0	0	0	1	0	0	0	0	1
<i>F. phuketensis n. sp.</i>	1	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	1	0	0	1	0	0
<i>F. rubra</i>	1	0	0	0	1	0	0	0	1	6	1	0	1	2	0	0	1	0	0	1	?	?
<i>F. tonerella</i>	1	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	1	0	0	?	?	0
<i>Pseudofabriciella analis</i>	0	1	0	1	1	2	1	0	2	0	1	0	3	1	0	0	1	0	0	0	0	0
<i>P. australiensis</i>	2	0	0	1	1	2	2	0	2	0	1	0	3	1	0	0	1	0	0	0	0	0
<i>P. californica</i>	0	0	0	1	1	1	1	0	2	0	2	0	2	1	0	0	1	0	0	0	0	0
<i>P. capensis</i>	0	0	0	1	1	1	1	0	2	0	2	0	3	1	0	0	1	0	0	0	0	0
<i>P. filamentosa</i>	0	?	0	1	1	2	1	0	2	0	1	0	1	1	0	0	1	0	0	0	0	0
<i>P. incisura</i>	2	0	0	1	1	2	2	0	2	0	1	0	3	1	0	0	1	0	0	0	0	0
<i>P. longa</i>	0	1	0	1	1	2	1	0	2	0	1	0	3	1	0	0	1	0	0	0	0	0
<i>P. longipyga</i>	0	1	0	1	1	2	2	0	2	0	1	0	1	1	0	0	1	0	0	0	0	0
<i>P. peduncula</i>	0	1	0	1	1	2	1	0	2	0	1	0	2	1	0	0	1	0	0	0	0	0
<i>P. quasincisura</i>	2	0	0	1	1	2	2	0	2	0	1	0	3	1	0	0	1	0	0	0	0	0
<i>P. soffa</i>	0	1	0	1	1	2	1	0	2	0	1	0	2	1	0	0	1	0	0	0	0	0
<i>Fabricia stellaris</i>	0	0	0	0	2	0	0	0	2	4	2	0	1	1	0	0	1	0	0	0	0	0
<i>Pseudofabricia aberrans</i>	1	0	0	0	2	0	0	0	2	0	2	0	3	1	0	0	1	0	0	0	0	0
<i>Augeneriella basifurcata</i>	3	0	0	0	2	0	0	0	3	4	2	0	3	1	0	0	1	0	0	0	0	0
<i>A. hummelincki</i>	3	0	0	0	2	0	0	0	2	3	2	0	1	1	0	0	1	0	0	0	0	0
<i>A. lagunari</i>	3	0	0	0	2	0	0	0	3	4	2	0	3	1	0	0	1	0	0	0	0	0
<i>A. mossambica</i>	3	0	0	0	2	0	0	0	2	4	2	0	3	1	0	0	1	0	0	0	0	0
<i>A. pectinata</i>	3	0	0	0	2	0	0	0	2	3	2	0	3	1	0	0	1	0	0	0	0	0
<i>Novafabricia bilobata</i>	0	1	0	0	2	0	0	0	2	4	2	0	3	1	0	0	1	0	0	0	0	0
<i>N. brunnea</i>	0	1	0	0	2	0	0	0	2	2	2	0	1	1	0	0	1	0	0	0	0	0
<i>N. chilensis</i>	0	1	0	0	2	0	0	0	2	3	2	1	3	1	0	0	1	0	0	0	0	0
<i>N. exiguus</i>	0	1	0	0	2	0	0	0	2	2	2	0	2	1	0	0	1	0	0	0	0	0
<i>N. gerdi</i>	0	1	0	0	2	0	0	0	2	2	2	1	3	1	0	0	1	0	0	0	0	0
<i>N. infratorquata</i>	0	1	0	0	2	0	0	0	2	2	2	0	1	1	0	0	1	0	0	0	0	0
<i>N. labrus</i>	0	1	0	0	2	0	0	0	2	3	2	0	3	1	0	0	1	0	0	0	0	0
<i>N. tenuiseta</i>	0	1	0	0	2	0	0	0	2	0	2	0	2	1	0	0	1	0	0	0	0	0
<i>N. triangularis</i>	0	1	0	0	2	0	0	0	2	2	2	0	2	1	0	0	1	0	0	0	0	0
<i>Parafabricia ventricingulata</i>	0	0	0	0	2	0	0	0	2	4	2	0	3	1	0	0	1	0	0	0	0	0
<i>Fabricinuda limnicola</i>	0	2	0	0	3	0	0	1	2	5	2	0	3	1	0	0	1	0	0	0	0	0
<i>F. bikini</i>	2	2	1	0	3	0	0	1	2	5	2	0	3	1	0	0	1	0	0	0	0	0
<i>F. trilobata</i>	2	2	1	0	3	0	0	1	2	5	2	0	3	1	0	0	1	0	0	0	0	0
<i>F. pseudocollaris</i>	2	2	0	0	3	0	0	1	2	5	2	0	3	1	0	0	1	0	0	0	0	0
<i>F. pseudopalpa</i>	0	0	0	0	3	0	0	1	2	5	2	0	3	1	0	0	1	0	0	0	0	0
<i>Pseudoaugeneriella unirama</i>	2	0	0	0	2	0	0	0	2	3	2	0	2	1	0	0	1	0	0	0	0	0
<i>P. brevirama n. sp.</i>	2	0	0	0	2	0	0	0	2	3	2	0	2	1	0	0	1	0	0	0	0	0
<i>Brifacia metastellaris</i>	0	0	0	0	2	0	0	0	2	4	2	0	3	1	0	0	1	0	0	0	0	0

- Appendix III. Characters and states used to determine cladistic relationships among *Fabriciola* species.
1. Ventral filamentous appendages: (0) vascularized, unbranched; (1) nonvascularized, unbranched.
  2. Peristomial eyes: (0) black, well developed; (1) red or reddish brown.
  3. Inferior thoracic notosetae: (0) elongate, narrowly hooded in all setigers; (1) broadly hooded, flagellate in some setigers.
  4. Pygidial eyes: (0) black; (1) red or reddish brown; (2) absent.
  5. Abdominal pinhead setae: (0) absent; (1) present.
  6. Branchial "skeleton": (0) absent; (1) present.

Appendix IV. Character-state matrix for *Fabriciola* species based on character states presented in Appendix III.

	1	2	3	4	5	6
Outgroup	0	0	0	0	0	0
<i>baltica</i>	1	0	0	0	0	1
<i>berkeleyi</i>	1	1	0	1	0	0
<i>F. sp. cf. F. berkeleyi</i>	1	1	0	1	1	0
<i>brevibranchiata</i>	1	1	0	1	0	0
<i>cri</i>	1	1	0	1	1	0
<i>flammula</i>	1	1	0	1	1	0
<i>ghardaqa</i>	1	1	0	1	0	0
<i>liguronis</i>	1	0	0	0	0	1
<i>mediaseta</i>	1	1	1	1	1	0
<i>minuta</i>	1	0	0	0	0	1
<i>parvus</i>	1	0	0	2	0	1
<i>phuketensis</i> n. sp.	1	1	0	1	1	0
<i>rubra</i>	1	1	1	1	1	?
<i>tonerella</i>	1	1	0	1	?	0

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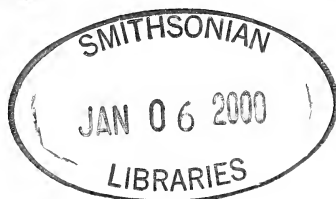
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FROM THE GALAPAGOS ISLANDS

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# LARVAL LABRISOMIDAE (PISCES: BLENNIOIDEI) FROM THE GALÁPAGOS ISLANDS

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GUILLERMO A. HERRERA AND ROBERT J. LAVENBERG

**ABSTRACT.** Larval Labrisomidae from the Galápagos Islands are described from field-collected specimens. The species included are *Starksia galapagensis*, *Dialommus fuscus*, *Labrisomus dendriticus*, *L. multiporosus*, *Malacotenus tetranemus*, and *M. zonogaster*. Identifications were based on meristic data and on comparison of morphology between adults and larger larvae. Labrisomid larvae are elongate, slightly compressed, with 30–47 myomeres, head small and generally rounded with a short snout, external melanophores at anterior tip of the cleithral symphysis; at least one pair of melanophores on head; a ventral row of melanophores on tail (between pterygiophores of anal fin); melanophores above gut (visible only in early stages); and a large swimbladder that is lost during development. Characters that separate *S. galapagensis* larvae from other labrisomids are a more advanced development at smaller size and a longer preanal length (47–53% vs <45% of standard length). Larvae of *Dialommus fuscus* have a high number of dorsal spines (24–27), a high number of anal rays (26–28), a high number of vertebrae (43), and a short preanal distance (33% of standard length). *Labrisomus* and *Malacotenus* larvae have no obvious synapomorphies. Species are identified by particular combinations of characters: preopercular spines, and melanophores on the upper jaw, dorsal margin of trunk, hypural border, and urostyle. In late larvae, the relative size of spines and rays in the dorsal fin is useful in identification.

**RESUMEN.** Se describen las larvas de los labrisómidos de las Islas Galápagos, utilizando especímenes recolectados en terreno. Las especies consideradas son: *Starksia galapagensis*, *Dialommus fuscus*, *Labrisomus dendriticus*, *L. multiporosus*, *Malacotenus tetranemus*, y *M. zonogaster*. La identificación de las larvas se estableció en base a información merística y comparación de morfología de adultos con la de larvas de mayor tamaño. Las larvas de labrisómidos son elongadas, levemente comprimidas lateralmente, con 30–47 miómeros, tienen una cabeza pequeña y generalmente redondeada, con un hocico corto, con un melanóforo externo en el extremo anterior de la sínfisis de los cleitros, con un par (al menos) de melanóforos sobre la cabeza, con una hilera ventral de melanóforos en el margen ventral del cuerpo (entre los pterigóforos de la aleta anal), con melanóforos sobre el intestino (visibles solo en etapas tempranas), y una vejiga gaseosa grande que se pierde durante el desarrollo. Caracteres útiles en la separación de las larvas de *S. galapagensis* de las de otros labrisómidos son un desarrollo más avanzado a una talla más pequeña y una mayor longitud preanal (47–53% vs <45% de la longitud estándar). Las larvas de *Dialommus fuscus* tienen un alto número de espinas en la aleta dorsal (24–27), un alto número de radios anales (26–28), un alto número de vértebras (43), y una corta distancia preanal (33% de la longitud estándar). *Labrisomus* and *Malacotenus* no muestran obvias sinapomorfias larvales a nivel de género. Las especies se pueden identificar por combinaciones particulares de caracteres; espinas preoperculares, y melanóforos en premaxilar, margen dorsal del tronco, borde de las placas hipurales, y urostilo. En larvas más grandes, la estructura de la aleta dorsal, i.e. el tamaño relativo de espinas y radios es también útil en la identificación.

## INTRODUCTION

Labrisomid blennies are small (5–12 cm), demersal reef and nearshore fishes, primarily of the New World. The group is represented by 98 species (14 genera), with approximately half of the species in the eastern Pacific (Nelson, 1984; Grove and Lavenberg, 1997).

Information about life history is available for some members of the family. Matarese et al. (1984) summarized briefly larval characters at a time when

not many larvae were described and the family was not well defined. More recent and more significant contributions include the works of Brogan (1992), who studied the larvae of several species of labrisomids and other blennies from the Gulf of California, and Watson (1996), who described the larvae of five species from the California Current Region.

We describe postflexion larvae of *Starksia galapagensis* (Rosenblatt and Taylor, 1971), *Dialommus fuscus* (Gilbert, 1891), *Labrisomus multiporosus* (Hubbs, 1953), *L. dendriticus* (Reid, 1935), *Malacotenus tetranemus* (Cope, 1877), and *M. zonogaster* (Heller and Snodgrass, 1903), based on field-collected specimens from the Galápagos Is-

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Table 1. Summary of meristic characters for the genera of eastern Pacific Labrisomidae.

Tribe/Genus	D	A	P1	P2	Vertebrae
Cryptotremi					
<i>Alloclinus</i>	XXIV–XXVI, 9–11	II, 21–23	13–14	I, 3	41–42
<i>Auchenionchus</i>	XXIV–XXVI, 11–12	II, 21–24	13–14	I, 3	42–43
<i>Calliclinus</i>	XXIV–XXV, 11–13	II, 20–22	15	I, 4	41–43
<i>Cryptotrema</i>	XXVI–XXVIII, 11–12	II, 24–27	—	I, 3	45–47
Labrisomini					
<i>Malaccoctenus</i>	XIX–XXII, 9–13	II, 17–23	13–16	I, 3	36–45
<i>Labrisomus</i>	XVII–XX, 10–13	II, 16–20	13–16	I, 3	33–46
Mnierpini					
<i>Dialommus</i>	XXIV–XVII, 12–14	I, 26–27	13	I, 3	43
<i>Mnierpes</i>	XXI–XXIII, 10–12	II, 22–23	12–13	I, 3	39
Paracilinini					
<i>Exerpes</i>	(III–IV)–(XXIII–XXVI), 1/2	II, 17–20	13–15	0–I, 2–3	35
<i>Paraclinus</i>	XXVI–XXXIII, 0–1	II, 16–21	11–15	0–I, 2–3	33–39
Starksini					
<i>Starksia</i>	XIX–XXII, 7–10	II, 16–21	12–15	I, 3	30–35
<i>Xenomedeia</i>	XX–XXIII, 8–11	II, 18–22	12–14	I, 3	34–37

lands. The larvae of another labrisomid species that occurs in the Galápagos Islands, *L. jenkinsi* (Heller and Sodgrass, 1903) were not found in the samples. *M. tetranemus* and *L. multiporosus* range from the Gulf of California to northern Chile, whereas the other species, except *L. dendriticus*, are endemic to the Galápagos Islands. *L. dendriticus* is an eastern Pacific oceanic island endemic, known only from Isla Malpelo and the Galápagos Islands (Grove and Lavenberg, 1997).

MATERIALS AND METHODS

Plankton samples were collected by the R/V VELERO III during the Allan Hancock expedition cruises to the eastern tropical Pacific and Galápagos Islands. Most samples were collected during 1933; however, a few specimens came from the expeditions of 1932 and 1934. The collections were made at night (at anchorage), using an electric light and dipnets. Sampling sites were mainly at Española, Santa Maria, Santa Cruz, Isabela, Baltra, and Genovesa Islands (Fraser, 1943).

The specimens (preserved in 70% ethanol) were sorted from the larval fish collections at the Natural History Museum of Los Angeles County (LACM). Specimens were identified by the size-series method (Powles and Markle, 1984), relying on the diagnostic meristics of each species. Meristic data were obtained from Hubbs (1952, 1953), Rosenblatt and Taylor (1971), Springer (1959), Stephens and Springer (1973), Brogan (1992), and Hastings and Springer (1994). Additional vertebral counts and fin meristics were obtained from radiographs of juvenile and adult specimens from the LACM holdings.

All measurements, standard length (SL) and preanal length, were recorded to the nearest 0.1 mm using a Wild M3 stereomicroscope. A representative size series of each species, when available, was illustrated with the aid of a camera lucida. Brief descriptions are given for species represented by a few larvae; they are usually about the same

size (e.g., *Dialommus fuscus*). Meristic data from radiographs of specimens, combined with data from the literature (for labrisomid genera and species from the Galápagos Islands), are summarized in Tables 1 and 2.

LABRISOMIDAE

The Labrisomidae are teleostean fishes of the sub-order Blennioidei, which are considered to be paraphyletic on the basis of DNA sequences and allozyme data (Stepien, Dixon, and Hillis, 1993). Springer (1993) found no evidence to support the monophyly of the Labrisomidae among the 34 characters he analyzed across all the Blennioidei. Stepien et al. (1997) recently hypothesized that the group composed of the Labrisomidae, Clinidae and Chaenopsidae is monophyletic. The paraphyly in the Labrisomidae is probably due to the inclusion of some genera based on plesiomorphic characters such as the presence of a scaled body and a lateral line (Hastings and Springer, 1994).

Currently the labrisomids include 14 genera, allocated into five tribes, and are diagnosed by a dorsal fin either entire or in a spinous and segmented ray portion with more spines than segmented rays, 17–33 dorsal-fin spines, 0–13 simple segmented dorsal-fin rays (never branched), two anal-fin spines (except for *Dialommus* with one), 16–27 segmented anal-fin rays, pectoral-fin rays unbranched, scales cycloid when present with radii only in anterior field, free bony margins of opercular bones not fimbriate, no projection of the pelvic girdle extending anteriorly in front of the juncture with the cleithra, pelvic fins insert in advance of the pectoral fins, dorsal- and anal-fin rays equal in number to the vertebrae between them, and more than 30 vertebrae (see Springer, 1993 for additional labrisomid

Table 2. Summary of meristic and relevant morphologic data for larval Labrisomidae found in the Galápagos Islands. From Hubbs (1952, 1953); Rosenblatt and Taylor (1971); Springer (1959); Stephens and Springer (1973); and this study.

Species	Vertebrae	Dorsal*	Anal*	Pectoral*	Pigmentation				Preopercular spines	Prenal distance
					D	UJaw	Hyp	Uro		
<i>Starksia galapagensis</i>	34–35	XX–XXI (XXII) 7–10	II, (16)17–19	13–14	–	–	–	–	–	47–53
<i>Dialommus fuscus</i>	43	XXIV–XXVII, 10–13(14)	I, 26–28	13	–	–	+	–	–	33
<i>Labrisomus dendriticus</i>	36	XX, (10)11–12	II, (19) 20–21	13	+	+	+	–	+	40–45
<i>Labrisomus jenkinsi</i>	—	XXIII–XIX, 10–11	II, 17	14–15	?	?	?	?	?	?
<i>Labrisomus multiporosus</i>	34–35	(XVII–XIX) 11–13	II, (17–19)	(13–15)	+	–	+	+	+	41–46
<i>Malacotenus tetranemus</i>	35–36	(XVIII–XX) 10–12	II, 18–20	(13–15)	+	+	–	–	+	41–45
<i>Malacotenus zonogaster</i>	37–38	XXI–XXII, 10–11(12)	II, (19) 20–21	14	+	+	+	+	–	38–41

Abbreviations: \* Counts in parentheses are less frequent; ranges in parentheses indicate that both extreme values are less frequent; underscored are most frequent counts. Pigmentation: melanophore presence (+) or absence (–) dorsally (D) on the body (c, continuous row of melanophores), UJaw (upper jaw, number in parentheses), Hyp (hypural), Uro (urostyle; D, dorsal; L, lateral); Preopercular spines: presence (+) or absence (–); preanal distance expressed as a percentage of standard length. Meristic data for *Labrisomus jenkinsi* are provided only for reference, as the larvae remain undocumented.

features). These fishes are restricted to the tropical and warm temperate waters of the New World and the west coast of Africa (see Stepien 1992, figure 1; we cannot verify the western Pacific record shown in figure 1).

Labrisomids have two modes of spawning; ovoviviparity in the tribe Starksiini and oviparity in the other four tribes. In the Starksiini the first anal-fin spine is modified into an elongate genital papilla to serve as an intromittent organ. Development proceeds in the follicles of the ovary, and the embryos hatch at an advanced larval stage. To our knowledge, all other labrisomids exhibit some degree of courtship and spawn adhesive demersal eggs into a nest site, which is guarded by the parents. At hatching, larvae have pigmented eyes and measure about 3–4 mm notochordal length (NL). Notochord flexion usually occurs shortly thereafter.

Larvae are elongate, slender, and slightly laterally compressed with at least 30–47 myomeres; gut initially straight, preanal length usually less than 50% of standard length, up to 53% in *Starksia*; a large swimbladder (absent in adults); a small, rounded head; a short snout; six branchiostegal rays; and 7+6 principal caudal rays. Pigmentation is weak or light; melanophores occur primarily on dorsal cranial surfaces; on the nape; anterior to the gut, behind the cleithra; over the swimbladder; at the tip of the cleithral symphysis; on the hind gut; and along the ventral margin of the tail, especially between the pterygiophores of the anal-fin rays. Labrisomid larvae show no pronounced morphological specializations to pelagic life.

### LARVAL DESCRIPTIONS

#### *Starksia galapagensis* (Rosenblatt and Taylor, 1971)

Figure 1

**GENERAL MORPHOLOGY.** Based on 237 specimens, larvae and juveniles (11.6 to 14.2 mm). *Starksia galapagensis* has single nasal, orbital, and nuccal cirri and no preopercular spines (Table 2). The smallest specimen (Fig. 1a., 11.6 mm) has completed notochord flexion. No significant changes in body shape occur during subsequent development (Fig. 1a–c). The largest larva was 14.2 mm (Fig. 1c), although metamorphosing specimens were slightly smaller (Fig. 1d–e). By 12.4 mm, all the pores of the circumorbital series (10), and three in the preoperculomandibular series (Fig. 1d) are developed.

**FIN DEVELOPMENT.** All fin spines and rays are present at 11.6 mm. The shape and relative proportions of spines and rays are constant, except for the posteriormost three to four anal-fin rays that grow longer than the rest, forming a lobe nearly as long as the caudal peduncle.

**PIGMENTATION.** Larval *Starksia galapagensis* are unique in having a large ventral melanophore on the surface of the basipterygium. A single small melanophore may develop on the ventral margin of

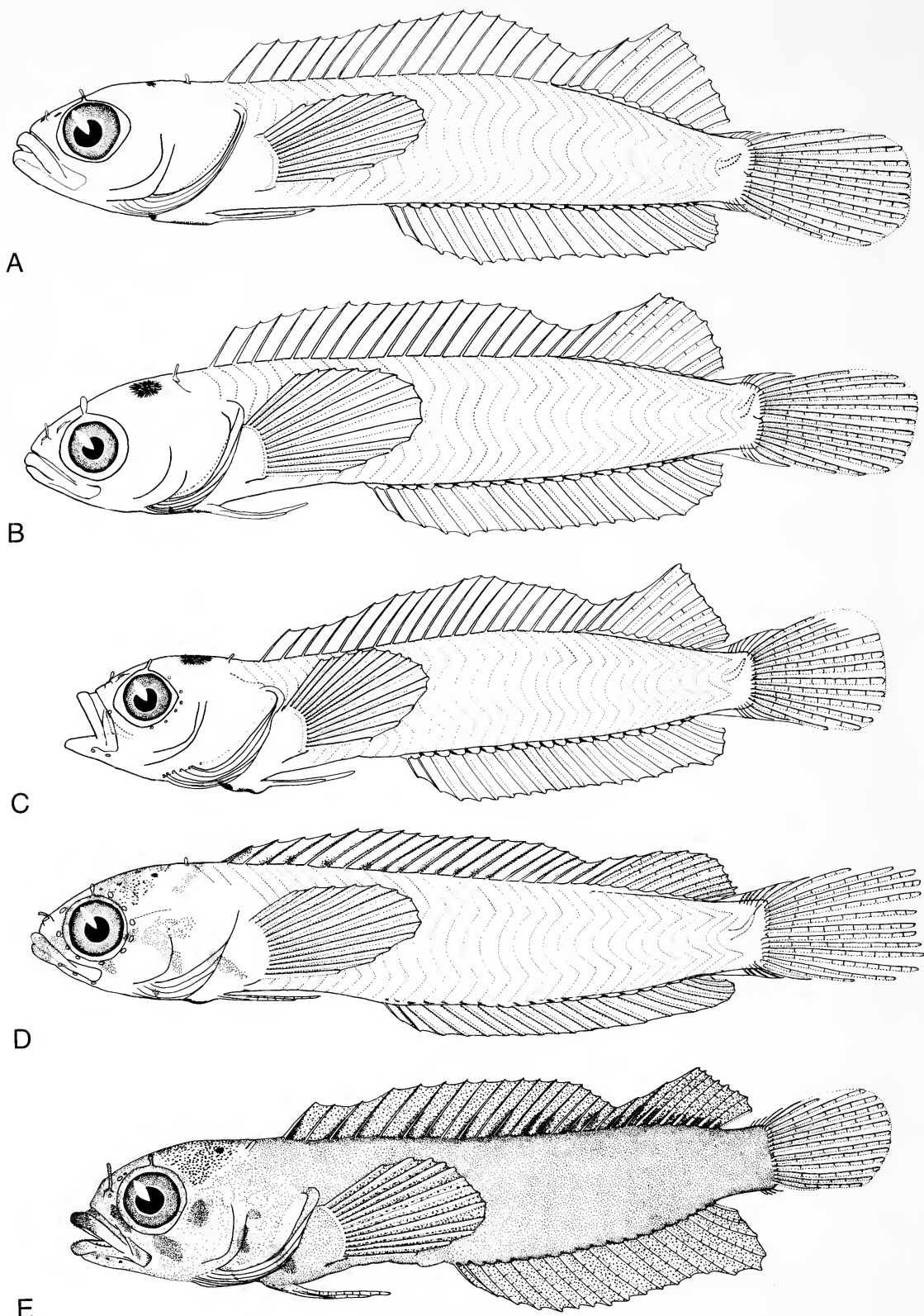


Figure 1. Field collected larvae and juvenile of *Starksia galapagensis*: (a) 11.6-mm larva (LACM 45644-12), (b) 13.0-mm larva (LACM 45663-13), (c) 14.2-mm larva (LACM 45621-20), (d) 12.4-mm transforming specimen (LACM 45634-15), (e) 12.6-mm juvenile (LACM 43688-1).

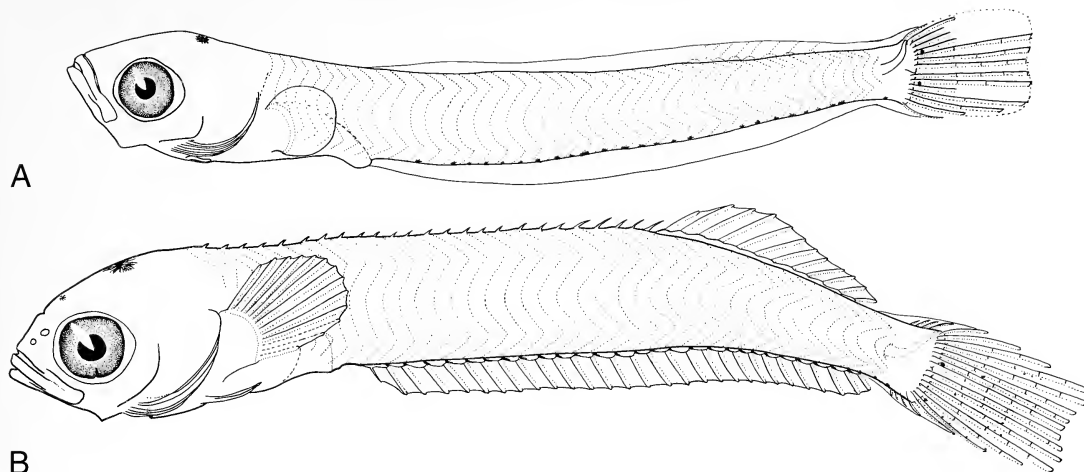


Figure 2. Field collected larvae of *Dialommus fuscus*: (a) 8.4 mm (LACM 45665-2), (b) 10.2 mm (LACM 45621-14).

the caudal peduncle. The 12.4-mm specimen (Fig. 1d) seems to be in the process of metamorphosis; this specimen also has a small melanophore ventral to the gut, at the pectoral-fin base level.

Part of the typical dark spots, composed of small melanophores and observed in the head of the adults, can be recognized in the two larger specimens; these spots are in lips; in front of, below and behind the eye; in the operculum; and in front of the pectoral fins (Fig. 1d-e).

At metamorphosis, small melanophores develop along the anterior and posterior margins of all fin spines and rays. Furthermore, there are blotches in the dorsal fin membrane with higher concentration of melanophores. In older specimens (Fig. 1e), small punctate melanophores develop on the entire body and fins; those dorsally on the head are a little larger. The ventral melanophore on the basipterygium is also lost.

**REMARKS.** Among the six Galápagos labrisomids, only *Starksia galapagensis* has fully developed larvae at sizes as small as 11.6 mm and metamorphic specimens smaller than 14 mm. Distinctive characters are the elongate melanophore ventrally on the basipterygium and a preanal length >47% standard length (SL).

### *Dialommus fuscus* (Gilbert, 1891)

#### Figure 2

**GENERAL MORPHOLOGY.** Description based on 13 specimens; two larvae (8.4 and 10.2 mm) described in detail. Compared with the other known larval Galápagos labrisomids, the larvae of this species are more slender, with a shorter preanal length (Table 2). Neither specimen has developed cirri. There are no preopercular spines, and apparently they are absent in all larval *Dialommus*.

**FIN DEVELOPMENT.** Flexion and caudal-fin ray development are complete at 8.4 mm, and the

dorsal-fin pterygiophores are developing posteriorly (Fig. 2a). At 10.2 mm, dorsal- and anal-fin spines and rays are present, but most of the dorsal-fin spines are poorly developed. Pectoral-fin rays are not completely formed (Fig. 2b).

**PIGMENTATION.** Two well-separated melanophores develop on the principal caudal-fin rays near the distal margins of the upper and lower hypural plates but not in contact with them. A pair of small melanophores develops in the interorbital region anterior to the two large cephalic melanophores at 10.2 mm (Fig. 2b). Three small melanophores can be found on the ventral margin of the caudal peduncle.

**REMARKS.** Larvae of *D. fuscus* can be identified by a long and slender body shape, a short preanal distance, high myomere count (43), and distinctive caudal-fin melanophores. In late larvae, the number of spines and rays in the dorsal and anal fins is diagnostic (Table 2).

### *Labrisomus dendriticus* (Reid, 1935)

#### Figure 3

**GENERAL MORPHOLOGY.** Based on 176 larvae (6.4–22.7 mm). Body is elongate with a shape intermediate between the slender *Dialommus fuscus* and the more robust *Starksia galapagensis*. Slope of the head is flat in early stages (Fig. 3a), becoming more rounded (Fig. 3e). Preanal length ranges from 40–45% SL. Cirri develop later than in the other species of *Labrisomus* and *Malacotenus*. At 18.1 mm, nasal and orbital cirri are small buds (Fig. 3d). By 22.7 mm, bifid nasal and orbital cirri and three nuccal cirri are present (Fig. 3e); the nuccal cirri are smaller in *L. dendriticus* than in *L. multiporosus* and *Malacotenus*.

**FIN DEVELOPMENT.** At 6.4 mm, a full complement of anal-fin rays are developing, and the dorsal-fin anlage is formed. Dorsal-fin spines begin

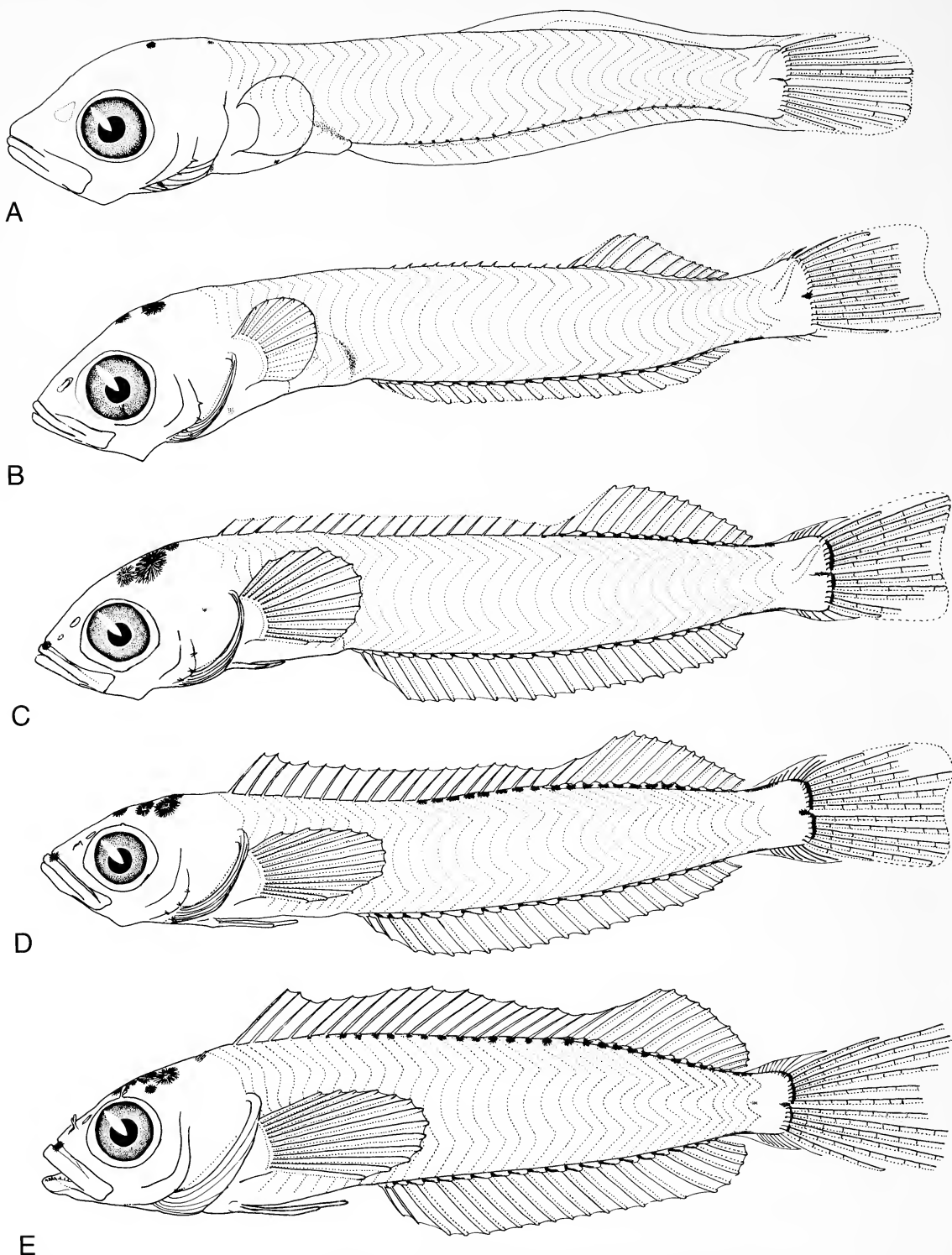


Figure 3. Field collected larvae of *Labrisomus dendriticus*: (a) 6.4 mm (LACM 45656-3), (b) 8.4 mm (LACM 45614-4), (c) 13.6 mm (LACM 45614-4), (d) 18.1 mm (LACM 45614-4), (e) 22.7 mm (LACM 45621-5).



to develop posteriorly by 8.4 mm; all spines are formed by 13.0 mm. By 18.1 mm, the first two dorsal-fin spines are longer (Fig. 3d), as in adults.

**SPINATION.** Preopercular spines are developed by 6.4 mm (Fig. 3a). They become embedded in late-stage larvae and remain visible to at least 18.1 mm; they disappear by 22.7 mm (Fig. 3e).

**PIGMENTATION.** The most distinctive character is the presence of a melanophore between the hypural plates, close to the posterior border (Fig. 3a). A pair of melanophores develops on the upper jaw at about 9.0 mm. A single pair of melanophores is present above the midbrain in larvae <7.0 mm, increasing to three pairs in larvae >16.0 mm (Fig. 3a–d). At 6.4 mm, a ventral melanophore is present on the gut (Fig. 3a), but it disappears before 8.4 mm.

At about 10 mm, two melanophores develop behind the distal hypural margins. Two to four melanophores are present on the ventral margin of the caudal peduncle (Fig. 3a, 6.4 mm); one to two melanophores develop on the dorsal margin after 10.0 mm (Fig. 3c–e). A continuous row of melanophores develops along the pterygiophores of the dorsal fin, spreading both caudad and cephalad from the anterior soft rays, beginning at 10.2 mm; in the largest specimen, this row extends from the fourth or fifth spine to the last dorsal-fin ray (Fig. 3e). At 22.7 mm, external melanophores form laterally on the caudal peduncle (Fig. 3e), probably signaling the beginning of metamorphosis.

**REMARKS.** Of the six species studied, *Labrisomus dendriticus* is the only one that has a melanophore between the hypural plates and a continuous dorsal row of melanophores on the trunk and tail. Other distinguishing characters are small nuchal cirri; presence of preopercular spines; a pair of melanophores on the upper jaw; and a series of melanophores along the posterior border of the hypural plates. Also, *L. dendriticus* develops one or two melanophores on the dorsal margin of the caudal peduncle, a feature that is absent in larvae of *L. multiporosus*.

The two species of *Labrisomus* have the same configuration of spines and rays in the dorsal fin. The terminal dorsal-fin spine is longer than the preceding spines and superficially appears to be part of the segmented ray portion of the dorsal fin. *Malacotenus* differs from *Labrisomus* in that the last two dorsal-fin spines are longer than the preceding ones and appear to belong to the segmented ray portion of the fin.

### *Labrisomus multiporosus* (Hubbs, 1953)

#### Figure 4

**GENERAL MORPHOLOGY.** Based on 915 larvae (5.4–18.4 mm). These larvae are morphologically similar to those of *L. dendriticus*. The largest specimen, 18.4 mm, has bifid nasal cirri, a single orbital cirri, and five nuchal cirri of moderate length (Fig. 4f). A diagnostic feature of adults is a complex

cranial pore pattern, which begins to develop in late-stage larvae. Pores form above the eye by 14 mm and proliferate as development proceeds, particularly around the orbit and laterally on the lower jaw (Fig. 4e–f).

**FIN DEVELOPMENT.** The development of dorsal and anal fins is similar to that of *L. dendriticus*. At 5.4 mm, only part of the dorsal-fin anlage is present, and notochord flexion is complete. At 7.2 mm, dorsal and anal fins are partially formed. By 14.5 mm, the anteriormost four dorsal-fin spines are of about uniform length (Fig. 4e–f), resulting in the characteristic straight fin margin.

**SPINATION.** Three preopercular spines are present in small larvae (5.4 mm), and the number increases to four spines by 14.5 mm (Fig. 4e) and to 8 at 18.4 mm (Fig. 4f). The spines are not lost, as occurs in other species; the adults of *L. multiporosus* are characterized by the presence of preopercular spines.

**PIGMENTATION.** Melanophores develop between the pterygiophores of the first three segmented dorsal-fin rays at 11 mm (Fig. 4d). They spread cephalad in a discontinuous row to the seventh or eighth spine, and they spread caudad in a continuous row to near the last ray.

Internal melanophores develop laterally on the urostyle (Fig. 4e–f), and a series of external melanophores develops along the posterior margin of the hypurals (Fig. 4a) in larvae as small as 5.4 mm. At 14.5 mm, a few small punctate melanophores pepper the caudal fin membrane, mainly in the lower lobe (Fig. 4e). Two to five melanophores are present on the ventral margin of the caudal peduncle; these may coalesce, and by 18.4 mm, only two large melanophores can be discerned (Fig. 4f).

Melanophores above the brain increase from one pair at 5.4 mm to two pairs at 7.2 mm (Fig. 4a–b) and to three pairs at 14.5 mm, with the appearance of progressively more anterior pairs (Fig. 4e–f). At 5.4 mm, there is one ventral melanophore on the gut and two below the anus; all of these disappear before 7.2 mm (Fig. 4b). At 18.4 mm, three large melanophores form ventrally on the gut and one forms ventrolaterally below the pectoral base (Fig. 4f).

**REMARKS.** Among the six Galápagos labrisomid species, *L. multiporosus* is the only one that retains preopercular spines as a juvenile. Furthermore, the number and size of spines increase in larger larvae.

In contrast to *L. dendriticus*, *L. multiporosus* lacks melanophores on the upper jaw and between the hypural plates. Further, the development and number of preopercular spines, the dorsal pigment pattern, and the size of dorsal-fin spines and rays serve to distinguish these two species. The two species show differences in the time of development of pigment along the hypural margin: in *L. multiporosus* melanophores develop early (by 5.4 mm), whereas in *L. dendriticus* they develop late (by 10 mm).

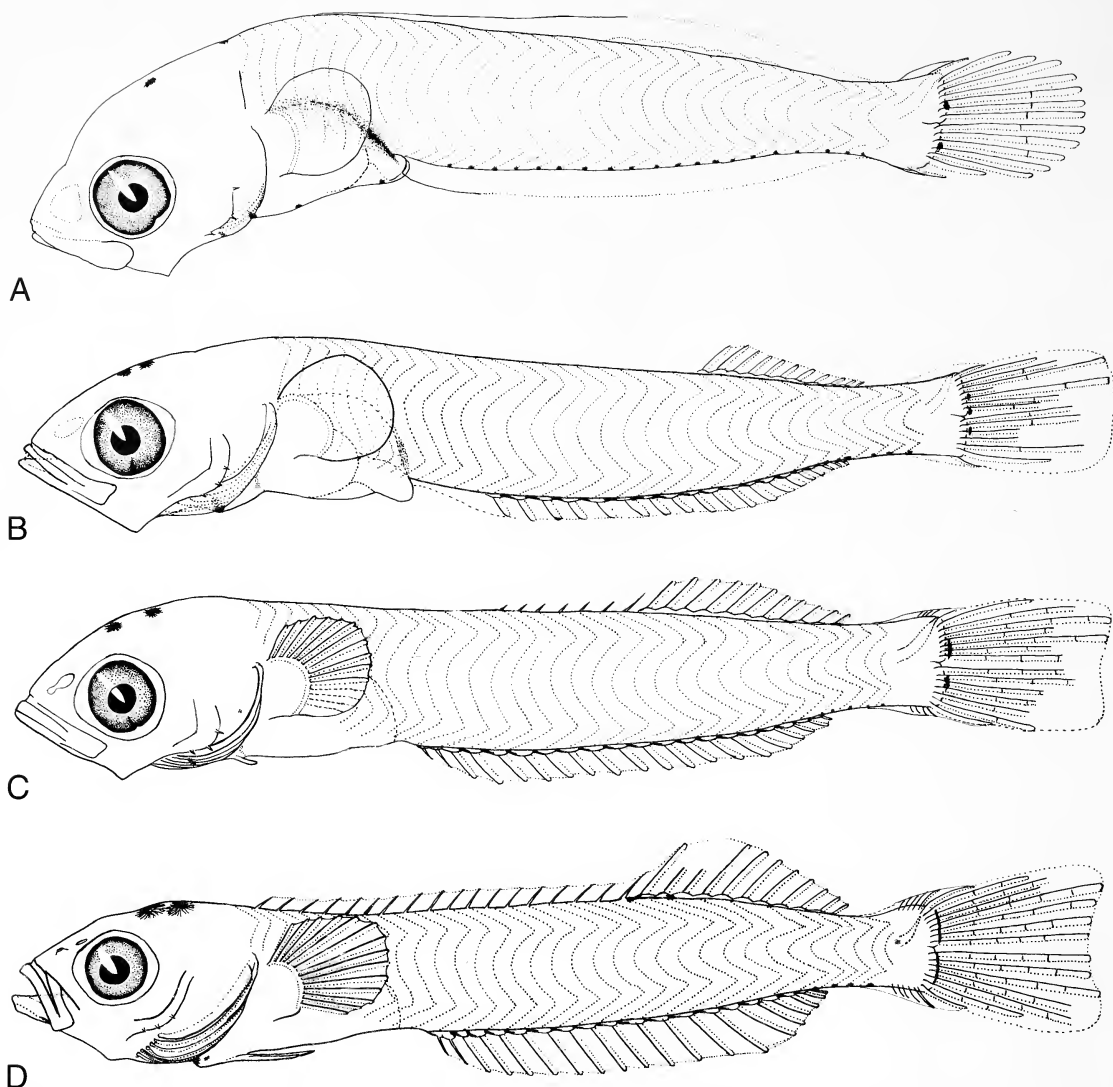


Figure 4. Field collected larvae of *Labrisomus multiporosus*: (a) 5.4 mm (LACM 45623-5), (b) 7.2 mm (LACM 45675-4), (c) 8.3 mm (LACM 45675-4), (d) 11.8 mm (LACM 45621-6), (e) 14.5 mm (LACM 45623-5), (f) 18.4 mm (LACM 45623-5).

### *Malacoctenus tetranemus* (Cope, 1877)

#### Figure 5

**GENERAL MORPHOLOGY.** Based on 228 larvae (5.4–17.3 mm). The larval shape as in other *Labrisomus* and *Malacoctenus* species. Preanal length ranges from 41–45% SL. *M. tetranemus* develops six long nuccal cirri, a bifid nasal cirrus, and a bifid orbital cirrus. Two mandibular pores develop laterally on the lower jaw in larger specimens (Fig. 5d–e).

**FIN DEVELOPMENT.** Dorsal-fin spines begin to develop at 9.0 mm. By about 16 mm, the spinous dorsal fin is notched near its anterior and posterior ends (Fig. 5d–e). In *Malacoctenus*, the first two elements of the posteriorly lobed portion of the dor-

sal fin are spines. This feature is established by 10.2 mm in *M. tetranemus*, even before dorsal-fin spine development is complete (Fig. 5 b–e).

**SPINATION.** At 5.4 mm, *Malacoctenus tetranemus* has three preopercular spines (Fig. 5a); however, these disappear during development and are no longer visible in larvae larger than 16 mm (Fig. 5d–e).

**PIGMENTATION.** A pair of melanophores develops on the premaxillary in larvae as small as 5.4 mm (always present after 6.2 mm). Two pairs of melanophores develop on the midbrain before 7.0 mm, and by 12.2 mm, two additional pairs have appeared above the forebrain. These melanophores increase in size with development (Fig. 5c–e).

A row of melanophores appears between the

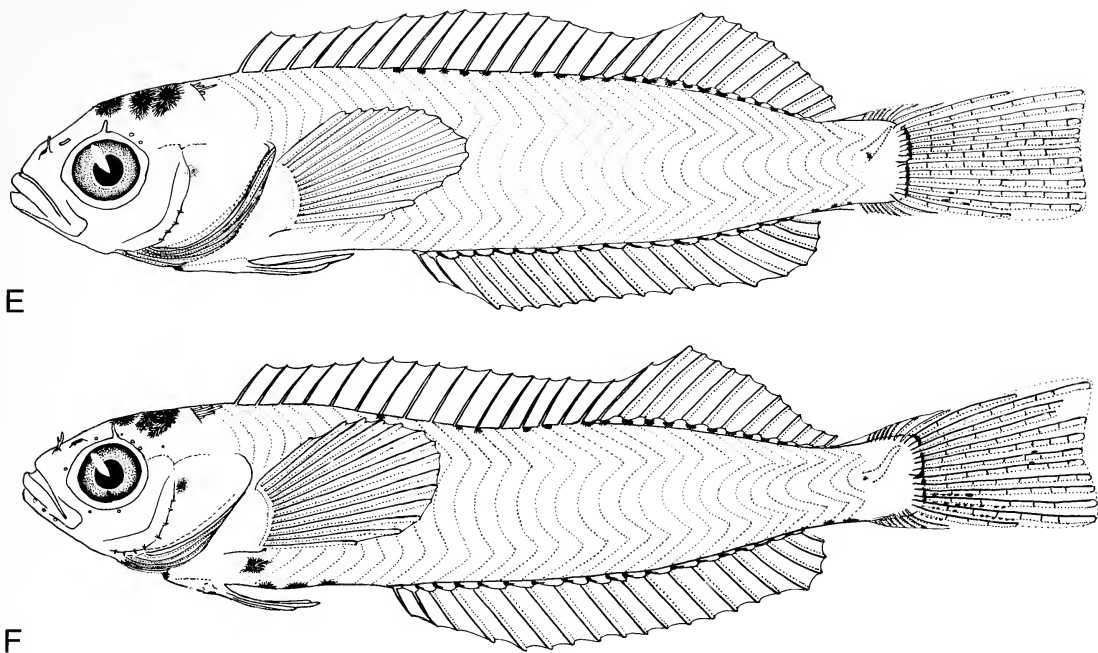


Figure 4. Continued.

first pterygiophores of the segmented ray portion of the dorsal fin by 10.2 mm (Fig. 5c) and subsequently spreads both cephalad and caudad (Fig. 5d–e). These melanophores are not arranged in a continuous row, nor is their position on the pterygiophores constant among individuals (Fig. 5d–e).

In larvae shorter than 7.0 mm, there is usually no pigmentation on the ventral margin of the caudal peduncle, but one small melanophore is present in some specimens. Two melanophores are present ventrally along the gut but disappear early by 10.2 mm (Fig. 5a). Melanophores typically are absent along the hypural margin.

**REMARKS.** Among the six species treated here, *M. tetranemus* has the largest and most numerous (6) nuccal cirri. It is easily distinguished from other species by the combination of preopercular spines, the absence of pigmentation along the hypural margin, and the presence of melanophores on the upper jaw. Further, *M. tetranemus* typically shows heavier cranial pigmentation.

*Malacoctenus zonogaster* (Heller and Snodgrass, 1903)

Figure 6

**GENERAL MORPHOLOGY.** Based on 414 larvae (7.0–17.7 mm). Preopercular spines are absent. Preanal length ranges from 39–41% SL. *Malacoctenus zonogaster* develops a single orbital cirrus, a bifid nasal cirrus, and three small nuccal cirri.

**FIN DEVELOPMENT.** Notochord flexion is

complete and segmented dorsal- and anal-fin rays are forming by 7.0 mm (Fig. 6a). Dorsal-fin spines begin to appear by 11.0 mm, and by 15.6 mm the typical adult pattern of having the first two dorsal-fin spines longer than the third and fourth spines is present (Fig. 6d–e). The generic character of having the last two dorsal-fin spines included in the segmented ray portion of the dorsal fin is present at 12.2 mm (Fig. 6d).

**PIGMENTATION.** Cranial pigment consists of a pair of melanophores on the frontals; another, larger pair on the parietals; and an embedded melanophore on the nape. A few smaller melanophores sparsely scattered on the head increase in number with growth (Fig. 6a–e).

A discontinuous row of melanophores develops between the anterior pterygiophores of the segmented ray portion of the dorsal fin at 12.2 mm and spreads cephalad to the fifth dorsal-fin spine and caudad (Figs. 6d–e), but not as far as the last two segmented rays. Larvae larger than 15 mm have a single, small, usually faint melanophore on the upper jaw. In contrast, other labrisomids with upper jaw pigment typically have a pair of melanophores.

A series of two to four melanophores appears on the ventral margin of the caudal peduncle after 7.0 mm (Fig. 6a), and this increases to four to six melanophores after 9.0 mm (Fig. 6b–e). On the dorsal peduncle margin, one or two melanophores develop at about 10.0 mm and are retained in later larval stages (Figs. 6b–e). Internal dorsal melano-

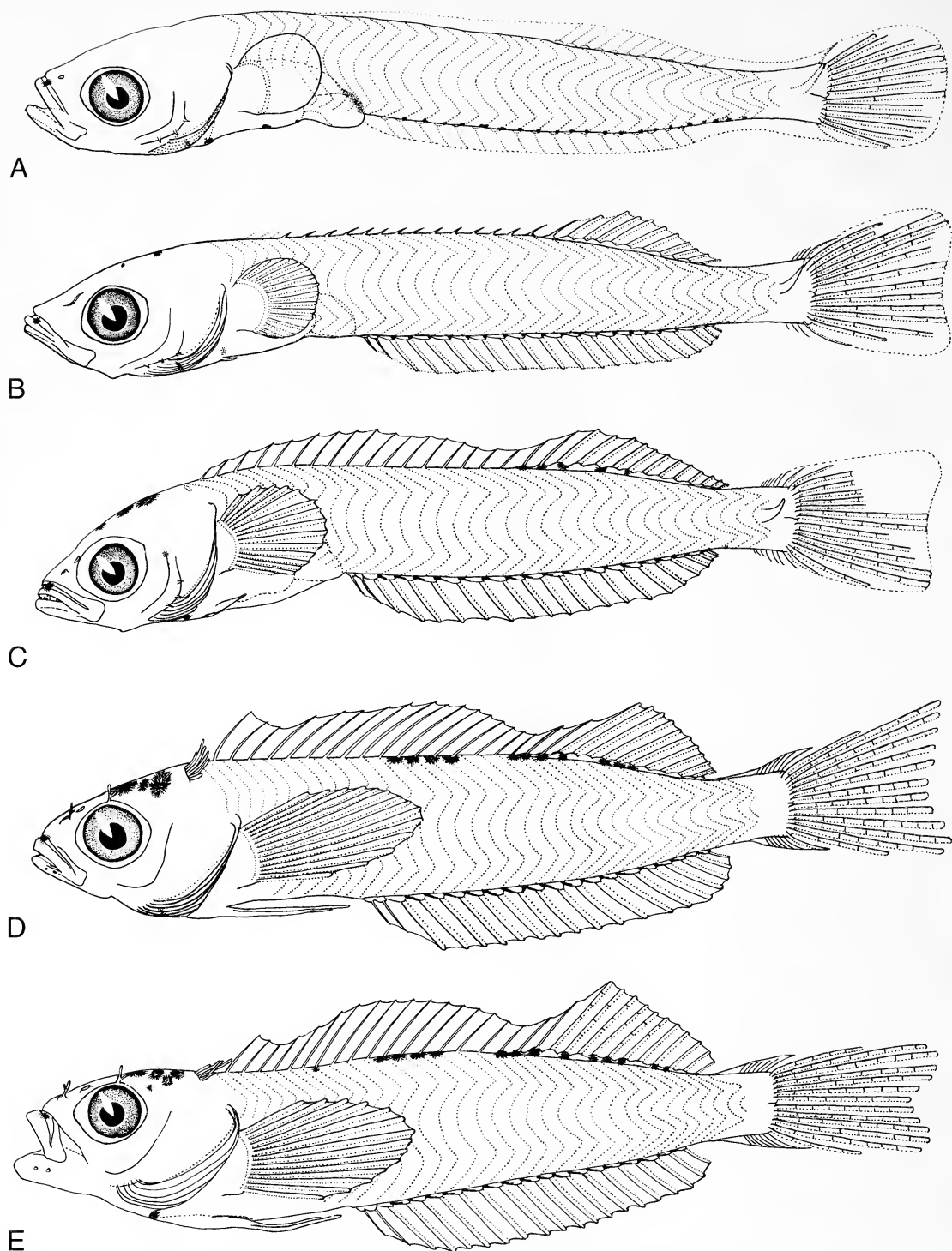


Figure 5. Field collected larvae of *Malaccoctenus tetranemus*: (a) 7.2 mm (LACM 45675-6), (b) 10.2 mm (LACM 45675-6), (c) 12.2 mm (LACM 45623-7), (d) 16.1 mm (LACM 45643-5), (e) 17.3 mm (LACM 45625-14).

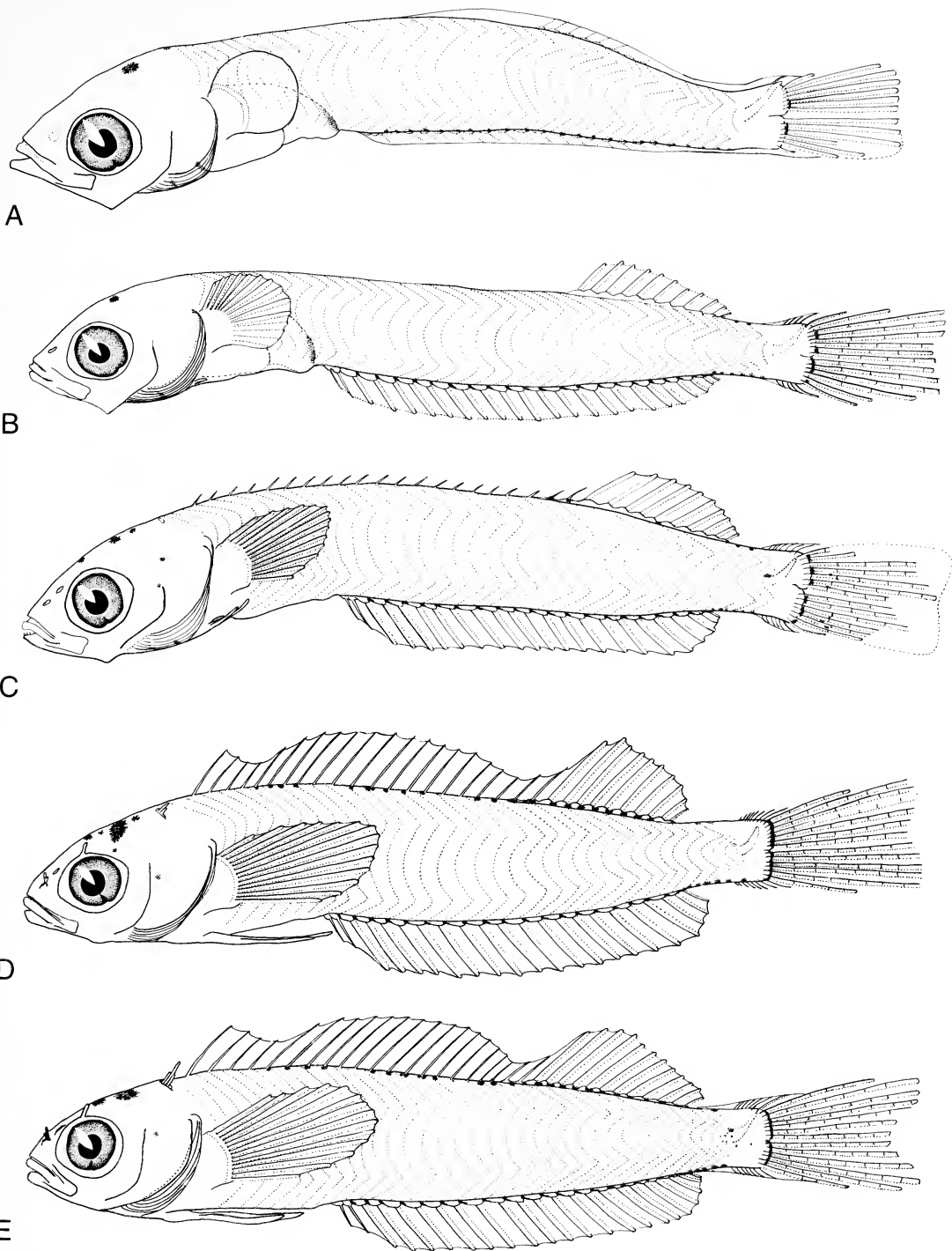


Figure 6. Field collected larvae of *Malacotenus zonogaster*: (a) 7.0 mm (LACM 45675-7), (b) 10.2 mm (LACM 45675-7), (c) 12.2 mm (LACM 45623-7), (d) 15.6 mm (LACM 45625-15), (e) 17.7 mm (LACM 45622-2).

phores associated with the urostyle are present in larvae larger than 9.0 mm (Fig. 6c–e). Hypural border pigmentation is present by 7.0 mm, initially as one melanophore on the margin of each plate. These increase in number and eventually overlap, covering the entire hypural margin (Fig. 6d–e). At 18.4 mm, small melanophores develop on the lower caudal rays (Fig. 6e).

**REMARKS.** Both species of *Malacotenus* develop pigmentation on the upper jaw, but *M. zonogaster* has a single medial melanophore that develops late (>15.0 mm), whereas *M. tetranemus* has two that appear early (<6.0 mm SL). *M. zonogaster* also differs from *M. tetranemus* in lacking preopercular spines, in retaining the dorsal and ventral pigmentation on the caudal peduncle throughout larval life, and in having melanophores between nearly all pterygiophores on the segmented-ray portion of the dorsal fin, a pigmented hypural border, smaller nuchal cirri, and a single orbital cirrus.

Those larvae of *M. zonogaster* that lack dorsal-fin spines resemble the triplefin blenny, *Lepidoneustes corallicola* (Tripterygiidae). They can be distinguished from one another by the relative distance between the snout and the origin of the soft portion of the dorsal fin; this distance is 68–71% of SL in *M. zonogaster* and 60–63% in *L. corallicola*.

## DISCUSSION

Even though the coverage here is limited both in number of species and stages of development examined, three larval types can be recognized according to their shapes, which coincide with traditional labrisomid classification. For example, a typical feature is the preanal distance, which reaches 38–46% in species of *Malacotenus* and *Labrisomus* (Labrisomini), 47–53% in *Starksia* (Starksini), and 33% in *Dialommus* (Mnierpini).

The larvae of *Starksia galapagensis* are morphologically different from those of other labrisomids, an observation that would be consistent with excluding the tribe Starksini from the family Labrisomidae. Based on molecular evidence, the tribe has been considered to be more closely related to Clinidae (Stepien et al., 1993) or Chaenopsidae (Stepien et al., 1997). The presence of a large and elongated ventral melanophore at the basipterygium in *S. galapagensis*, a striking feature of larval chaenopsids (Brogan, 1992), suggests a close relationship with the family Chaenopsidae.

The larvae of *Dialommus fuscus* differ from others in this study in having a more elongate body with a short preanal length (33%), a high number of vertebrae (43), pigmented hypural plate margins, a high number of spines in the dorsal fin (24–27), and a high number of rays in the anal fin (26–28). More comparisons are not possible because the available larvae of this species were few and the size range was narrow.

The species of *Labrisomus* and *Malacotenus* show specific arrays of preopercular spines and me-

lanophores on the upper jaw, dorsal margin of the trunk, hypural plate border, and urostyle. In larger larvae, the relative size of the first spines of the dorsal, and the number of spines included in the second lobe of the dorsal fin are helpful in identification. There are no characters that define *Labrisomus* and *Malacotenus* as early larvae. However, in larger specimens, an adult feature develops: the posterior lobe of the dorsal fin includes one spine in *Labrisomus* and two spines in *Malacotenus*.

Watson (1996) described larvae of *L. multiporosus* in the size range from 5.5–12.3 mm from the California Current Region, which differ in some aspects with those from the Galápagos. These larvae develop several relatively large melanophores around the gut early in their development, whereas larvae from the Galápagos do not have them in the same size range. Some can be seen after 14.5 mm, but this seems to be more a juvenile feature. Furthermore, at the same stage of development, the larvae of *L. multiporosus* from the Galápagos have fewer preopercular spines than their counterparts from the California Current Region. It remains to be determined whether these differences are due to variation within the same species, which has an extended geographic range in the Eastern Pacific, or whether a separate species is present in the Galápagos.

Brogan (1992) described larvae of two species of *Labrisomus* (not identified) from the Gulf of California, with one to three large ventral melanophores ventrally on the trunk and no preopercular spines. Watson (1996) reports the same for *L. xanti*. A generalized pattern for blennioids is the presence of a continuous series of melanophores associated with the bases of the anal fin elements (Cavalluzzi, 1997), as it occurs in the two species from the Galápagos illustrated in this study. Then, the pigment pattern shared by the larvae of the three species described by Brogan (1992) and Watson (1996) would represent a derived condition suggesting a closer relationship among them.

Brogan (1992) described the larvae of two species of *Malacotenus* and found that one of them, *M. hubbsi*, never develops preopercular spines. Because this character is generalized in *Malacotenus* (and *Labrisomus*), its absence suggests a closer relationship between *M. hubbsi* and *M. zonogaster*. The knowledge of the larvae of *Malacotenus* and *Labrisomus* is still limited. For each of these two genera, there are about nine species in the eastern Pacific and nine in the western Atlantic. With the larvae of only five species of each genus known so far, any generalization about relationships based on ontogenetic characters is still speculative.

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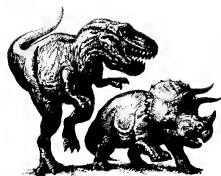
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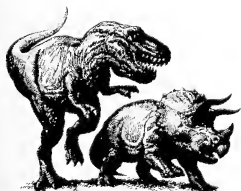
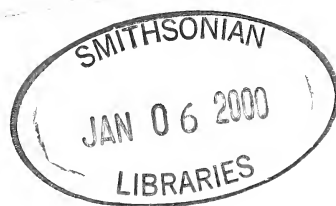
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# CONTRIBUTIONS IN SCIENCE

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UPPER PALEOCENE TO LOWER EOCENE  
("MEGANOS STAGE") MARINE MEGAFOSSILS IN  
THE UPPERMOST SANTA SUSANA FORMATION,  
SIMI VALLEY, SOUTHERN CALIFORNIA

RICHARD L. SQUIRES



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# UPPER PALEOCENE TO LOWER EOCENE ("MEGANOS STAGE") MARINE MEGAFOSSILS IN THE UPPERMOST SANTA SUSANA FORMATION, SIMI VALLEY, SOUTHERN CALIFORNIA

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RICHARD L. SQUIRES<sup>1</sup>

**ABSTRACT.** Uppermost Paleocene to lowermost Eocene ("Meganos Stage") marine rocks are rare on the Pacific coast of North America, and the upper 100 m of the Santa Susana Formation in Simi Valley represents the only known "Meganos Stage" rocks in southern California. This report concerns the first detailed study of mega-invertebrate fossils in this part of the formation. The fossils are in thin lenses that formed as storm-lag accumulations in a relatively shallow, offshore environment. Thirty localities yielded a total of 38 megafossil taxa identifiable to species or subspecies. These include one isidid octocoral, one solitary coral, two colonial corals, 17 gastropods, 14 bivalves, two crabs, and one spatangoid echinoid. A new species of solitary coral, *?Antillophyllia californica* new species, is described and named. A possible new species of the colonial coral *Astrocoenia* is described. *Turritella andersoni susanae* is locally abundant and one of the most diagnostic species of the "Meganos Stage" in the Simi Valley area.

Most of the studied megafauna is known from elsewhere in Pacific coast Eocene strata, primarily in California. The molluscan-stage ranges of approximately one third of the studied mega-invertebrates are extended downward to the "Meganos Stage," based on their presence in the upper 100 m of the Santa Susana Formation. The molluscan-stage ranges of the gastropod *Ringicula* (*R.*) *pinguis*, the bivalve *Saulella undulifera*, and the crab *Cyclocorystes aldersoni* are extended upward from the Paleocene "Martinez Stage" to the "Meganos Stage." In addition, a few of the mega-invertebrates have their geographic ranges extended. The isidid octocoral *?Mopsea* sp., aff. *M. costata* is the first record of an isidid from Paleogene rocks on the Pacific coast of North America. The studied megafauna is indicative of warm-water conditions, and some of the taxa are conspecific with or closely allied to Old World Tethyan mollusks.

## INTRODUCTION

Since the early 1900s, paleontologists have collected marine megafossils from the Santa Susana Formation in the Simi Valley area (Fig. 1), Ventura County, southern California. These fossils, which are predominantly mollusks, have been studied by Waring (1917), Nelson (1925), Fantozzi (1955), and Zinsmeister (1983a, 1983b), but their studies dealt only with "Martinez Stage" rocks of late Paleocene age in the lower part of the formation on the south side of Simi Valley. Although various workers have found a few mollusks in the upper 100 m of the Santa Susana Formation, to date there has not been a comprehensive study of these fossils. Poor exposures, absence of fossils at many locales, and generally poor preservation have discouraged such study, and prior to this study no one had ever "walked out" the stratigraphic interval throughout the Simi Valley area. In addition, outcrops of the upper 100 m of the Santa Susana Formation have the same color and general appearance of essen-

tially unfossiliferous outcrops stratigraphically lower in the Santa Susana Formation. Many previous workers seemed to have assumed that the upper 100 m are not particularly fossiliferous. Locally, however, megafossils are abundant there, and their preservation can be good. The purpose of this present study is to document the taxonomic composition of the megafossil content in these upper 100 m. This information will help greatly in refining the molluscan stage ranges of these taxa because the upper 100 m of this formation correlate to the "Meganos Stage" of latest Paleocene to earliest Eocene age. Rocks deposited on the Pacific coast of North America during this time interval are relatively rare, and those in the study area represent the only known "Meganos Stage" rocks in southern California.

The molluscan stage terminology used in this report includes the upper Paleocene "Martinez Stage," the uppermost Paleocene to lowermost Eocene "Meganos Stage," the middle lower "Capay Stage," the upper lower to lower middle "Domenigine Stage," the lower middle "Transition Stage," and the middle middle Eocene to upper Eocene "Tehjon Stage." The stage names are in quotes because they are informal terms and in essence equivalent to formation names. Clark and Vokes (1936) gave

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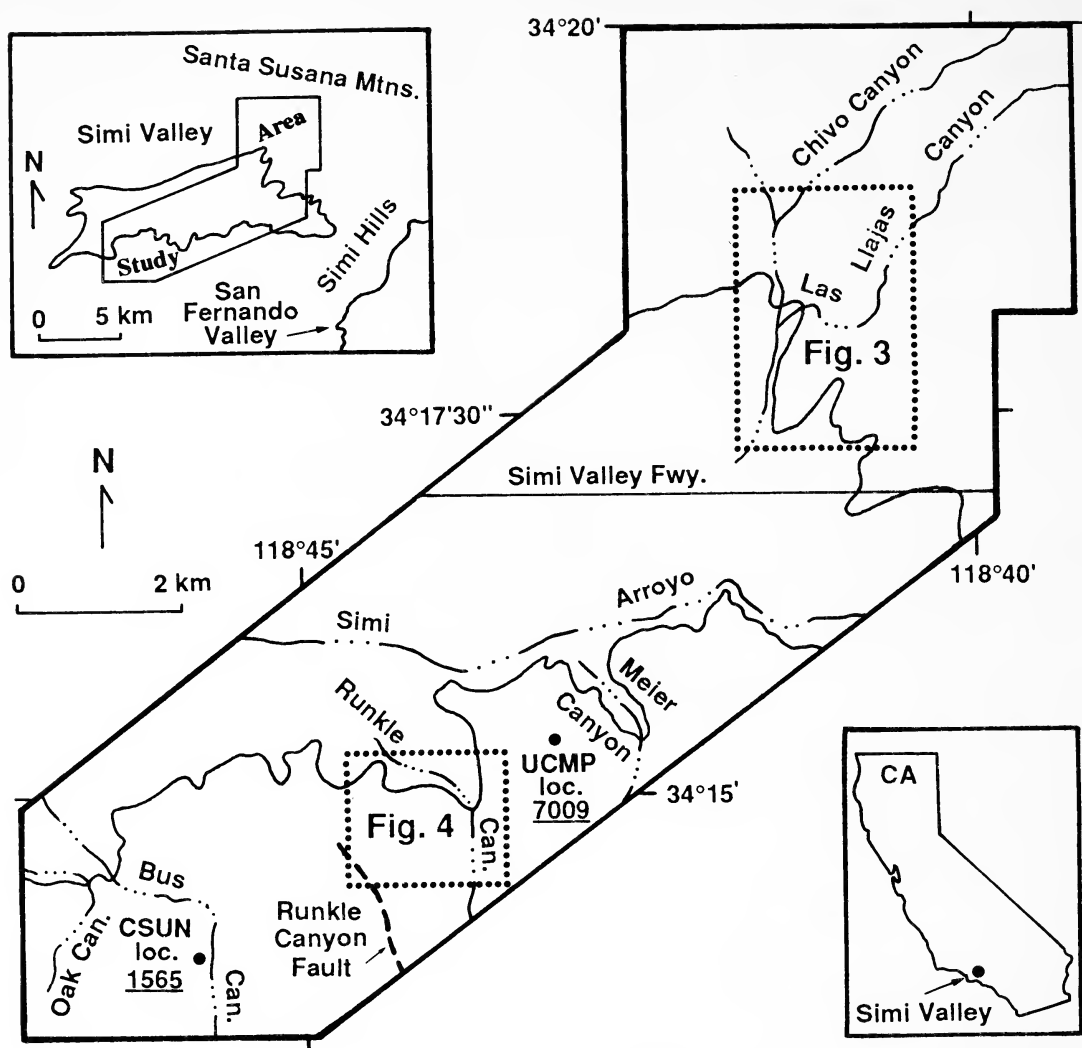


Figure 1. Index map of Simi Valley, also showing areas used for Figures 3 and 4.

a historical overview of these stage names. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used here. Saul (1983) and Squires (1984, 1987, 1988a) regarded the modified "Capay Stage" of Givens (1974) as middle lower Eocene.

### STRATIGRAPHY

The upper 100 m of the approximately 1000-m-thick Santa Susana Formation in the Simi Valley area consists mostly of gray, very fine-grained sandstone, with some gray muddy to sandy siltstone. Locally, there are concentrations of fossil-shell hash, and rocks surrounding these localized concentrations are barren of megafossils. The lower part of the upper 100 m of the Santa Susana Formation has a gradational lithology from the underlying gray mudstone and siltstone. The Santa Su-

sana Formation is disconformably overlain by basal conglomerate of the Lajas Formation (Fig. 2), and the contact is an uneven erosion surface with as much as 1 m of relief. Thin beds of laminated sandstone alternating with thin beds of bioturbated sandstone containing vertical *Ophiomorpha* burrows are present at the top of the Santa Susana Formation at two places on the north side of the valley. One location is at CSUN locality 968, and the other location is just north of the Marr Ranch (Fig. 3) in the northeast corner of section 31, T3N, R17W, where the type section of the overlying Lajas Formation is located (see Squires, 1981:fig. 3) (Fig. 3).

Sedimentary rocks in the upper 100 m of the Santa Susana Formation are not resistant and are usually poorly exposed or covered. The best exposures are on the north side of Simi Valley, where 19 fossil-

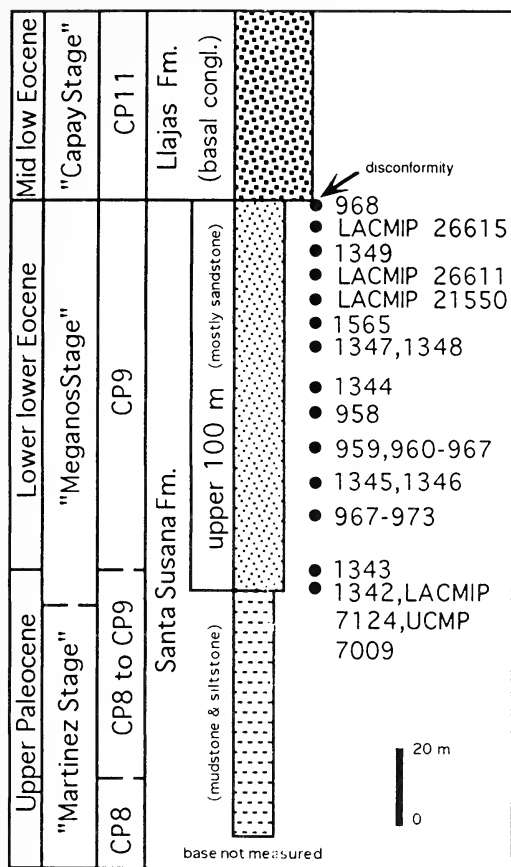


Figure 2. Stratigraphic column of the upper 100 m of the Santa Susana Formation (and of the immediately underlying and overlying strata), showing subseries, provincial molluscan stages, calcareous nannofossil biozones (CP Zones), and stratigraphic position of each of the megafossil-collecting localities. Age of the lower part of the Lajas Formation from Squires (1984).

collecting localities have been found (Fig. 3). CSUN localities 962 through 967 are approximately aligned along the same strike and form a series of localities that parallels the top of the Santa Susana Formation. CSUN localities 969 through 973 are similarly aligned. Four localities (CSUN 968, LACMIP 21550, LACMIP 26611, and LACMIP 26615) are near the top of the formation. At nearly all of the localities on the north side of Simi Valley, fossils are concentrated in lenses about 20 cm thick and several meters in lateral extent. The tops and bottoms of the lenses are indistinct. The bivalves in the lenses are almost always single valves and usually broken, and many of the associated gastropods consist of fragments. Although the fossils are mostly broken, none shows any obvious signs of abrasion. Specimens of *Turritella andersoni susanae* Merriam, 1941 are plentiful and dominate the otherwise usually meager megafauna. At CSUN local-

ity 959, there is a thin lens containing abundant *Turritella uvasana infera* Merriam, 1941 and the lens is traceable laterally for about 6 m. This locality is now under home sites.

On the south side of Simi Valley, 11 fossil-collecting localities have been found in the upper 100 m of the Santa Susana Formation (Figs. 1, 4). An isolated locality (CSUN 1565) is in Bus Canyon, and another isolated locality (UCMP loc. 7009) is near Meier Canyon (Fig. 1); the other localities are in two groups, with six localities found mostly near the top of the Santa Susana Formation in the Runkle Canyon area and three localities just east of the Runkle Canyon fault (Fig. 4). At most of these localities on the south side of Simi Valley, the fossils are similar to those on the north side of the valley, and there are concentrations of unabraded fossil-shell hash in thin lenses whose tops and bottoms are indistinct. Abundant weathered-out specimens of the solitary coral *Antillophyllia californica* new species, abundant tips (apices) of turritellas, and commonly occurring mostly right valves of the bivalve *Pycnodonte* (*Phygraea*) sp., aff. *P. (P.) pacifica* Squires and Demetron, 1990 were found in float at CSUN locality 1343.

The relative stratigraphic position of each megafossil locality in the upper 100 m of the Santa Susana Formation, on both the north and south side of Simi Valley, is shown in Fig. 2.

## DEPOSITIONAL ENVIRONMENT

Parker (1983) did the most current and detailed study of the depositional environment of the Santa Susana Formation and reported that the vertical sequence of the Simi Conglomerate, Las Virgenes Sandstone, and Santa Susana Formation represents a transition from nonmarine to deep-marine facies. The distribution of these facies is, in part, defined by the Runkle Canyon-Burro Flats fault zone in the central part of the south side of Simi Valley. Parker (1983) referred to strata west of this fault zone as the "western facies," and these include, from base to top, braided river, meandering stream, near-shore, transition zone, offshore to shelf, and slope deposits. He referred to strata east of this fault zone as the "eastern facies," and these consist mostly of slope and inner-fan deposits. The fault zone juxtaposes coeval nonmarine and deep-marine rocks and accounts for the fact that nonmarine to nearshore Las Virgenes Sandstone, for example, is present only west of the fault (Fig. 5).

Parker (1983) reported that although the Santa Susana Formation was mostly deposited in deep water, the sedimentology of the upper 100 m of the formation throughout the Simi Valley area reflects uplift to shelf depths prior to deposition of the non-marine basal part of the Lajas Formation. New sedimentologic information obtained during this present study shows that the shallowing event Parker (1983) recognized produced, toward the top of the Santa Susana Formation, sediments deposited

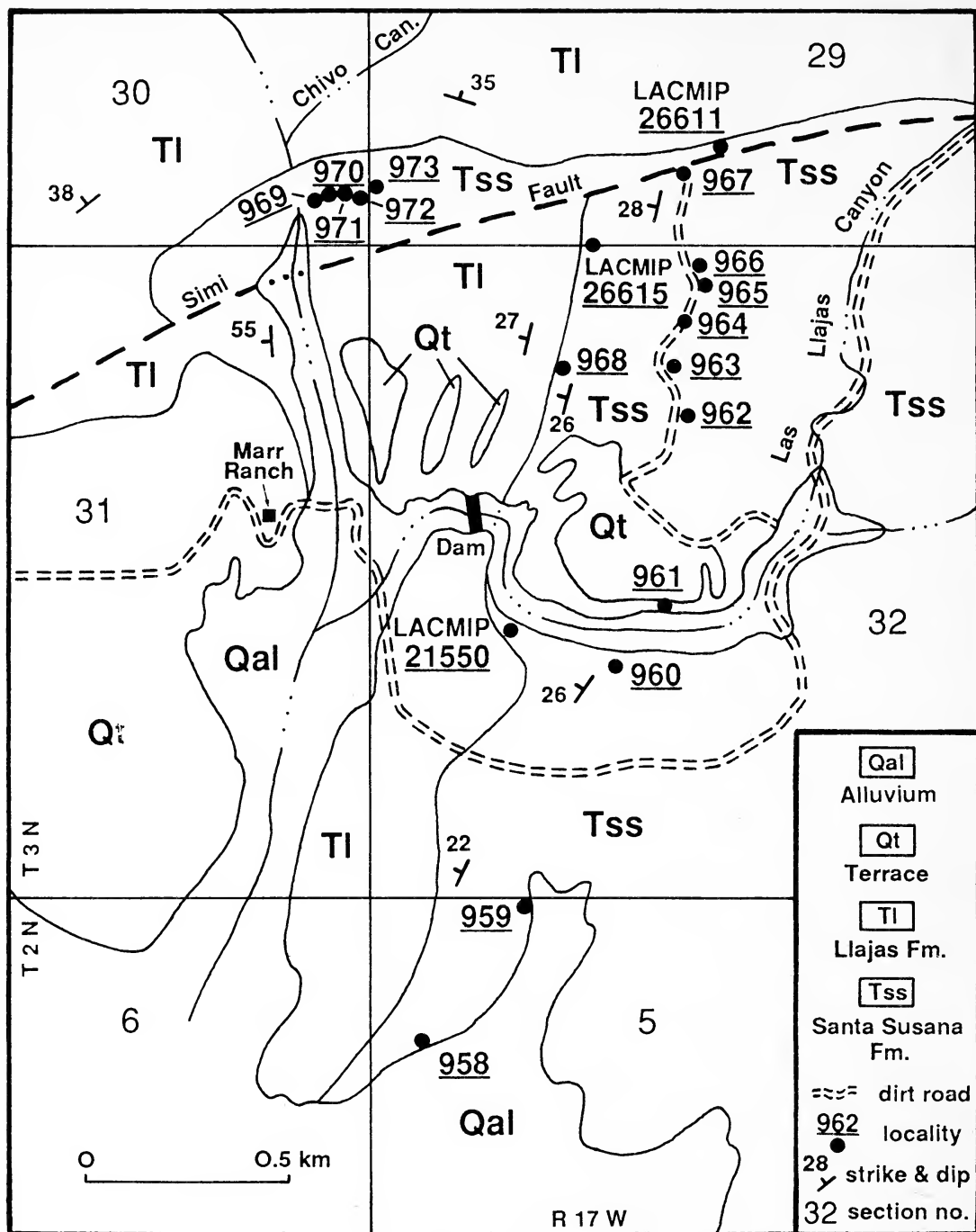


Figure 3. Geologic map showing location of megafossil localities (CSUN localities unless otherwise noted) on the north side of Simi Valley. Base map is U.S. Geological Survey, 7.5-minute, Santa Susana quadrangle, 1951 (photorevised 1969), Ventura County, southern California. Geology from Squires (1983b).

in progressively more shallow water. Beds of alternating laminated sandstone and bioturbated sandstone (e.g., at CSUN loc. 968) were found at the top of the formation, and this alternation of lithologies, which is also present in the shallowest marine

part of the overlying Lajas Formation, is characteristic of modern and ancient shoreface to upper offshore environments (Squires, 1981).

Heitman (1983), on the basis of benthic foraminiferal assemblages, also reported that the upper-

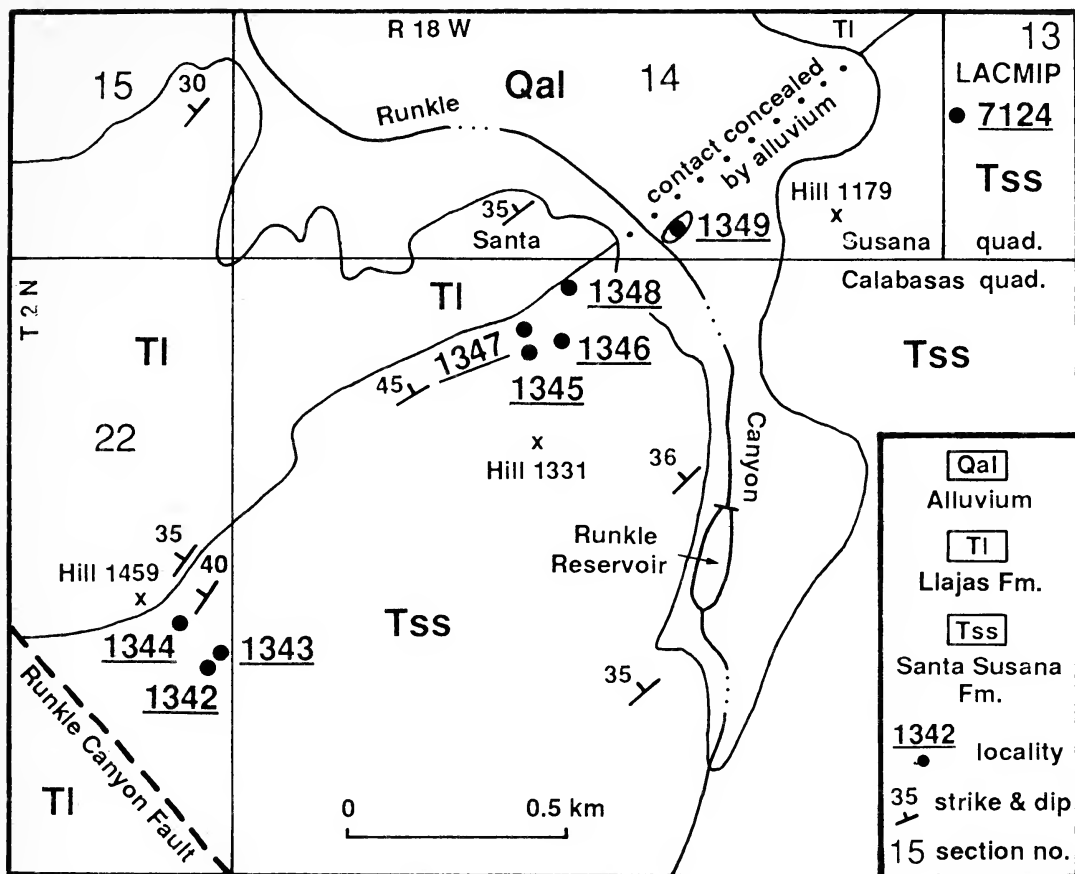


Figure 4. Geologic map showing location of megafossil localities (CSUN localities unless otherwise noted) on the south side of Simi Valley. Base maps are U.S. Geological Survey, 7.5-minute Calababas quadrangle, 1952 (photorevised 1967); and Santa Susana quadrangle, 1951 (photorevised 1969), Ventura County, southern California. Geology from Squires (1983b).

most part of the Santa Susana Formation represents a shoaling event associated with basin filling that deposited a silty sandstone just above the shelf-slope break. Filewicz and Hill (1983), on the basis of calcareous nannofossil datums and sediment-accumulation rates, reported that silty sandstones in the upper Santa Susana Formation (20 m below the base of the overlying Llajas Formation) were deposited just above the shelf-slope break.

Squires (1991a) and Saul and Squires (1997) interpreted that megafossils in the upper 100 m of the Santa Susana Formation on the north side of Simi Valley are shallow-marine forms deposited as storm-lag accumulations in a relatively shallow, off-shore environment. This more detailed present study further supports these earlier interpretations.

Squires (1990) suggested that the fossiliferous lens at CSUN locality 1342, in the upper 100 m of the formation on the south side of Simi Valley, represents a storm deposit in a middle to outer shelf environment, and that the distance of postmortem

transport of the shallow-marine mollusks was not great.

At all of the fossil localities mentioned in this present report, fossils occur as concentrations in small lenses of sandstone surrounded by siltstone usually barren of megafossils. The tops and bottoms of these lenses are indistinct, and Squires (1981) reported similar lenses in the overlying Llajas Formation, where the shallow-marine facies grades into outer shelf to slope facies. In this transitional paleoenvironment, the contacts of the fossiliferous lenses were rendered indistinct by the activities of burrowing organisms shortly after deposition of the sediments, undoubtedly just like those in the upper 100 m of the Santa Susana Formation.

It is readily apparent that the fossils in the upper 100 m of the Santa Susana Formation have undergone some postmortem transport, based on their broken condition and localized concentrations. The distance of this transport was not great based on the absence of any evidence of significant abrasion.

Waring 1917	Clark 1918	Clark 1921, Kew 1924		Nelson 1925		Clark 1926	Parker, 1983, Saul, 1983, & This Report		Mollusk "Stages"
		W	E	W	E		W	E	
Tejon	Tejon	Meganos Fm.		Domengine Fm.		Domen- gine Fm.	Llajas Fm.		"Domen- gine"
Martinez	Meganos								Santa Susana Fm.
	Martinez	Martinez Fm.	Martinez marine member	Santa Susana Shales	Santa Susana Fm.	"Martinez"			
							Las Virgenes Sandstone	Las Virgenes Sandstone	
							Simi Conglomerate		Simi Conglom.
Chico		Chico Fm		Chico			Chatsworth Fm.		Campanian

Figure 5. Comparative concepts of lower Paleogene stratigraphic units in the Simi Valley area. The letters "W" and "E" refer to west and east of the Runkle Canyon fault (shown in Fig. 1).

In addition, the fossils are ecologically similar. Burial was rapid because there is a scarcity of epibionts. Most of the fossils represent storm-lag accumulations in a middle-to-outer shelf environment, where fine sands accumulated in close proximity to siltstone. Bioturbation must have obliterated any initially sharp contacts that would have been formed along the bottoms of the fossiliferous lenses.

CSUN locality 1343, however, is unusual because the abundant specimens of the solitary coral? *Antillophyllia californica* new species found there constitute a growth series. These corals must have lived in close proximity to where they were buried and experienced much less distance of postmortem transport than the other associated fossils.

In summary, the overall fine-grained rock type, the assemblages of benthic foraminifera, the localized concentrations of unabraded shallow-marine megafossils, and alternating rock types at the top of the formation indicate that the bulk of the upper 100 m of the Santa Susana Formation in the Simi Valley area was deposited in a relatively shallow, offshore environment (middle-to-outer shelf depths). Storm surges transported the megafossils,

but the distance of transport was not far. Beds at the top of the formation were deposited in a shallower environment (shoreface).

### MEGAFAUNA

A total of 560 megafossil specimens were collected from 30 localities. Preservation ranges from poor to good, and many of the fossils are badly weathered or in hard concretions. Thirty-eight megafossil taxa were identified to genus and species/subspecies. These include one octocoral, one solitary coral, two colonial corals, 17 gastropods, 14 bivalves, two crabs, and one spatangoid echinoid. Other taxa too poorly preserved for generic identification include one solitary coral, one scaphopod, three gastropods (a naticid, a cymatiid, and a turrid), and four bivalves (a pinnid, a lucinid, a pitarinid, and a solenid). The poorly preserved solitary coral was mentioned by Durham (1943:199, pl. 32, fig. 22), who reported two specimens from UCMP locality 7000 (exact location not known). Only the exterior morphology of this coral is known. It is alate and somewhat flabelliform, but better preserved speci-



mens and studies of their interiors are needed to determine the familial or generic assignments. No new specimens were found during this present study. Durham (1943) identified the coral as *Flabellum stantoni* Durham, 1943, a name that he also gave to specimens that Vaughan (1900:67–68, pl. 4, figs. 5, 6) had misidentified as *Flabellum remondianum* Gabb (1864:207, pl. 26, fig. 199). Vaughan's specimens were probably collected from "Martinez Stage" rocks near Benicia in northern California. Durham (1943) was probably correct in giving the name *F. stantoni* to Vaughan's specimens from Benicia, but whether or not this name is appropriate for the two poorly known coral specimens from the upper part of the Santa Susana Formation is an open question. These two coral specimens are not the same as the new species of solitary coral described here.

Although early workers (Clark, 1921:table 1; 1926:114–116; Kew, 1924:25; Nelson, 1925:pl. 61, and foldout between pages 402 and 403) gave faunal lists for so-called "Meganos" age-strata in the Simi Valley area, there are serious problems in trying to use these lists because (1) detailed locality information is lacking, and (2) previously used formation names (e.g., Meganos and Domengine) are not exact equivalents of the upper 100 m of the Santa Susana Formation (Fig. 5). In addition, because these species names have only been listed, without illustration or reference to catalogued museum specimens, there is no way to verify the identifications.

Three previously named megafossil species have their type localities in the upper 100 m of the Santa Susana Formation in the Simi Valley area. They are the gastropod *Corsania* (*Januncia*) *susana* Saul and Squires, 1997 and the bivalves *Arca* (*Arca*) *filewicz* Squires, 1991a and *Netastoma* *squiresi* Kennedy, 1993. In addition, the following two species could probably be added to this list. Although the description of the type locality of the bivalve *Venericardia* (*Pacificor*) *susanaensis* Verastegui, 1953, is somewhat vague, this locality is most likely in the upper 100 m of the formation. As will be discussed under "Age," the type locality of the gastropod *Turritella* *andersoni susanae* was reported (Merriam, 1941) from the basal part of the Lajas Formation, but the actual stratigraphic position of this locality is probably in the upper 100 of the Santa Susana Formation.

## AGE

The upper 100 m of the Santa Susana Formation is latest Paleocene through earliest Eocene ("Meganos Stage") in age, based on calcareous nannofossils, mollusks, sporomorphs, and magnetostratigraphy. Assignments to the calcareous nannofossil biozones and provincial Pacific coast of North America lower Paleogene molluscan stages are shown in Figure 2.

The term "Meganos Stage" stems from Clark

(1918), and the type section of this stage is in the Deer Valley area north of Mount Diablo, Contra Costa County, northern California, where Clark (1918, 1921) subdivided the Meganos Formation into five major lithologic members. Starting at the base, he designated the members as Divisions A, B, C, D, and E. The molluscan fauna from this series, which was studied in detail by Clark and Woodford (1927), comes from Division D. Almgren et al. (1988: fig. 4) assigned Division D strata of the Meganos Formation to the CP9 Zone (lowest Eocene) of the standard calcareous nannofossil zonation. Most of the "Meganos Stage" correlates with the CP9 Zone, but the lower part of the stage correlates to the CP8 Zone (uppermost Paleocene). The age of the "Meganos Stage," therefore, corresponds to the latest Paleocene to earliest Eocene (Saul, 1983; Squires, 1988a, 1997). Modern workers now refer to the strata of Division D of the Meganos Formation as the Margaret Hamilton Sand (Edmondson, 1984).

Filewicz and Hill (1983:fig. 5) reported calcareous nannofossils diagnostic of the lower Eocene *Discoaster diastypus* (CP9) Zone of the standard calcareous nannofossil zonation from siltstones immediately below the upper 100 m of the Santa Susana Formation on the north side of Simi Valley. The upper 100 m on the north side of Simi Valley are barren of any calcareous nannofossils (Filewicz and Hill, 1983), as well as any planktonic foraminifera (Heitman, 1983). Filewicz and Hill (1983) did not study the upper 100 m of this formation on the south side of Simi Valley. In the course of this present study, I collected 12 microfossil samples from the upper 100 m of the Santa Susana Formation on the south side of Simi Valley. The calcareous nannofossils are rare, poorly preserved, and, as with those from the north side of Simi Valley, only present near the bottom of the 100-m-thick interval, where the siltstone content is higher. Only two samples, those from CSUN localities 1342 and 1343, yielded any calcareous nannofossil data pertinent to geologic age determination. Both samples yielded a late Paleocene age, probably equivalent to the *Discoaster multiradiatus* (CP8) Zone of the standard calcareous nannofossil zonation (M. V. Filewicz, personal communication). No planktonic foraminifera were recovered from any of the 12 microfossil samples (H. L. Heitman, personal communication).

As mentioned earlier, the stratigraphic nomenclature of the upper part of the Santa Susana Formation in the Simi Valley area has been confusingly inconsistent. Similarly, the concept of the "Meganos Stage" in this area has lacked biostratigraphic precision. Saul's (1983) study of the turritellas and venericardias in the various Paleogene formations in the Simi Valley area helped greatly in clarifying the proper assignment of provincial molluscan stages to these formations. She reported that *Turritella andersoni susanae*, *T. uvasana infera*, *T. meganosensis* Merriam, 1941 and *Venericardia* (*Pacificor*)

*hornii susanaensis* are important megafaunal components of the upper 100 m of the Santa Susana Formation and enable correlation of these rocks to the northern California-based concept of the "Meganos Stage." *Turritella meganosensis*, furthermore, is also found at the type section (Margaret Hamilton Sand) of this stage in northern California. *Turritella andersoni susanae* is locally plentiful in the upper 100 m of the formation and is probably confined to the "Meganos Stage." A single specimen, which is the holotype of this gastropod, however, was reported from the basal part ("Capay Stage") of the overlying Llajas Formation on the north side of Simi Valley. It seems highly probable that the stratigraphic position of this locality is in error, and that the holotype is actually from the upper part of the Santa Susana Formation. *Turritella wasana inifera* is found in both the "Meganos Stage" and in the overlying "Capay Stage."

The only well-described (Clark and Woodford, 1927) megafauna of "Meganos" age is that of the Margaret Hamilton Sand at the type section of the "Meganos Stage" in Deer Valley, Contra Costa County, although strata ("Meganos Formation") of this age are also known from south of Round Valley on the Middle Fork of Eel River in Mendocino County, northern California. Other than *Turritella meganosensis*, species found in both the Margaret Hamilton Sand and the upper 100 m of the Santa Susana Formation are *Calyptrea diegoana* (Conrad, 1855) [= *Calyptrea* (*Galerus*) *calabasaensis* Nelson, 1925], *Brachysphingus mammillatus* Clark and Woodford, 1927, *Nuculana* (*Saccella*) *gabbii* (Gabb, 1869) [= *Leda gabbii* (Gabb, 1869)], and *Schizaster diabloensis* Kew, 1920. *Gemmula* sp., aff. *G. diabloensis* Clark and Woodford, 1927 from the upper 100 m of the Santa Susana Formation has close affinity to *G. diabloensis* from the Margaret Hamilton Sand.

Frederickson (1983) reported early Eocene sporomorphs from the upper 100 m of the Santa Susana Formation on the north side of Simi Valley. The presence of these early Eocene sporomorphs is best documented near the top of the upper 100 m of the formation.

Bottjer et al. (1991) reported that, in terms of magnetostratigraphy, the lowermost part of the upper 100 m of the Santa Susana Formation on the north side of Simi Valley is correlative to Chron C24R, which is equivalent to an interval that encompasses the Paleocene-Eocene boundary (Berggren et al., 1995).

Simi Valley is part of the Western Transverse Ranges tectonic block, which has been rotated by Neogene displacements. Before rotation, this block lay adjacent to San Diego and Anaheim in southern California. During the Miocene, the block was rotated clockwise. Its northern end (which included Simi Valley) acted as the pivotal area and remained essentially in place (Atwater, 1998). The Eocene paleolatitude of the Simi Valley area, therefore, was probably not much different than it is today. De-

position of the upper 100 m of the Santa Susana Formation was also coincident with an overall global sea-level rise (supercycle TA2 of Haq et al., 1987).

The latest Paleocene to earliest Eocene age ("Meganos Stage") of the upper 100 m of the Santa Susana Formation corresponds to an absolute age of 53 to 55 Ma (Berggren et al., 1995). Based on their presence in the upper 100 m of the Santa Susana Formation, the molluscan-stage ranges of nine species can be extended downward to the "Meganos Stage." These species are: *Velates perversus* (Gmelin, 1791), *Pachycrommium clarki* (Stewart, 1927), *Architectonica* (A.) *llajasensis* Sutherland, 1966, *Cylichnina tantilla* (Anderson and Hanna, 1925), *Spondylus carlosensis* Anderson, 1905, *Macoma rosa* Hanna, 1927, *Pitar wasana coquillensis* Turner, 1938, *Corbula* (*Caryocorbula*) *dickersoni* Weaver and Palmer, 1922, and *Corbula* (*Caryocorbula*) *parilis* Gabb, 1864. Similarly, the presence of *Astrocoenia* sp. and *Pycnodonte* (*Phygraea*) sp., aff. *Pycnodonte* (*Phygraea*) *pacifica* Squires and Demetron, 1990, in the upper 100 m of the formation represents the earliest occurrences of *Astrocoenia* and *Phygraea* in the Paleogene rock record of the Pacific coast of North America.

The molluscan-stage ranges of three species in the study area can be extended upward from the Paleocene "Martinez Stage" to the "Meganos Stage." These species are: *Ringicula* (R.) *pinguis* (Gabb, 1864), *Saulella undulifera* (Gabb, 1869), and *Cyclocorystes aldersoni* Squires, 1980.

## PALEOCLIMATE AND PALEOBIOGEOGRAPHY

As reviewed by Squires (1987), the world climate was relatively warm and equable during most of the Paleocene through early middle Eocene time, and a worldwide late Paleocene warming trend culminated in a period of peak warming during the early Eocene. Also reviewed by Squires (1998), during late Paleocene to early middle Eocene time, humid tropical climatic conditions were prevalent in coastal-lowland areas from Baja California, Mexico, to southwestern Washington.

Megafossils in the upper 100 m of the Santa Susana Formation strongly support the presence of tropical waters. The hermatypic colonial coral genus *Astrocoenia* lives today only in the West Indies and is a reef dweller in shallow, tropical seas (Durham, 1942). Although Paleocene and early Eocene reef corals seldom formed true reefs, by middle through late Eocene times they started to build reefs, and *Astrocoenia* was one of these reef builders in the Caribbean region (Budd et al., 1992). The extinct gastropod genus *Corsania* is indicative of warm climate (Saul and Squires, 1997), and modern *Campanile* is also indicative of warm waters and very shallow depths (Squires, 1993). The bivalve *Arca* s.s. most frequently inhabits tropical waters today (Keen, 1971; Abbott and Dance,

1982), and the same is true of the bivalves *Spondylus* (see Squires, 1984:table 5) and *Fimbria* (see Nicol, 1950).

The late Paleocene and early Eocene were times of major immigration of Old World Tethyan megainvertebrates into the Pacific coast region of North America via a seaway, most likely through the Central America seaway (Clark and Vokes, 1936; Givens, 1978, Zinsmeister, 1983a; Squires, 1984, 1987). One of the most important of these is the gastropod *Velates perversus*, which dispersed westwardly from Pakistan into California (Squires, 1987; Squires and Demetron, 1992). The new occurrence of this species in the "Meganos"-age upper 100 m of the Santa Susana Formation provides it with a slightly earlier arrival date in California.

Additional mollusk taxa in the upper part of the Santa Susana Formation that have been recognized as Tethyan or of Tethyan affinity (Clark and Vokes, 1936; Squires, 1984; 1987, 1990, 1991a; Givens, 1989) and must have accompanied *Velates perversus* into the waters of the Pacific coast of North America are *Pachycrommium*, *Arca* s.s., and *Fimbria*. Although *Campanile* is also indicative of Old World Tethyan connections, this genus had already arrived onto the Pacific coast region by the late Paleocene ("Martinez Stage") (Squires, 1993).

As will be indicated in the "Systematics" section, some other megafossils found in the upper part of the Santa Susana Formation are strongly suggestive of Old World Tethyan connections. The octocoral ?*Mopsea* sp., aff. *M. costata* Milne-Edwards and Haime, 1850 is remarkably similar to *M. costata* from the lower Eocene London Clay in southern England. The crab *Cyclocorystes aldersoni* Squires, 1980 is most similar to *C. pulchellus* Bell, 1858, also from the lower Eocene London Clay. *Cyclocorystes* is only known from these two species. The gastropod ?*Ancillarina* sp., which might be the only known record of this genus in the Western Hemisphere, is most similar to *A. canalifera* (Lamarck, 1802) from the Paris Basin, France.

SYSTEMATIC MATERIALS AND METHODS

Systematic arrangement of the higher taxa follows that of Bayer (1956) for the octocoral, Wells (1956) for the scleractinians, Vokes (1980) for the bivalves, and Glaessner (1969) for the crabs. The higher classification of gastropods is in a state of flux, and some of the categories used here for suprafamilial names are referred to as superorders and generally correspond to major clade names used by Ponder and Lindberg (1996, 1997).

Synonymies (primarily including only figured specimens), primary type material, molluscan stage range, and geographic distribution data are given for the identifiable species. Terms used to denote specimen abundance are defined as follows (number of specimens in parentheses): rare (1-4), uncommon (5-9), common (10-29), and abundant (30 or more). Abbreviations for catalog and/or locality numbers are:

ANSP: Academy of Natural Sciences, Philadelphia

ANSP CAS: California Academy of Sciences, San Francisco  
ANSP CSUN: California State University, Northridge  
ANSP LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology Section  
ANSP UCMP: University of California, Museum of Paleontology, Berkeley  
ANSP UCR: University of California, Riverside  
ANSP USNM: United States National Museum, Washington, D.C.

The bulk of the collections used in this study are housed at CSUN. New species primary type material and hypotypes of the invertebrates used for illustrations in this report are deposited at LACMIP.

SYSTEMATICS

Phylum Cnidaria Hatschek, 1888

Class Anthozoa Ehrenberg, 1834pqc

Subclass Octocorallia Haeckel, 1866

Order Gorgonacea Lamouroux, 1816

Family Isididae Lamouroux, 1812

Genus *Mopsea* Lamouroux, 1816

TYPE SPECIES. *Isis dichotoma* Linnaeus, 1758, by subsequent designation Milne-Edwards and Haime, 1850; Recent, Antarctica.

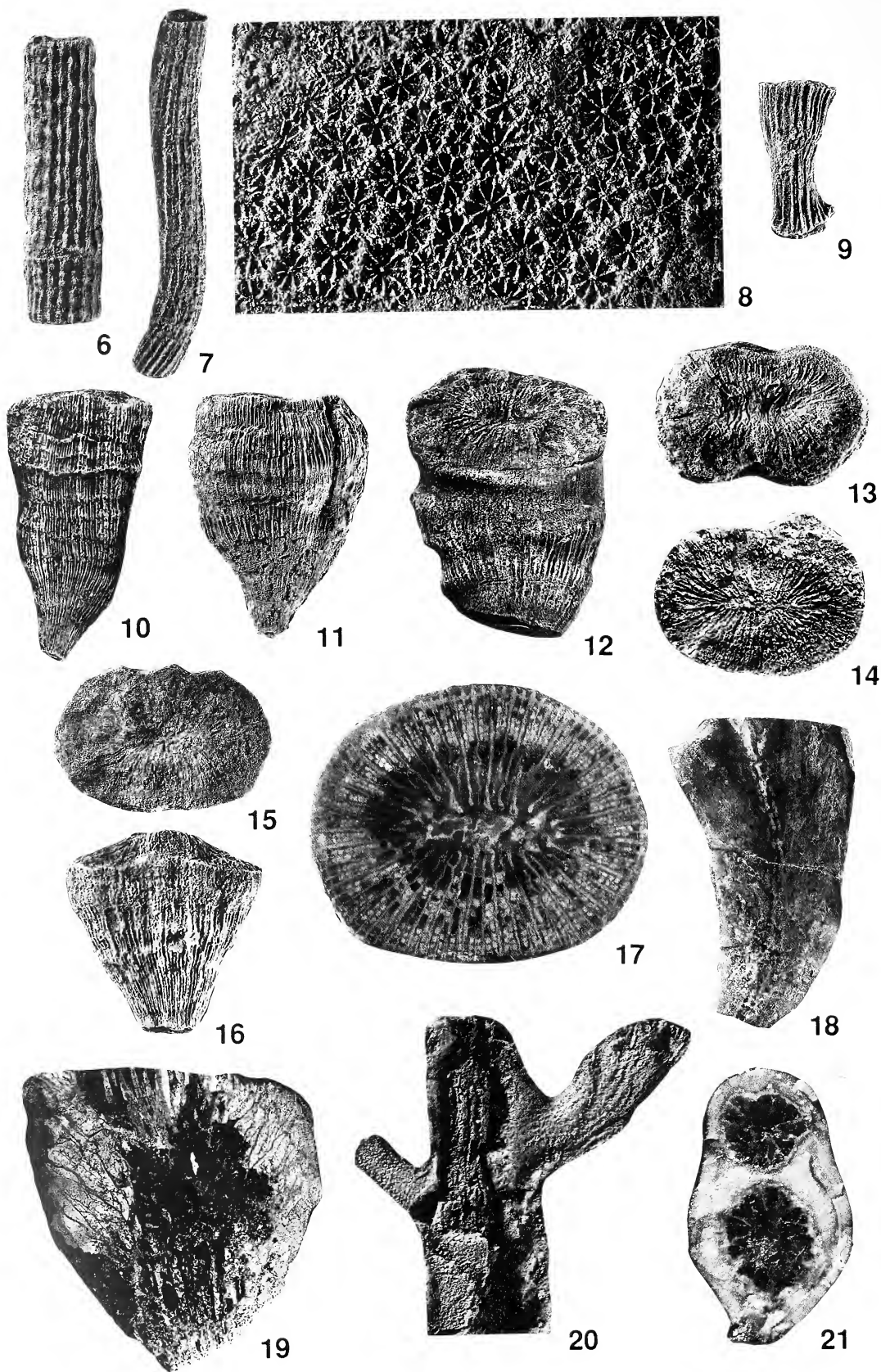
?*Mopsea* sp., aff. *M. costata* Milne-Edwards and Haime, 1850  
Figures 6, 7

LOCAL OCCURRENCE. CSUN loc. 1343.

REMARKS. Twenty-six fragments were collected, and they consist of straight-to-curved, cylindrical calcareous internode axial stems up to 23 mm long. The stems are longitudinally marked by closely spaced ribs that bear small spines.

Few published reports exist describing fossil octocoral remains. The isidid octocorals are probably the most common forms preserved because of extensive calcification of the axis (Kocurko, 1988). Unfortunately, generic determinations of isidid octocorals cannot be reliably made using only calcareous internode-stem material. Soft-part morphology and microscopic spicular material are also needed (Bayer, 1956, and personal communication).

The Santa Susana Formation specimens are remarkably similar to the calcareous axial parts of *Mopsea costata* Milne-Edwards and Haime, 1850, from the lower Eocene London Clay in southern England. The Santa Susana Formation specimens differ from *M. costata* Milne-Edwards and Haime (1850:42, pl. 7, figs. 3, 3a) only by having more elongate spines. To a slightly lesser degree, the Santa Susana Formation specimens also resemble *Mopsea encrinula* (Lamarck, 1815) that lives today in New Caledonian waters. The Santa Susana Formation specimens differ from *M. encrinula*, which



has been illustrated by Bayer and Stefani (1987:65–66, pl. 21, figs. 1–2), by having more closely spaced ribs that bear blunter spines.

The Santa Susana Formation specimens of ?*Mopsea* sp., aff. *M. costata* represent the first record of an isidid octocoral from Paleogene rocks on the Pacific coast of North America. The only other reported octocoral from this region is the parisidid *Parisis batequensis* Squires and Demettrion, 1992, found in the lower Eocene part of the Bateque Formation of Baja California Sur, Mexico.

Subclass Zoantharia Blainville, 1830

Order Scleractinia Bourne, 1900

Family Astrocoeniidae Koby, 1890

Genus *Astrocoenia* Milne-Edwards and Haime, 1848

**TYPE SPECIES.** *Astrea numisma* Defrance, 1826, by monotypy; upper Eocene (lower Bartonian Stage), Gap, southeastern France (Maritime Alps).

*Astrocoenia* sp.

Figure 8

**LOCAL OCCURRENCE.** CSUN loc. 1342.

**REMARKS.** Only a small fragment of a hemispherical colony was found. The fragment, which is weathered and possibly worn, is 40 mm long, 20 mm wide, and approximately 5 mm thick. The corallites are mostly filled with hard matrix, but some of them have been etched by weathering. The corallites are polygonal in shape, and the inside diameter of the calices are up to 1.75 mm. The thecal walls are about 0.25 mm thick, and their upper surfaces are irregular with short protuberances. The calices have two cycles of septa, octamerally arranged in two subequal groups. The first cycle consists of very thin septa that extend to the styliform columella, which appears in the bottom of the calice as a tubercle. The upper margins of these septa are beaded. The septa in the second cycle are very short and rudimentary, consisting of trabecular spines projecting inward from the thecal walls.

The presence of *Astrocoenia* sp. in the upper 100

m of the Santa Susana Formation represents the earliest record of this genus on the Pacific coast of North America and its first record in the “Meganos Stage.” Only two other species of *Astrocoenia* have been reported from this region. One is *Astrocoenia* sp., aff. *A. portoricensis* Vaughan, 1919, from middle lower Eocene (“Capay Stage”) strata in the *Turritella uvasana infera* fauna of the Juncal Formation in the Whitaker Peak area, Ventura County, California. Squires (1987:19, fig. 6) described and illustrated a specimen from the Juncal Formation. *Astrocoenia* sp. from the Santa Susana Formation differs from the Juncal Formation species by having larger corallites, by the presence of secondary septa, and by having eight primary septa. The Juncal Formation species usually has eight primary septa, but rare specimens can have 10 primary septa.

The other species of *Astrocoenia* reported from the Pacific coast of North America fossil record is *A. dilloni* Durham (1942), from lower Eocene “Capay Stage” and possibly “Domengine Stage” strata on the south side of the headwaters of Media Aqua Creek, Kern County, California (Durham, 1942) and from lower Eocene “Capay Stage” strata in the Bateque Formation of Baja California Sur, Mexico (Squires and Demettrion, 1992). *Astrocoenia* sp. differs considerably from *A. dilloni* Durham (1942: 505, pl. 44, fig. 3; Squires and Demettrion, 1992: 17, fig. 26) by having only eight rather than 10 septa and by having much weaker secondary septa.

Lower Tertiary astrocoenids are better represented in the Caribbean Sea region than on the Pacific coast region of North America. Of the various fossil astrocoenids reported by Duncan (1873), Vaughan (1919), Wells (1934, 1945), Frost and Langenheim (1974), and Budd et al. (1992) from the Caribbean region, *Astrocoenia* sp. is most similar to *A. jukesbrownei* Wells, 1945, and *A. incrustans* (Duncan, 1873) [= *A. guantanamoensis* Vaughan, 1919]. These two species are discussed below.

*Astrocoenia jukesbrownei* Wells (1945:3–4, pl. 1, figs. 4, 5; Budd et al., 1992:575, fig. 2.9–2.10), is known from middle Eocene strata in Barbados and upper Eocene strata in Panama. *Astrocoenia* sp. differs from *A. jukesbrownei* by having thinner thecal

←

Figures 6–21. Octocoral, colonial corals, and solitary coral from the upper 100 m of the Santa Susana Formation, Simi Valley. All specimens coated with ammonium chloride, unless otherwise noted. 6, 7. Octocoral? *Mopsea* sp., aff. *M. costata* Milne-Edwards and Haime, 1850, CSUN loc. 1343. 6. Side view,  $\times 3.9$ , LACMIP hypotype 12661. 7. Side view,  $\times 3.3$ , LACMIP hypotype 12662. 8. Colonial coral. *Astrocoenia* sp., dorsal view of corallum,  $\times 4.3$ , LACMIP hypotype 12663, CSUN loc. 1342. 9–19. Solitary coral? *Antillophyllia californica* new species, adult specimens unless otherwise noted, CSUN loc. 1343. 9. Lateral view of juvenile showing basal attachment area,  $\times 2.1$ , LACMIP paratype 12665. 10. Lateral view,  $\times 0.9$ , LACMIP paratype 12666. 11. Lateral view,  $\times 1.1$ , LACMIP paratype 12667. 12. Lateral view,  $\times 1.4$ , LACMIP paratype 12668. 13. Lateral view,  $\times 1.2$ , LACMIP paratype 12669. 14. Lateral view,  $\times 1.5$ , LACMIP paratype 12670. 15, 16. LACMIP holotype 12664,  $\times 1.3$ . 15. Dorsal view. 16. Lateral view. 17. Uncoated, polished section, transverse view through lower fossa area,  $\times 3.9$ , LACMIP paratype 12671. 18. Uncoated, polished section, longitudinal view through columella,  $\times 2$ , LACMIP paratype 12672. 19. Photomicrograph, longitudinal view through columella,  $\times 2$ , LACMIP paratype 12673. 20, 21. Colonial coral. *Archohelia clarki* Vaughan, 1927, CSUN loc. 1348. 20. Lateral view,  $\times 5.2$ , LACMIP hypotype 12674. 21. Dorsal view,  $\times 4$ , LACMIP hypotype 12675.

walls and shallower calices. *Astrocoenia incrustans* (Duncan, 1873:554, pl. 20, fig. 6; Budd et al., 1992:575, fig. 2.6–2.8) is known with certainty from middle Eocene strata in Cuba, St. Bartholomew, and Chiapas, Mexico; upper Eocene strata in Cuba and Antigua; and middle Miocene strata in Panama (Budd et al., 1992). *Astrocoenia* sp. differs from *A. incrustans* by having much weaker secondary septa and no secondary septa that extend to the columella. The relation of *Astrocoenia* sp. to these two species, as well as to other early Tertiary astrocoenids of similar size, growth habit, septal number, and calicular structure, needs to be clarified. More specimens and better preserved material of *Astrocoenia* sp. are needed to fully describe the external and internal features. Only then will it be possible to determine whether this astrocoenid represents a new species.

### Family Faviidae Gregory, 1900

#### Genus *Antillophyllia* Vaughan, 1932

**TYPE SPECIES.** *Antillia lonsdaleia* Duncan, 1864, by original designation; Miocene, Dominican Republic.

#### ?*Antillophyllia californica* new species

Figures 9–19

**DIAGNOSIS.** *Antillophyllia*-like with a shallow fossa, a columella usually trabecular below and sublamellar or nearly indiscernible above, a synaptical corallum wall, and a corallum with prominent girdling bands.

**COMPARISON.** The new species is most similar to ?*Antillophyllia olssoni* Clark and Durham (1946) from upper Eocene strata in Colombia. The similarity between the new species and ?*A. olssoni* Clark and Durham (1946:80, pl. 25, figs. 8, 9) is strong in terms of the large size of the corallum, the prominent costae corresponding to septa, the presence of a ring of synapticalae inside the wall, and thickened inner ends of the septa near the columella. The new species differs from ?*A. olssoni* by having a slightly smaller size, a narrower base to the corallum, a narrower columellar region, and the presence of swollen, girdling bands on the corallum.

The new species is most similar to *Antillophyllia sawkinsi* (Vaughan in Vaughan and Hoffmeister, 1926) from the uppermost Oligocene and lower Miocene La Quinta Formation in Chiapas, Mexico, and lower Miocene strata (apparently the Brasso Formation) in Trinidad (Frost and Langenheim, 1974). The swollen, girdling bands on the corallum of the new species are similar to those reported by Frost and Langenheim (1974) as epithelial bands on specimens of *A. sawkinsi*. The new species differs from *A. sawkinsi* (Vaughan in Vaughan and Hoffmeister, 1926:118, pl. 2, figs. 6, 6a; Wells, 1934:pl. 28, figs. 6, 6a; Vaughan and Wells, 1943:fig. 305, 3a–3b; Frost and Langenheim, 1974:282, 285, pl.

106, figs. 3–8, pl. 108, figs. 1–8) by having a narrower base, an elevated fossa (at least on some specimens), and a columella that is trabecular below and sublamellar above. Frost and Langenheim (1974) reported that *A. sawkinsi* is closely related to ?*Antillophyllia olssoni* Clark and Durham. Frost and Langenheim (1974) did not questionably assign Clark and Durham's species to *Antillophyllia*, although Clark and Durham (1946) originally did question the generic assignment.

?*Antillophyllia californica* new species superficially resembles ?*Trochocyathus striatus* (Gabb, 1864) reported (Squires, 1984) from the middle Eocene ("Domengine Stage") part of the Lajas Formation on the north side of Simi Valley. The new species differs from ?*T. striatus* (Gabb, 1864:207–208, pl. 26, fig. 195; Squires, 1984:14, fig. 5c) by having a larger size, a more compressed corallum, much shallower fossa, many more septa, narrower costae, a more horizontally elongate columella, and girdling bands on the corallum. In addition, the new species has no confirmed presence of pali, whereas ?*T. striatus* has pali.

**DESCRIPTION.** Solitary, trochoid (basal angle approximately 40 degrees) to subtrubinate, up to 50 cm in height and 2.5 cm in diameter. A few specimens moderately curved (ceratoid) and enlarging rapidly. Rare specimens bilobate. Corallum attached in early juvenile stage, with small holdfast conforming in shape to substrate; ?free in mature stage. Corallum external surface of most specimens shows swollen and irregularly spaced, ?epithelial girdling bands (1.5 to 3 mm wide). Corallum costate, septa lowly exsert. Costae tend to alternate in size and correspond to all septal cycles. Calice elliptical to subcircular, usually elliptical. Fossa very small to small, very slightly concave to shallowly concave. Some specimens with an elevated fossa; rare specimens with only a protruding central calice area and no fossa. Columella very shallow to moderately shallow; barely detectable in some specimens (septae nearly fill the columellar area on these specimens). Columella trabecular below and sublamellar above; sublamellar columella usually most obvious on juvenile specimens (less than about 18 mm in height). Wall septothecal? and parathecal (endothecal dissepiments moderately common). Septal margins moderately dentate; synapticalae in corallum wall. Specimens about 22 mm high show five cycles of septa: First cycle (six septa) and second cycle (six septa) reach the columella; third cycle (12 septa) reaches or nearly reaches the columella; fourth cycle (24 septa) 75 to 80% as long as the proseptra of the first cycle; and fifth cycle (48 septa) short and only in the wall. Inner ends of the first through third cycles of septa adjacent to the columella are swollen, and swellings (paliform lobes?) much better developed on juvenile specimens (less than about 18 mm in height).

**HOLOTYPE DIMENSIONS.** Height 24.3 mm (incomplete), long diameter 23.2 mm, short diameter 15.8 mm.



**PRIMARY TYPE MATERIAL.** LACMIP holotype 12664 (illustrated), LACMIP paratypes 12665 to 12673 (all illustrated); all types from CSUN loc. 1343.

**TYPE LOCALITY.** CSUN loc. 1343.

**MOLLUSCAN STAGE RANGE.** “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** South side of Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN loc. 1343.

**REMARKS.** Specimens are abundant (155 collected) and show a growth series that grades from juvenile (8 mm in height) to very mature adult (5 cm in height). The base of nearly every specimen is missing, but one juvenile (Fig. 9) shows a small holdfast. Although weathering has affected all specimens, external preservation is generally good. On many specimens, however, the fossa area and the corresponding septa have been crushed, infilled with difficult to remove, well-cemented mudstone, or both. In addition, no specimen is preserved well enough in the fossa area to determine whether the swollen inner ends of the major septa truly correspond to paliform lobes. One of the main diagnostic features of genus *Antillophyllia* is having paliform lobes, and until better preserved specimens are found, the new species can only be questionably assigned to this genus. Recrystallization and crushing have obscured much of the internal features of the specimens of the new species. There are “ghost structures” that resemble septothecate structures, and many of the dissepiments have been obliterated.

*Antillophyllia* was reported previously only from upper Eocene strata in Colombia, South America, Oligocene and Miocene strata in Chiapas, Mexico, and lower Miocene strata in Trinidad and Florida (Clark and Durham, 1946; Weisbord, 1971; Frost and Langenheim, 1974). If the new species does belong to this genus, it would be the earliest and westernmost occurrence of *Antillophyllia*.

**ETYMOLOGY.** The new species is named for the state of California.

Family Oculinidae Gray, 1847a

Genus *Archohelia* Vaughan, 1919

**TYPE SPECIES.** *Archohelia limonensis* Vaughan, 1919, by original designation; Pliocene, Costa Rica.

*Archohelia clarki* Vaughan, 1927

Figures 20, 21

*Archohelia clarki* Vaughan, 1927:143, pl. 23, figs. 1–5.

**PRIMARY TYPE MATERIAL.** UCMP holotype 31414 and UCMP paratype 31415; exact location unknown, “Meganos Formation,” north of Mt. Diablo, Contra Costa County, California.

**MOLLUSCAN STAGE RANGE.** “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** South side of Simi Valley, California, and north of Mt. Diablo, Contra Costa County, California.

**LOCAL OCCURRENCE.** CSUN loc. 1348.

**REMARKS.** Two specimens were found. After removal from the enclosing rock, their state of preservation is somewhat poor. Nevertheless, parts of the specimens show the branching, colonial form and the septa. *Archohelia clarki* is the only known species of this oculinid coral genus from the fossil record of the North American Pacific coast.

Prior to this present study, *Archohelia clarki* was only known from its type locality north of Mt. Diablo in Contra Costa County, California.

Phylum Mollusca Linnaeus, 1758

Class Gastropoda Cuvier, 1797

Superorder Neritopsina Cox and Knight,  
1960

Family Neritidae Rafinesque, 1815

Genus *Velates* Montfort, 1810

**TYPE SPECIES.** *Nerita perversa* Gmelin, 1791, by original designation and monotypy; Eocene, Paris Basin, France.

*Velates perversus* (Gmelin, 1791)

Figures 22, 23

*Nerita perversa* Gmelin, 1791:3686.

*Velates perversus* (Gmelin). Cox, 1931:36–37; Vokes, 1935:382–383, pl. 25, figs. 1–5; pl. 26, figs. 1–2; Clark and Vokes, 1936:875, pl. 1, figs. 7–8; Givens, 1974:61, pl. 5, figs. 5–6, 13; Squires, 1984:16–17, figs. 6b–c; 1987:23–24, figs. 15–19; 1991b:pl. 1, figs. 10, 11; Woods and Saul, 1986:643–647, figs. 4.17, 5.20, 5.22–5.25, 6.1–6.3, 6.8; Squires and Demettrion, 1992:26, figs. 55, 56.

**PRIMARY TYPE MATERIAL.** Lamarck’s Cabinet in the Natural History Museum of Geneva, Switzerland.

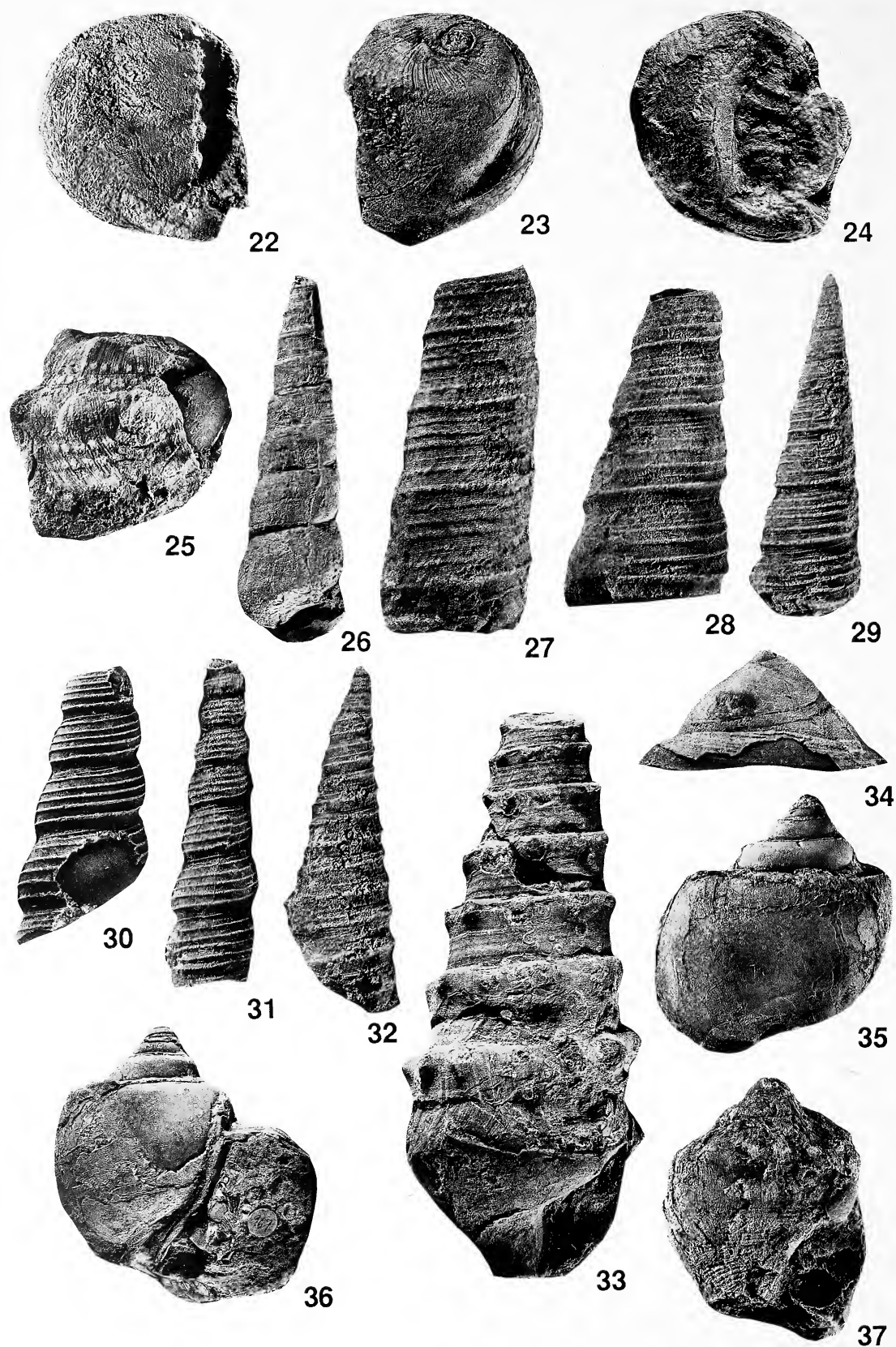
**MOLLUSCAN STAGE RANGE.** “Meganos” and “Capay,” possibly “Domengine.”

**GEOGRAPHIC DISTRIBUTION.** Pakistan, India, Myanmar, Tibet, Middle East, northern Africa, western Europe, Florida, ?Panama, Baja California Sur (Mexico), and southern California (possibly south-central California).

**LOCAL OCCURRENCE.** CSUN loc. 1342, LACMIP loc. 7124.

**REMARKS.** Two specimens were found. One, from CSUN locality 1342 is a large internal mold, but the diagnostic teeth on the inner lip are visible. The second specimen, from LACMIP locality 7124, is small, but it has the shell and shows all the diagnostic morphology.

See Squires (1987) for a more complete synonymy of this cosmopolitan species. The synonymy given here is primarily for the Pacific coast of North America. This is the first report of *Velates perversus* from the “Meganos Stage.” In the Simi Valley area, it is also known from low in the Lajas Formation





in "Capay Stage" rocks (Squires, 1984; Woods and Saul, 1986).

The only other species of *Velates* in the Simi Valley area is *V. californicus* Vokes (1935), which has been found at UCMP localities 7009 and 3792 (Vokes, 1935), as well as at LACMIP locality 23173 (Saul, 1983; Woods and Saul, 1986). The stratigraphic position of UCMP locality 7009 is known (Fig. 1), and is approximately on strike with that of LACMIP locality 7124 (Fig. 4). The stratigraphic positions of UCMP locality 3792 and LACMIP 23173, however, are not known. These two localities are probably in the upper part of the Santa Susana Formation on the south side of Simi Valley, and the specimens are probably late Paleocene in age (Woods and Saul, 1986).

Although *Velates californicus* and *V. perversus* might have the same geologic range (late Paleocene to early Eocene), they have never been collected at the same locality. As Woods and Saul (1986) reported, *V. californicus* always occurs stratigraphically below *V. perversus*, and the present study confirms this observation.

#### Genus *Corsania* Vidal, 1917

**TYPE SPECIES.** *Corsania doubillei* Vidal, 1917, by original designation; late Early Cretaceous (Albian), Cors, Lérída, Spain.

#### Subgenus *Januncia* Woods and Saul, 1986

**TYPE SPECIES.** *Corsania (Januncia) janus* Woods and Saul, 1986, by original designation; late Paleocene?, Baja California Sur, Mexico.

*Corsania (Januncia) susana* Saul and Squires, 1997

Figures 24, 25

*Corsania (Januncia) susana* Saul and Squires, 1997: 142–143, figs. 28–30.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 7890, CSUN loc. 969; LACMIP paratype 7891, CSUN loc. 973; LACMIP paratype 6441, CSUN loc. 966. All localities in the upper 100 m

of the Santa Susana Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** "Meganos."

**GEOGRAPHIC DISTRIBUTION.** North side of Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN locs. 966, 969, 973.

**REMARKS.** Three specimens were found. Only the holotype shows the inner lip, which is prominently set off from the deck area.

#### Superorder Caenogastropoda Cox, 1959

#### Family Turritellidae Woodward, 1851

**TYPE SPECIES.** *Turbo terebra* Linnaeus, 1758, by monotypy; Recent, southwest Pacific.

*Turritella meganosensis* Clark and Woodford, 1927

Figure 26

*Turritella meganosensis* Clark and Woodford, 1927:119–120, pl. 21, figs. 2–5; Merriam, 1941: 75, pl. 8, figs. 3, 4, 7, 9; Saul, 1983:pl. 1, fig. 13; Clark, 1929:pl. 5, figs. 1, 11; Schenck and Keen, 1940:pl. 22, figs. 5–7.

**PRIMARY TYPE MATERIAL.** UCMP holotype 12445 and UCMP paratype 12441, UCMP loc. 3159, Margaret Hamilton Sand [= Clark and Woodford's (1927) Division D of the Meganos Formation], Deer Valley, Contra Costa County, California; paratypes UMCP 31225–31226, UCMP loc. 7000, upper Santa Susana Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** "Meganos."

**GEOGRAPHIC DISTRIBUTION.** North side of Simi Valley, California; Deer Valley, Contra Costa County, California; south of Covelo (Round Valley) on Middle Fork of Eel River, Mendocino County, California.

**LOCAL OCCURRENCE.** Upper 100 m of the Santa Susana Formation (exact location not known).

**REMARKS.** In the upper 100 m of the Santa Susana Formation, this rare and large-sized turritellid

Figures 22–37. Gastropods from the upper 100 m of the Santa Susana Formation, Simi Valley. All specimens coated with ammonium chloride. 22, 23. *Velates perversus* (Gmelin, 1791),  $\times 1.8$ , LACMIP hypotype 12676, LACMIP loc. 7124. 22. Apertural view. 23. Abapertural view. 24, 25. *Corsania (Januncia) susana* Saul and Squires, 1997,  $\times 1.4$ , LACMIP holotype 7890, CSUN loc. 969. 24. Apertural view. 25. Abapertural view. 26. *Turritella meganosensis* Clark and Woodford, 1927, apertural view,  $\times 0.7$ , UCMP holotype 37430, UCMP loc. 7000. 27. *Turritella andersoni susanae* Merriam, 1941, apertural view,  $\times 3.2$ , LACMIP hypotype 12677, CSUN loc. 969. 28, 29. *Turritella buwaldana* Dickerson, 1916. 28. Abapertural view,  $\times 3.7$ , LACMIP hypotype 10434 [= UCLA hypotype 59372], LACMIP loc. 26615. 29. Abapertural view,  $\times 4.5$ , LACMIP hypotype 12678, CSUN loc. 1343. 30, 31. *Turritella uvasana infera* Merriam, 1941. 30. Abapertural view,  $\times 3$ , LACMIP hypotype 12679, CSUN loc. 967. 31. Apertural view,  $\times 2$ , LACMIP hypotype 12680, CSUN loc. 959. 32. *Turritella susanensis* Nelson, 1925 *nomen dubium*, abapertural view,  $\times 3.6$ , LACMIP hypotype 12681, CSUN loc. 1343. 33. *Campanile dilloni* (Hanna and Hertlein, 1949), apertural view,  $\times 0.6$ , LACMIP hypotype 12335, CSUN loc. 1565. 34. *Calyptrea diegoana* (Conrad, 1855), lateral view,  $\times 2.2$ , LACMIP hypotype 12682, CSUN loc. 958. 35, 36. *Pachycrommium clarki* (Stewart, 1927),  $\times 0.7$ , LACMIP hypotype 12683. 35. Apertural view. 36. Abapertural view. 37. *Phalium (Semicassis) tuberculiformis* (Hanna, 1924), apertural view,  $\times 1.7$ , LACMIP hypotype 12684, CSUN loc. 967.

(up to 90 mm in height) has been found only at UCMP locality 7000, which is 7.5 m below the Llajas Formation according to Saul (1983). The exact location of this locality, however, is not known. No additional specimens were found during this present study. This species is the only *Turritella* in the upper 100 m of the Santa Susana Formation that is restricted to the "Meganos Stage." Mid-adult stage specimens have a pronounced posterior swelling, but this feature becomes obsolete in late-adult stage specimens (Clark and Woodford, 1927; Merriam, 1941).

*Turritella andersoni susanae* Merriam, 1941

Figure 27

*Turritella andersoni susanae* Merriam, 1941:79, pl. 11, fig. 6; Saul, 1983:pl. 2, fig. 5.

*Turritella andersoni* n. subsp. Saul, 1983:pl. 1, figs. 15–18.

**PRIMARY TYPE MATERIAL.** UCMP holotype 15295, UCMP loc. A-993, basal Llajas Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** "Meganos."

**GEOGRAPHIC DISTRIBUTION.** Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN locs. 962, 963, 964, 965, 966, 969, 970, 971, 972, 973, 1347, 1349, LACMIP loc. 21551.

**REMARKS.** Specimens are abundant at most localities but generally have poor preservation because their weathered shells are chalky and disintegrate when removed from the outcrop. The largest specimens are up to 45 mm in height and were found at locality 966.

This subspecies is characterized by adult whorls with a concave whorl profile bearing two relatively heavy spiral ribs anteriorly (the anteriormost is the most prominent) and two primary spiral ribs posteriorly. All of these ribs can be noded. The medially concave area between these two sets of primary ribs is usually smooth, or, in some cases, with a secondary and numerous tertiary spiral ribs. A sutural spiral rib is also present.

Squires (1984) regarded this subspecies as conspecific with *Turritella andersoni* s.s. Dickerson, 1916. As stated by Merriam (1941), and later confirmed by Squires (1987), the two are separate taxa. *Turritella andersoni susanae* differs from *T. andersoni* s.s. in the relatively stronger development of the two posterior primary spiral ribs. In the synonymy of *T. andersoni* s.s. given by Squires and Goedert (1994), *T. a. susanae* was inadvertently included as a synonym of *T. andersoni*.

Although *Turritella andersoni susanae* is locally abundant and is one of the most diagnostic species of the "Meganos Stage" in the Simi Valley area, the holotype of this subspecies is reported to be from the basal part of the overlying Llajas Formation, at UCMP loc. A-993 on the north side of Simi Valley. The holotype is the only specimen of *T. a. susanae* ever reported from the Llajas Formation, and

Squires (1984), in his monographic work on the Llajas Formation, never encountered any specimens of this subspecies. The description of the type locality is imprecise and could apply equally to the upper 100 m of the Santa Susana Formation or to the lower part of the Llajas Formation. It is likely that the type locality of *T. a. susanae* is in error and should have been reported as from the upper 100 m of the Santa Susana Formation.

*Turritella buwaldana* Dickerson, 1916

Figures 28, 29

*Turritella buwaldana* Dickerson, 1916:500–501, pl. 42, figs. 7a–b; Hanna, 1927:307:pl. 19, figs. 7–8, 12; Vokes, 1939:161; Kappeler et al., 1984: table 2; Merriam, 1941:86–87, pl. 21, figs. 3–9; pl. 33, figs. 1–14; Stewart, 1946:pl. 11, fig. 24; Givens, 1974:63, pl. 5, fig. 15; Saul, 1983:pl. 2, figs. 13–15; Squires, 1983a:fig. 9f; 1984:18, fig. 6h; 1987:27, fig. 24; 1988b:10–11, fig. 15; 1991b:pl. 1, fig. 14; Squires and Demettrion, 1992:27, fig. 61.

?*Turritella uvasana* Conrad. Dickerson, 1915:pl. 5, figs. 1c, 3, 4.

*Turritella kewi* Dickerson, 1916:501, pl. 42, fig. 8.

*Turritella subuvasana* Nelson, 1925:423, pl. 56, figs. 5, 6, 7; Merriam, 1941:74, pl. 41, figs. 1–3.

*Turritella buwaldana crooki* Merriam and Turner, 1937:105, pl. 5, fig. 6; Merriam, 1941:87, pl. 21, figs. 1, 2; Turner, 1938:85; Vokes, 1939:161–162; Saul, 1983:pl. 2, figs. 2, 3.

*Turritella? buwaldana subuvasana* Nelson. Saul, 1983:pl. 1, fig. 11.

**PRIMARY TYPE MATERIAL.** UCMP holotype 12130, UCMP loc. 672, Domingine Formation, Fresno County, California.

**MOLLUSCAN STAGE RANGE.** "Meganos" through "Tejon."

**GEOGRAPHIC DISTRIBUTION.** San Ignacio Lagoon area, Baja California Sur, Mexico, to Glide, Oregon.

**LOCAL OCCURRENCE.** CSUN locs. 958, 959, 961, 962, 967, 970, 972, 1342, 1343, 1345, 1346, LACMIP loc. 26615.

**REMARKS.** Specimens are rare to common and are most abundant at locality 961. All specimens are fragmentary and show moderately good preservation.

The range of variability of *Turritella buwaldana* is "confusingly great," as noted by Merriam (1941: 86), and he found variation among individuals from the type locality, as well as variation within and among other known regional assemblages. Considerable variation of *T. buwaldana* is also present in specimens found in the upper 100 m of the Santa Susana Formation. Many of the specimens fit the original description of *T. buwaldana* and have three primary spiral ribs on the anterior half of the mature whorls and two (in some cases only one) secondary spiral ribs posterior to the primary ribs. Tertiary ribs, usually only one, are in the

interspaces. There are also rare specimens that have three primary ribs and three secondary ribs. These latter specimens are indistinguishable from *T. buwaldana crooki* Merriam and Turner. In the upper 100 m of the Santa Susana Formation, there are also specimens of *T. buwaldana* whose posterior-most primary rib is only as strong as a secondary rib, thereby producing whorls with two primary ribs and three secondaries.

Some specimens of *Turritella buwaldana* from the upper Santa Susana Formation have minute nodes on the primaries (usually only the posterior-most one) and on the secondaries. Squires (1987, 1988b) and Squires and Demetrios (1992) also reported the presence of minute nodes on specimens of this species from elsewhere on the Pacific coast of North America.

Nelson (1925: checklist opposite p. 402) reported *Turritella subuvasana* Nelson, 1925, from UCMP loc. 3791 [= CSUN loc. 1343] in the Santa Susana Formation. Specimens of Nelson's species consist of only the tips (apices) of the shells, even though Merriam (1941) reported that specimens show adult-whorl sculpture. During the present study, about 20 specimens were collected at CSUN locality 1343, and they also consist of only the tips of shells. The largest known specimens of *T. subuvasana* from this locality are only 12 mm in height, and the sculpture on the largest whorls usually consists of five spiral ribs. The two posterior-most ribs can be slightly weaker than the other three, or all can be subequal. The sculptural patterns of the tips of Paleogene turritellas from the Pacific coast of North America are not species specific, but in the case of *T. subuvasana*, the tips are sufficiently close to the variability of *T. buwaldana* to allow identification as *T. buwaldana*. One of these specimens is illustrated in Fig. 29.

Nelson (1925) and Merriam (1941) also reported *Turritella subuvasana* from UCMP loc. 3796 in the Santa Susana Formation. The exact stratigraphic position of this locality, which is the type locality of this gastropod, is not known because of structural complications caused by the nearness of the Runkle Canyon fault zone.

#### *Turritella uvasana infera* Merriam, 1941

Figures 30, 31

*Turritella uvasana infera* Merriam, 1941:90, pl. 40, figs. 2-4; Givens, 1974:65-66, pl. 6, figs. 5-7; Saul, 1983:pl. 1, fig. 19; pl. 2, fig. 4; Squires, 1984:19, fig. 6j; 1987:27-28, fig. 25.

**PRIMARY TYPE MATERIAL.** UCMP holotype 33993, UCMP loc. A-994, lower part of the Lajas Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** "Meganos" and "Capay."

**GEOGRAPHIC DISTRIBUTION.** Simi Valley, Whitaker Peak area, and Pine Mountain area, Ventura County, California.

**LOCAL OCCURRENCE.** CSUN locs. 959, 960, 961, 967, 1346, LACMIP loc. 21551.

**REMARKS.** Specimens are rare to abundant, and, at all localities, they are moderately well preserved. They are most abundant at CSUN locality 959. This species is characterized by five equal and strong primary spiral ribs on rounded whorls.

This species has been reported (Merriam, 1941; Givens, 1974; Saul, 1983; Squires, 1984, 1987) as present in the uppermost part of the Santa Susana Formation in the Simi Valley area. Merriam (1941) and Saul (1983) mentioned that these specimens have a more rounded whorl profile and heavier ribbing than those from the type locality low in the overlying Lajas Formation. Squires (1987), however, reported that the upper Santa Susana Formation specimens are indistinguishable from specimens elsewhere.

#### *Turritella susanaensis* Nelson, 1925 *nomen dubium*

Figure 32

*Turritella susanaensis* Nelson, 1925:423, pl. 56, figs. 1, 2; Merriam, 1941:73-74, pl. 41, figs. 4, 10.

**REMARKS.** Nelson (1925) and Merriam (1941) reported this taxon from the Santa Susana Formation at UCMP loc. 3791 [= CSUN loc. 1343] and UCMP loc. 3796. Specimens are abundant and moderately well preserved at locality 3791. As discussed under *Turritella buwaldana*, the exact stratigraphic position of UCMP loc. 3796 within the Santa Susana Formation is unclear. At both localities, only the broken-off tips of shells have been found, even though Merriam (1941) reported that specimens show adult-whorl sculpture. The largest known specimens are only 13 mm in height.

So far, even after more than 60 years of collecting, only tips of *T. susanaensis* are known. Their sculptural pattern is not distinctive. The sculptural pattern of the tips of Paleocene turritellas from the Pacific coast of North America are, in fact, not species specific. Nelson (1925) should not have based his species on such material; therefore, *T. susanaensis* becomes a *nomen dubium*.

#### Family Campanilidae Douvillé, 1904

##### Genus *Campanile* Fischer, 1884

**TYPE SPECIES.** *Cerithium giganteum* Lamarck, 1804a, by subsequent designation (Sacco, 1895); Eocene, Paris Basin, France.

#### *Campanile dilloni* (Hanna and Hertlein, 1949)

Figure 33

*Campanilopa dilloni* Hanna and Hertlein, 1949: 393, pl. 77, figs. 2, 4, text-fig. 1; Givens, 1974: 69, pl. 7, fig. 10; Squires and Advocate, 1986: 853, 855, fig. 2.1.

*Campanile dilloni* Hanna and Hertlein. Squires, 1991b:pl. 1, fig. 18; 1993:327–329, figs. 6–11.

**PRIMARY TYPE MATERIAL.** CAS holotype 9425 and CAS paratypes 9428 and 9429, all from CAS loc. 30667, Mabury Formation, Agua Media Creek, Temblor Range, Kern County, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” and “Capay.”

**GEOGRAPHIC DISTRIBUTION.** Orocopia Mountains, Riverside County, California, to Agua Media Creek, Temblor Range, Kern County, California.

**LOCAL OCCURRENCE.** CSUN loc. 1565.

**REMARKS.** A single specimen was found. It is 15.1 cm in height and well preserved.

## Family Calyptraeidae Lamarck, 1809

### Genus *Calyptraea* Lamarck, 1799

**Type Species.** *Patella chinensis* Linnaeus, 1758, by monotypy; Recent, Europe.

#### *Calyptraea diegoana* (Conrad, 1855)

Figure 34

*Trochita diegoana* Conrad, 1855:7, 17; 1857:327, pl. 5, fig. 42.

*Galerus excentricus* Gabb, 1864:136, pl. 20, fig. 95; pl. 29, fig. 232a; Arnold, 1907a:pl. 10, fig. 3a.

*Calyptraea calabasaensis* Nelson, 1925:419, pl. 54, figs. 8a–b.

*Calyptraea* (*Galerus*) *calabasaensis* Nelson. Clark and Woodford, 1927:120, pl. 21, figs. 10–13.

*Calyptraea diegoana* (Conrad). Stewart, 1927:340–341, pl. 27, fig. 15; Turner, 1938:89–90, pl. 20, figs. 1–2; Effinger, 1938:378; Weaver, 1943:351–352, pl. 71, figs. 16, 20; pl. 103, fig. 3; 1953:29; Stewart, 1946:pl. 11, fig. 5; Kleinpell and Weaver, 1963:186, pl. 24, fig. 7; Hickman, 1969:79, 82, pl. 11, figs. 7–8; 1980:33–34, pl. 2, figs. 18–21; Deméré et al., 1979:pl. 2, fig. 7; Squires, 1984:21, fig. 6q; 1987:32, fig. 4; 1988b:11, fig. 19; 1991b:pl. 1, fig. 20; 1994:pl. 1, fig. 2; Squires and Goedert, 1994:16, 18, fig. 36.

**PRIMARY TYPE MATERIAL.** USNM holotype 1856, Eocene strata (probably the Delmar Formation), San Diego, California.

**MOLLUSCAN STAGE RANGE.** “Martinez” through lower Oligocene.

**GEOGRAPHIC DISTRIBUTION.** San Diego, California, to Little River area, Grays Harbor County, Washington.

**LOCAL OCCURRENCE.** CSUN locs. 958, 963, 1342, 1349.

**REMARKS.** Specimens are rare but moderately well preserved.

## Family Naticidae Forbes, 1838

### Genus *Pachycrommium* Woodring, 1928

**Type Species.** *Amaura guppyi* Gabb, 1873, by original designation; Recent, Miocene, Dominican Republic.

#### *Pachycrommium clarki* (Stewart, 1927)

Figures 35, 36

*Amauropsis alveata* (Conrad). Arnold, 1910:pl. 4, fig. 21; Dickerson, 1915:pl. 5, fig. 9; Waring, 1917:pl. 15, fig. 25 [Misidentifications]. Not *Amauropsis alveata* (Conrad, 1855).

*Amaurellina* (*Euspirocrommium*) *clarki* Stewart, 1927:336–339, pl. 26, figs. 8, 9 [new name, in part, for *Amauropsis alveata* (Conrad, 1855), preoccupied and misidentified]; Clark, 1929:pl. 11, fig. 10; Turner, 1938:86, pl. 20, fig. 3; Weaver, 1943:345, pl. 70, figs. 10, 18; Kleinpell and Weaver, 1963:188, pl. 27, fig. 15.

*Amaurellina clarki* Stewart. Gardner and Bowles, 1934:246, figs. 6, 8.

?*Amaurellina multiangulata* Vokes, 1939:174, pl. 22, figs. 2, 8, 13.

?*Pachycrommium clarki* (Stewart). Vokes, 1939:175, pl. 22, figs. 11, 30; Givens, 1974:73, pl. 8, figs. 6, 10.

*Amaurellina*? (*Euspirocrommium*) *clarki* Stewart. Stewart, 1946:pl. 11, fig. 3.

*Pachycrommium clarki* (Stewart). Marincovich, 1977:238–241, pl. 20, figs. 4–10; Squires, 1983a:fig. 9b; 1984:25, fig. 7e; 1987:36, fig. 44; 1988b:12, fig. 25; 1991b:pl. 1, fig. 25; Squires et al., 1992:pl. 1, fig. 18.

**PRIMARY TYPE MATERIAL.** UCMP holotype 31385 and UCMP paratype 31386 of *Amaurellina* (*Euspirocrommium*) *clarki* Stewart, both from UCMP loc. 7004, Llajas Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” through “Tejon.”

**GEOGRAPHIC DISTRIBUTION.** Laguna San Ignacio area, Baja California Sur, Mexico, to southwestern Washington.

**LOCAL OCCURRENCE.** CSUN locs. 958, 967, 1346, 1347.

**REMARKS.** Specimens are rare to uncommon and most numerous at CSUN locality 967, where they also show the best preservation. This is the first report of this species from the “Meganos Stage.”

## Family Cassidae Swainson, 1832

### Genus *Phalium* Link, 1807

**TYPE SPECIES.** *Buccinum glaucum* Linnaeus, 1758, by subsequent designation (Dall, 1909); Recent, Indo-Pacific.

Subgenus *Semicassis* Mörch, 1852

**TYPE SPECIES.** *Cassis japonica* Reeve, 1848, by subsequent designation (Harris, 1897); Recent, China and Japan.

?*Phalium* (*Semicassis*) *tuberculiformis*  
(Hanna, 1924)

Figure 37

**LOCAL OCCURRENCE.** CSUN loc. 967.

**REMARKS.** A single specimen was found. It is mostly an internal mold without the outer lip and anterior end of the shell. Some shell is present on the ventral surface, but it is weathered. The specimen has three carinae on the body whorl, and the shell material shows fine spiral ribbing between the carinae. Morphologically, the specimen resembles comparably preserved specimens of *Phalium* (*Semicassis*) *tuberculiformis*, from the "Domengine Stage" "Stewart bed" in the Lajas Formation on the north side of Simi Valley. This similarity is significant enough to warrant tentative identification.

Order Neogastropoda Thiele, 1929

Family Buccinidae Rafinesque, 1815

Genus *Brachysphingus* Gabb, 1869

**TYPE SPECIES.** *Brachysphingus sinuatus* Gabb, 1869, by subsequent designation (Cossmann, 1901); Paleocene, California and Baja California, Mexico.

*Brachysphingus mammilatus* Clark and  
Woodford, 1927

Figure 38

*Brachysphingus mammilatus* Clark and Woodford, 1927:116–117, pl. 20, figs. 8–15; Clark, 1929: 13, pl. 4, figs. 3, 10; Schenck and Keen, 1940: 22, figs. 1, 2; Givens, 1974:84, pl. 10, fig. 3; Squires, 1997:856, 858, figs. 5, 1–14.

*Pseudoliva* sp. Smith, 1975:pl. 1, figs. 14, 15.

**PRIMARY TYPE MATERIAL.** UCMP holotype 31234 from UCMP loc. 3157; UCMP paratype 31235 from UCMP loc. 3577; UCMP paratype 31236 from UCMP loc. 3159; UCMP paratype 31237 from UCMP loc. 3159, UCMP paratype 31238 from UCMP loc. 3577. All from Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark and Woodford (1927)], Deer Valley, Contra Costa County, California.

**MOLLUSCAN STAGE RANGE.** "Meganos" and "Capay."

**GEOGRAPHIC DISTRIBUTION.** Simi Valley, California, to south of Covelo (Round Valley) on Middle Fork of Eel River, Mendocino County, California.

**LOCAL OCCURRENCE.** CSUN locs. 958, 1345.

**REMARKS.** Specimens are rare and well preserved. Squires (1997) did a detailed study of *Brachysphingus*, noting its occurrence in the upper 100 m of the Santa Susana Formation.

*chysphingus*, noting its occurrence in the upper 100 m of the Santa Susana Formation.

*Brachysphingus mammilatus* has been found associated with *Turritella meganosensis* in the area south of Covelo (Round Valley) on the Middle Fork of the Eel River, Mendocino County, California (Merriam and Turner, 1937).

Family Olividae Latreille, 1825

Genus *Ancillarina* Bellardi, 1882

**TYPE SPECIES.** *Ancilla canalifera* Lamarck, 1802, by subsequent designation (Palmer, 1937); Eocene, Paris Basin, France.

?*Ancillarina* sp.

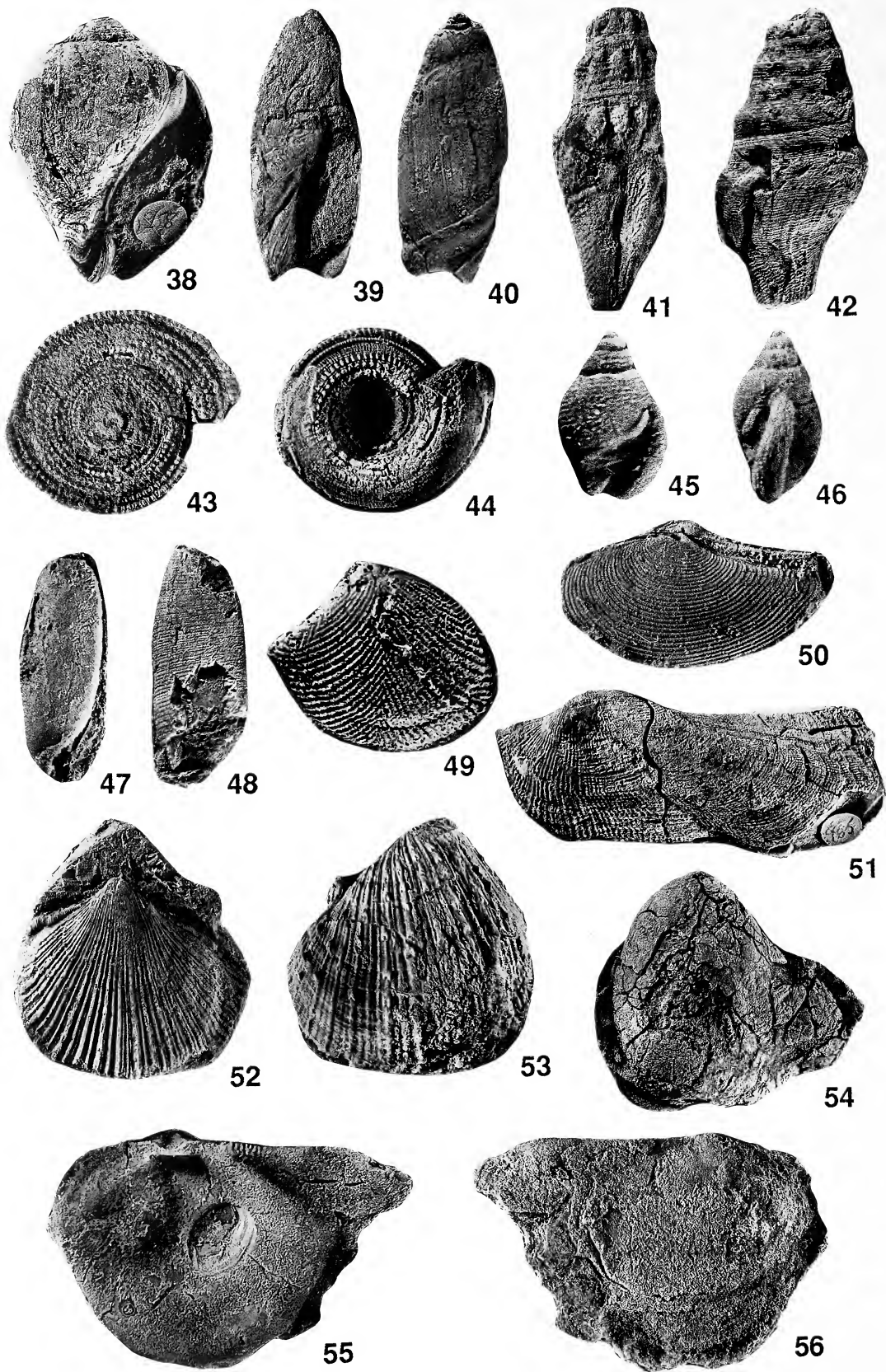
Figures 39, 40

**LOCAL OCCURRENCE.** CSUN loc. 961.

**REMARKS.** Three specimens were found. The best preserved of the three is crushed in the middle, and most of the spire is represented as an internal mold. The other two specimens are internal molds. The best preserved specimen is similar in overall shape and in the columella area to the Paris Basin, France, Eocene *Ancillarina canalifera* (Lamarck, 1802). *Ancillarina canalifera*, which is the type species of *Ancillarina*, has a total lack of callus on the spires whorls and sutures, and, according to Kilburn (1981), this is a major diagnostic feature of this genus. The specimen from CSUN locality 961 differs slightly from *A. canalifera* (Lamarck, 1802: 475, pl. 2, fig. 8; Cossmann and Pissarro, 1910–1913:pl. 67, figs. 211–9, 211–9', 211–9"; Kilburn, 1981:figs. 24–27) by having a less distinct suture between the penultimate whorl and body whorl. The somewhat indistinct suture on the specimen from locality 961 might be the result of poor preservation or of a slight amount of callus. Until better preserved specimens are found, it is not possible to assign this species with certainty to *Ancillarina*.

If the specimen from locality 961 does prove to belong to *Ancillarina*, it would be the first record of this genus in the Western Hemisphere. Wenz (1943) reported the temporal range of this genus as Eocene to Miocene and the geographic distribution as confined to Europe.

The specimen of ?*Ancillarina* sp. superficially resembles *Ancilla burroensis* Nelson (1925) from the "Martinez marine member" ("Martinez Stage") part of the Santa Susana Formation on the south side of Simi Valley. The specimen of ?*Ancillarina* sp. differs from *A. burroensis* Nelson (1925:433, pl. 60, figs. 2, 3) by having columellar teeth that are less prominent, longer, and more parallel to the shell axis, as well as by having a more deeply notched anterior sinus. In addition, if ?*Ancillarina* sp. does have any callus on the spire, it is much lighter than the heavily calloused spire found on *A. burroensis*.





Family Turridae Swainson, 1840

Genus *Gemmula* Weinkauff, 1875

**Type Species.** *Gemmula hindsiana* Berry, 1958 [= *Pleurotoma gemmata* Reeve, 1843], by subsequent designation (Cossmann, 1896); Recent, southern Baja California, Mexico, to Colombia, South America.

*Gemmula* sp., aff. *G. diabloensis* Clark and Woodford, 1927

Figure 41

**LOCAL OCCURRENCE.** CSUN loc. 961.

**REMARKS.** A single specimen was found, and it is missing the uppermost spire and tip of the anterior canal. About half of the shell material is missing, and the half that present is weathered. The specimen has close affinity to *Gemmula diabloensis* Clark and Woodford (1927:107, pl. 19, figs. 3, 4) from the "Meganos Stage" Margaret Hamilton Sand [= Division D of the Meganos Formation as used by Clark and Woodford, 1927] in Contra Costa County, California. The specimen from CSUN locality 961 differs from *G. diabloensis* by having 12 rather than about 10 axial ribs on the penultimate whorl, three rather than four spiral ribs between the shoulder angulation and the sutural collar, and spiral ribs on the body whorl grading anteriorly from medium to fine rather than being differentiated into pairs or sets of three.

Genus *Turricula* Schumacher, 1817

**TYPE SPECIES.** *Turricula flammea* Schumacher, 1817, by monotypy; Recent, Sri Lanka.

*Turricula* sp., aff. *T. burroensis* (Nelson, 1925)

Figure 42

**LOCAL OCCURRENCE.** CSUN loc. 969.

**REMARKS.** A single specimen was found, and it is missing the upper part of the spire and about half

of the anterior canal. The specimen is also somewhat weathered, and the nodes on the spire are correspondingly subdued. The specimen has affinity to *Turricula burroensis* (Nelson, 1925) from the so-called "Martinez Marine Member" ("Martinez Stage") part of the Santa Susana Formation on the south side of Simi Valley. The specimen from CSUN locality 969 differs from *T. burroensis* (Nelson, 1925:435, pl. 60, figs. 8, 9) by having more spiral ribs (26 rather than 16) on the penultimate whorl and more spiral ribs (about 60 rather than 45) on the body whorl.

Nelson (1925) originally assigned his species to *Turris* Röding, 1798, but Zinsmeister (1983b) re-assigned the species to *Turricula* based on the diagnostic presence of the anal sinus on the shoulder slope.

Although *Turricula calafia* Nelson (1925:434, pl. 60, figs. 1a, 1b), known only from the same locality as *T. burroensis*, is similar to *T. burroensis*, the specimen of *Turricula* from CSUN locality 969 is more similar to *T. burroensis* in that it is slimmer.

Subclass Heterobranchia Gray, 1840

Order Heterostropha Fischer, 1885

Family Architectonicidae Gray, 1850

Genus *Architectonica* Röding, 1798

**Type Species.** *Trochus perspectivus* Linnaeus, 1758, by subsequent designation (Gray, 1847b); Recent, Indo-Pacific.

Subgenus *Architectonica* s.s.

*Architectonica (Architectonica) llajasensis*  
Sutherland, 1966

Figures 43, 44

*Architectonica llajasensis* Sutherland, 1966:1-4, figs. 1, 2.

*Architectonica (Architectonica) llajasensis* Sutherland. Squires, 1984:19, fig. 6k; Squires and Demettrion, 1994:131-132, fig. 16.

Figures 38-56. Gastropods and bivalves from the upper 100 m of the Santa Susana Formation, Simi Valley. All specimens coated with ammonium chloride. 38-48. Gastropods. 38. *Brachysphingus mammilatus* Clark and Woodford, 1927, apertural view,  $\times 1.4$ , LACMIP hypotype 12685, CSUN loc. 958. 39, 40. *Ancillarina* sp.,  $\times 2.5$ , LACMIP hypotype 12686, CSUN loc. 961. 39. Apertural view. 40. Abapertural view. 41. *Gemmula* sp., aff. *G. diabloensis* Clark and Woodford, 1927, apertural view,  $\times 4.5$ , LACMIP hypotype 12687, CSUN loc. 969. 42. *Turricula* sp., aff. *T. burroensis* (Nelson, 1925), abapertural view,  $\times 2$ , LACMIP hypotype 12688, CSUN loc. 961. 43, 44. *Architectonica (A.) llajasensis* Sutherland, 1966,  $\times 2$ , LACMIP hypotype 12689, LACMIP loc. 26609. 43. Apical view. 44. Umbilical view. 45, 46. *Ringicula (R.) pinguis* (Gabb, 1864),  $\times 13.2$ , LACMIP hypotype 12690, LACMIP loc. 1344. 45. Apertural view. 46. Right-lateral view. 47, 48. *Cylichnina tantilla* (Anderson and Hanna, 1925). 47. Apertural view,  $\times 5.4$ , LACMIP hypotype 12691, CSUN loc. 964. 48. Abapertural view,  $\times 4.8$ , LACMIP hypotype 12692, CSUN loc. 970. 49-54. Bivalves. 49. *Acila (Truncaila) decisa* (Conrad, 1855), latex peel of external mold, right valve,  $\times 3.8$ , LACMIP hypotype 12693, CSUN loc. 959. 50. *Nuculana (Saccella) gabbii* (Gabb, 1869), latex peel of external mold, left valve,  $\times 6$ , LACMIP hypotype 12694, CSUN loc. 967. 51. *Arca (A.) filewiczii* Squires, 1991a, left valve,  $\times 1$ , LACMIP holotype 8365, CSUN loc. 965. 52, 53. *Spondylus carlosensis* Anderson, 1905,  $\times 2.1$ , LACMIP hypotype 12695, CSUN loc. 1343. 52. Left (free) valve. 53. Right (attached) valve. 54-56. *Pycnodonte (Phygraea)* sp., aff. *Pycnodonte (Phygraea) pacifica* Squires and Demettrion, 1990, CSUN loc. 1343. 54. Left (lower) valve,  $\times 1.4$ , LACMIP hypotype 12696. 55, 56. Right (upper) valve,  $\times 2.5$ , LACMIP hypotype 12697. 55. Interior. 56. Exterior.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 1140, LACMIP loc. 461-B, Llajas Formation, Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” and “Domengine” (no specimens known from “Caypay Stage”).

**GEOGRAPHIC DISTRIBUTION.** Baja California Sur, Mexico, to Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN locs. 966, 958.

**REMARKS.** A single specimen was found at CSUN locality 966, and this is the first record of *Architectonica* (*Architectonica*) *llajasensis* from “Meganos Stage” strata. An internal mold was found at CSUN locality 958.

Family Ringiculidae Philippi, 1853

Genus *Ringicula* Deshayes, 1838

Subgenus *Ringicula* s.s.

Type Species. *Auricula ringens* Lamarck, 1804b, by subsequent designation, Gray (1847b); Eocene, Paris Basin, France.

*Ringicula* (*Ringicula*) *pinguis* (Gabb, 1864)

Figures 45, 46

*Cinulia pinguis* Gabb, 1864:112, pl. 29, figs. 221a, 221b.

*Ringinella pinguis* Gabb, 1869:175; Dickerson, 1914:17, figs. 4a, 4b.

*Tornatellaea pinguis* (Gabb). Nelson, 1925:436, pl. 60, figs. 5, 6; Stewart, 1927:433–434, pl. 25, fig. 10; Schenck and Keen, 1940:pl. 20, fig. 11.

*Tornatella pinguis* (Gabb). Zinsmeister, 1983a:pl. 4, fig. 31.

**PRIMARY TYPE MATERIAL.** ANSP lectotype 4265, Martinez Formation, “in the bluffs, a mile west of Martinez” (Gabb, 1864), Contra Costa County, California.

**MOLLUSCAN STAGE RANGE.** “Martinez” to “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** Southern California to Martinez, California.

**LOCAL OCCURRENCE.** CSUN loc. 1344.

**REMARKS.** Eight specimens were found, all early juveniles of minute size.

*Ringicula* s.s. is characterized by a small, low-spire globose to subglobose shape with a sculpture of spirally incised furrows, a greatly thickened outer lip, an internally dentate outer lip, a columella with two strong folds, and an anterior notch to the aperture (Sohl, 1964; Davies and Eames, 1971). The Santa Susana Formation specimens have all of these characteristics. Genus *Tornatellaea* Conrad, 1860, of family Acteonidae Orbigny, 1835, is similar to *Ringicula* s.s., but *Tornatellaea* lacks a varixlike outer lip and has no notch at the anterior end of the aperture.

The presence of *Ringicula* (*R.*) *pinguis* at CSUN loc. 1344 is the first record of this species in “Meganos Stage” strata.

Order Opisthobranchia Milne-Edwards, 1848

Family Cylichnidae A. Adams, 1854

Genus *Cylichnina* Monterosato, 1884

Type Species. *Bulla umbilicata* Montagu, 1803, by original designation; Recent, Norway.

*Cylichnina tantilla* (Anderson and Hanna, 1925)

Figures 47, 48

*Cylichnella tantilla* Anderson and Hanna, 1925: 140, pl. 7, figs. 4, 8, 9.

*Cylichnina tantilla* (Anderson and Hanna). Stewart, 1927:439–441, pl. 27, figs. 2–4; 1946:pl. 11, fig. 11; Turner, 1938:67–68, pl. 20, figs. 9, 10; Vokes, 1939:110, pl. 16, figs. 28, 33, 39; Weaver, 1943:548–549, pl. 100, figs. 10–12, 14–15; Squires, 1983a, fig. 9a; 1984:40, fig. 9p; 1988b: 17, fig. 43; 1991b:pl. 2, fig. 14; Squires et al., 1992:pl. 1, fig. 24; Squires and Demetron, 1992: 34, fig. 94.

**PRIMARY TYPE MATERIAL.** CAS holotype 958, CAS paratypes 959 and 960, all from CAS locality 711, Tejon Formation, Grapevine Canyon, southern end of San Joaquin Valley, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” through “Tejon.”

**GEOGRAPHIC DISTRIBUTION.** San Laguna Ignacio area, Baja California Sur, Mexico, to southwestern Washington.

**LOCAL OCCURRENCE.** CSUN locs. 961?, 964, 967, 970, 1344, 1346.

**REMARKS.** Specimens are rare and generally not well preserved. This is the first report of this species from “Meganos Stage” strata.

Class Bivalvia Linnaeus, 1758

Order Nuculoida Dall, 1889

Family Nuculidae Gray, 1824

Genus *Acila* H. Adams and A. Adams, 1858

Type Species. *Nucula divaricata* Hinds, 1843, by subsequent designation (Stoliczka, 1871); Miocene to Pliocene, Japan; Recent, Japan, China, and Korea.

Subgenus *Truncacila* Grant and Gale, 1931

Type Species. *Nucula castrensis* Hinds, 1843, by original designation; Pliocene to Pleistocene, California; Recent, northeastern Pacific.

*Acila* (*Truncacila*) *decisa* (Conrad, 1855)

Figure 49

*Nucula decisa* Conrad, 1855:11–12; 1857:pl. 3, fig. 19.

*Acila gabbiana* Dickerson, 1916:481, pl. 36, fig. 1; Anderson and Hanna, 1925:176, pl. 9, fig. 12.



*Nucula (Acila) stillwaterensis* Weaver and Palmer, 1922:6, pl. 8, fig. 8.

*Acila lajollaensis* Hanna, 1927:270, pl. 25, figs. 1, 3, 5, 7–8, 12, 15.

*Acila (Truncacla) decisa* (Conrad). Schenck, 1936: 53–56, pl. 3, figs. 1–9, 11–15; pl. 4, figs. 1–2; text fig. 7 (22, 23, 25); Turner, 1938:41–42, pl. 5, figs. 2–3; Vokes, 1939:41, pl. 1, figs. 7–8; Weaver, 1943:22–23, pl. 6, figs. 1, 4, 8; pl. 7, figs. 8–9; Moore, 1968:30, pl. 13a; 1983:A10, pl. 1, fig. 14; Givens, 1974:38, pl. 1, fig. 1; Squires, 1984:41, fig. 10a; 1987:54, fig. 86; 1988b:17, fig. 44; 1991b:pl. 2, fig. 15; Throckmorton, 1988:pl. 1, fig. 19; Squires and Goedert, 1997:fig. 2g.

**PRIMARY TYPE MATERIAL.** UCMP neotype 31132, designated by Schenck (1936), UCMP loc. 5062, Ardath Shale, San Diego County, California.

**MOLLUSCAN STAGE RANGE.** “Martinez” through upper Eocene (*Turritella schencki delaguerrae* Zone of Kleinpell and Weaver, 1963).

**GEOGRAPHIC DISTRIBUTION.** San Diego, California, to Kamchatka, Russia.

**LOCAL OCCURRENCE.** CSUN locs. 958, 959, 961.

**REMARKS.** Specimens are scarce to uncommon and are preserved as external molds. They are most abundant at locality 961, where six specimens were found. The Kamchatka occurrence of this species is in lower Eocene strata along the shore of the Penzhin Inlet (northern Sea of Okhotsk) and the nearby Koryak Uplands to the east (Devyatilova and Volobueva, 1981).

Family Nuculanidae H. Adams and A.  
Adams, 1858

Genus *Nuculana* Link, 1807

Type Species. *Arca rostrata* Chemnitz, 1784, by original designation; Recent, North Atlantic.

Subgenus *Saccella* Woodring, 1925

**TYPE SPECIES.** *Arca fragilis* Chemnitz, 1784, by original designation; Recent, Mediterranean Sea.

*Nuculana (Saccella) gabbii* (Gabb, 1869)  
Figure 50

*Leda? protexta* Conrad. Gabb, 1864:199 (in part), pl. 26, fig. 185.

Not *Leda? protexta* Gabb, 1860:303, pl. 48, fig. 23.

*Nuculana gabbii* Conrad, 1866:3, *nomen nudum*.  
*Leda gabbii* (Conrad). Gabb, 1869:197.

*Leda gabbii* (Conrad). Stanton, 1896:1041, pl. 64, fig. 8; Arnold, 1907a:pl. 10, fig. 1; 1910:pl. 2, fig. 8; Arnold and Anderson, 1910:pl. 24, fig. 8; Waring, 1917:76, pl. 13, fig. 6; Dickerson, 1915: pl. 1, fig. 1; 1916:pl. 36, fig. 3; Clark, 1929:pl. 3, fig. 12; Clark and Woodford, 1927:85–86, pl. 14, fig. 2.

*Leda vogdesi* Anderson and Hanna, 1925:177–179, pl. 2, figs. 8, 9.

*Saccella gabbii* (Gabb). Stewart, 1930:55–58, pl. 7, fig. 3, pl. 10, fig. 4.

*Nuculana (Saccella) gabbii* (Gabb). Vokes, 1939: 41–42; Kleinpell and Weaver, 1963:195, pl. 28, fig. 1; Givens, 1974:39, pl. 1, fig. 3; Moore, 1983:A16, pl. 2, figs. 7, 8; Squires, 1984:41, fig. 10b.

*Nuculana gabbii* (Gabb). Deméré et al., 1979:pl. 1, fig. 13.

?*Nuculana (Calorhadia) gabbii* (Gabb). Zinsmeister, 1983a:pl. 1, fig. 3.

**PRIMARY TYPE MATERIAL.** ANSP lectotype ANSP 4476 (of *Leda gabbii* Gabb, 1869), designated by Stewart (1930), “Tejon Formation,” Martinez, California.

**MOLLUSCAN STAGE RANGE.** “Martinez” through upper Eocene (*Turritella schencki delaguerrae* Zone of Kleinpell and Weaver, 1963).

**GEOGRAPHIC DISTRIBUTION.** Simi Valley, California, to Kamchatka, Russia.

**LOCAL OCCURRENCE.** CSUN locs. 958, 960, 961, 967, 1342?

**REMARKS.** Only a few poorly preserved internal molds were found, except at CSUN locality 967 where a well-preserved external mold was found. The Kamchatka occurrence of this species is in lower Eocene strata along the shore of the northern Sea of Okhotsk (Devyatilova and Volobueva, 1981).

Order Arcoida Stoliczka, 1871

Family Arcidae Lamarck, 1809

Genus *Arca* Linnaeus, 1758

**TYPE SPECIES.** *Arca noae* Linnaeus, 1758, by subsequent designation (Schmidt, 1818); Recent, Mediterranean Sea and northwest Africa.

Subgenus *Arca* s.s.

*Arca (Arca) filewiczii* Squires, 1991a

Figure 51

*Arca (Arca) filewiczii* Squires, 1991a:68–69, figs. 2–6.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 8365 and LACMIP paratype 8366; both from CSUN loc. 965, upper 100 m of the Santa Susana Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** North side of Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN loc. 965

**REMARKS.** Two specimens were found; one is closed valved.

Family Spondylidae Gray, 1826

Genus *Spondylus* Linnaeus, 1758

Type Species. *Spondylus gaederopus* Linnaeus, 1758, by subsequent designation (Schmidt, 1818); Recent, Mediterranean Sea and northwest Africa.

*Spondylus carlosensis* Anderson, 1905

Figures 52, 53

*Spondylus carlosensis* Anderson, 1905:194, pl. 13, fig. 1; Arnold, 1910:pl. 2, figs. 6,7; Dickerson, 1915:pl. 1, fig. 7; Anderson and Hanna, 1925:189–190, text fig. 10; Vokes, 1939:57, pl. 3, figs. 10, 13; Kleinpell and Weaver, 1963:199, pl. 31, fig. 6; Squires, 1984:43, fig. 10j; Moore, 1987:C6–C7, pl. 1, fig. 5; Squires and Goedert, 1994:23, fig. 55.

*Spondylus* cf. *S. carlosensis* Anderson. Squires, 1991b: pl. 2, fig. 17.

**PRIMARY TYPE MATERIAL.** CAS holotype 56, west and north of Coalinga, NW 1/4 of section 35, T 20 S, R 14 E, Domengine Formation, Fresno County, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” through middle part of “Tejon.”

**GEOGRAPHIC RANGE.** Simi Valley, California, to southwestern Washington.

**LOCAL OCCURRENCE.** CSUN loc. 1343.

**REMARKS.** Two specimens were found. One is small (height 20 mm), closed valved, and well-preserved overall. This specimen affords new morphologic information because, unlike previously described and illustrated specimens of this species, it shows both the left (Fig. 52) and right (Fig. 53) valves rather than only the left valve. The right (attached) valve is less circular and much more convex than the left. The radial ribs on the right valve are less closely spaced, wider, less sharp sided, and more spinose than those on the left. Usually, every fourth or fifth radial rib on both valves (especially on the right valve) is more prominent than the other ribs. Although the auricles are mostly missing on the right valve, those on the left valve are intact (a rare condition). The auricles on the left valve are small, and the anterior one has coarse growth lines and two strong and wide radial ribs, one of which delineates the hinge-line. The posterior auricle on the left valve is smooth, but it is set off from the rest of the valve by a moderately strong radial rib. On both valves, the beak is anterior of the valve center.

The other specimen of *Spondylus carlosensis* found at CSUN locality 1343 is a portion of a right valve attached to a specimen of the solitary coral ?*Antillophyllia californica* new species.

The presence of *Spondylus carlosensis* in the upper 100 m of the Santa Susana Formation is the first record of this species from “Meganos Stage” strata.

Order Ostreoida Férussac, 1822

Family Gryphaeidae Vyalov, 1936

Genus *Pycnodonte* Fischer de Waldheim, 1835

**TYPE SPECIES.** *Pycnodonte radiata* Fischer de Waldheim, 1835, by original designation; Late Cretaceous, Crimea.

Subgenus *Phygraea* Vyalov, 1936

**TYPE SPECIES.** *Gryphaea* (*Gryphaea*) sec. *Phygraea frauscheri* Vyalov, 1936, by original designation; late Paleocene, Austria.

*Pycnodonte* (*Phygraea*) sp., aff. *Pycnodonte* (*Phygraea*) *pacifica* Squires and Demetron, 1990

Figures 54–56

**LOCAL OCCURRENCE.** CSUN loc. 1343.

**REMARKS.** A single left (lower valve) was found, and 13 right (upper) valves were found. The left valve is weathered, missing some shell material, probably not complete, and infilled with very hard matrix. It is smooth, very convex, and has a prominent winglike extension separated from the main part of the valve by a moderately shallow sulcus that deepens ventrally. Only one of the right valves is mostly complete. It is smooth, flattish, has vermicular anachomata, and has a prominent winglike extension bearing a finely granular appearance because of vesicular shell structure. In addition, there is a prominent ridge interiorly where the right valve joins the left valve. The specimens have affinity with *Pycnodonte* (*Phygraea*) *pacifica* Squires and Demetron, 1990, from the “Capay Stage” through the lower middle part of the “Tejon Stage” within the Bateque Formation in Baja California Sur, Mexico. The Santa Susana Formation specimens differ from *Pycnodonte* (*Phygraea*) *pacifica* Squires and Demetron (1990:386, fig. 3.1–3.4) by having a smaller size, more prominent anachomata, and, apparently, a radial sulcus that originates farther from the umbo. These differences, however, might be related to growth stage. It is possible that all the Santa Susana Formation specimens are juveniles. All known specimens of *Pycnodonte* (*Phygraea*) *pacifica* are adults. Until more Santa Susana Formation specimens (especially of the left valve) are found, it cannot be positively determined if the already-collected material represents a new species or whether it represents only the juvenile stage of *Pycnodonte* (*Phygraea*) *pacifica*.

The only other species of *Pycnodonte* (*Phygraea*) known from the Paleogene rock record of the Pacific coast of North America is *P. (P.) cuarentaensis* Squires and Demetron, 1994, from the “Capay Stage” part of the Bateque Formation in Baja California Sur, Mexico. *Pycnodonte* (*Phygraea*) *cuarentaensis* Squires and Demetron (1994:132–133, figs. 17–22) differs from both *Pycnodonte* (*Phygraea*) *pacifica* and the Santa Susana Formation specimens by having fine radial ribbing on the left valve.

The specimens of *Pycnodonte* (*Phygraea*) sp., aff. *Pycnodonte* (*Phygraea*) *pacifica* in the upper 100 m of the Santa Susana Formation in Simi Valley represent the earliest occurrence of *Phygraea* on the Pacific coast of North America, and its first occur-

rence on the Pacific coast of North America outside of Baja California Sur, Mexico.

Order Veneroida H. Adams and A. Adams,  
1856

Family Fimbriidae Nicol, 1950

Genus *Fimbria* Megerle von Mühlfeld, 1811

**TYPE SPECIES.** *Fimbria magna* Megerle von Mühlfeld, 1811 [= *Venus fimbriata* Linnaeus, 1758], by original designation; Recent, Indo-Pacific.

*Fimbria susanensis* Squires, 1990

Figure 57

*Fimbria susanensis* Squires, 1990:554, fig. 2.1–2.3.

**PRIMARY TYPE MATERIAL.** UCMP holotype 38568 from UCMP loc. 7009; UCMP paratype 38569 from UCMP loc. 3792. Both specimens from the upper 100 m of the Santa Susana Formation, south side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** “Meganos.”

**GEOGRAPHIC RANGE.** South side Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN loc. 1342 and UCMP loc. 7009.

**REMARKS.** Seven specimens were found, and a few show the hinge. *Fimbria susanensis* has been reported from UCMP localities 3792 and 7009, but, as mentioned under *Velates perversus*, the exact location of UCMP locality 3792 is not known.

Squires (1990) incorrectly equated CSUN locality 1342 with UCMP loc. 3791. The latter locality, which is in close proximity to CSUN locality 1342, actually is the same as CSUN locality 1343.

*Fimbria susanensis* is the earliest occurrence of *Fimbria* in North America (Squires, 1990).

Family Carditidae Fleming, 1828

Genus *Venericardia* Lamarck, 1801

**TYPE SPECIES.** *Venericardia imbricata* Lamarck, 1801 [= *Venericardia imbricata* Gmelin, 1791], by subsequent designation (Schmidt, 1818); Eocene, Paris Basin France.

Subgenus *Pacificor* Verastegui, 1953

**TYPE SPECIES.** *Venericardia mulleri* Verastegui, 1953, by original designation; Paleocene, California.

*Venericardia (Pacificor) calafia susanaensis*  
Verastegui, 1953

Figure 58

*Venericardia (Pacificor) susanaensis* Verastegui, 1953:22–23, pl. 5, figs. 1–4.

*Venericardia (Pacificor) hornii susanaensis* Verastegui, Saul, 1983:pl. 1, fig. 14.

*Venericardia (Pacificor) calafia susanaensis* Verastegui, 1953:22–23, pl. 5, figs. 1–4.

regui, Moore, 1992:E19–E20, pl. 1, figs. 14, 16–18.

**PRIMARY TYPE MATERIAL.** CAS holotype 8004, “Santa Susana shale,” McCray Oil Wells, Oil Canyon, north side of Simi Valley (exact locality unknown), California.

**MOLLUSCAN STAGE RANGE.** “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** North side of Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN locs. 959, 967.

**REMARKS.** Only a few fragments were found at localities 959 and 967. Elsewhere, in the northeast corner of section 31, T 3 N, R 17 W, a few meters below the base of the Lajas Formation, I found an internal mold of a closed-valved specimen. No other megafossils were found with this internal mold. In addition, new housing construction in the southwest corner of section 32, T 3 N, R 17 W uncovered a nearly complete, closed-valved specimen of this bivalve (James Rohrer, Petras Company, personal communication), which I was able to inspect and identify.

The holotype of *Venericardia (P.) calafia susanaensis* is incomplete. The exact location of its type locality is not known, but it is most likely in the upper 100 m of the Santa Susana Formation based on the recent discovery of this subspecies in this part of the formation (see above). The locality of the specimen illustrated by Saul (1983:pl. 1, fig. 14) is UCMP locality 7000, and the exact location of this locality, which is 7.5 m below the Lajas Formation according to Saul (1983), is also not known. Locality 7000 is also where the only specimens of *Turritella meganosensis* known from the upper Santa Susana Formation have been found.

Family Cardiidae Lamarck, 1809

Genus *Nemocardium* Meek, 1876

**TYPE SPECIES.** *Cardium semiasperum* Deshayes, 1858, by subsequent designation (Sacco, 1899); Eocene, Paris Basin, France.

*Nemocardium linteum* (Conrad, 1855)

Figure 59

*Cardium linteum* Conrad, 1855:3, 9; 1857:pl. 2, fig. 1; Anderson and Hanna, 1925:166–167, pl. 3, fig. 3.

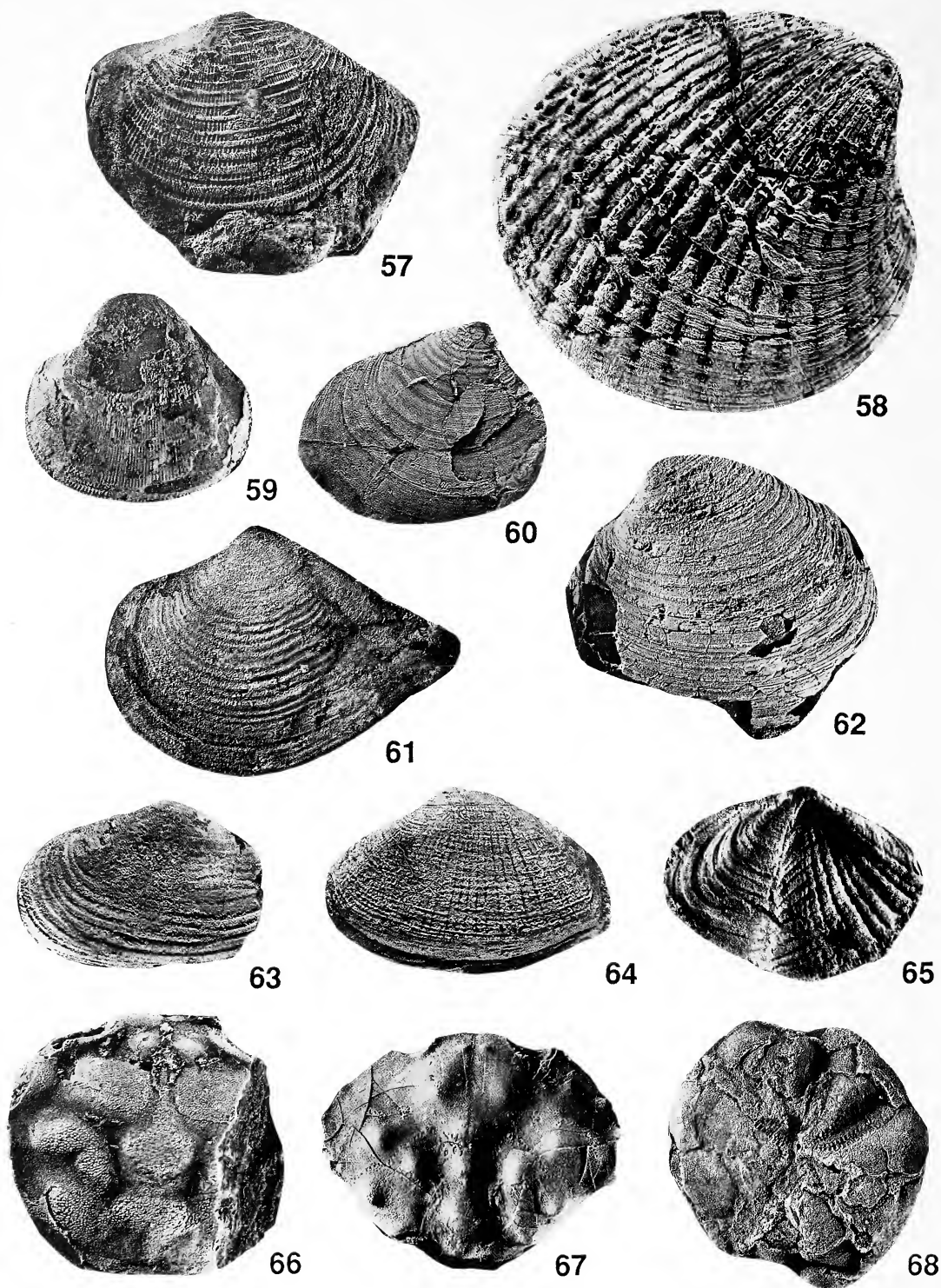
*Cardium cooperii* Gabb, 1864:172, pl. 24, figs. 154–154a; Arnold, 1907b:pl. 38, figs. 2–2a; Waring, 1917:pl. 13, fig. 3; Hanna, 1927:285, pl. 41, figs. 6, 7.

*Cardium dalli* Dickerson, 1913:289, pl. 14, fig. 4a–c.

Not *Cardium dalli* Heilprin, 1887:131, pl. 16a, fig. 70.

*Cardium marysvillensis* Dickerson, 1916:482 [new name for *Cardium dalli* Dickerson, 1913, preoccupied].

*Cardium (Protocardium) marysvillensis* Dickerson, Clark and Woodford, 1927:94, pl. 15, fig. 12.



Figures 57–68. Bivalves, crabs, and spatangoid echinoid from the upper 100 m of the Santa Susana Formation, Simi Valley. All specimens coated with ammonium chloride. 57–65. Bivalves. 57. *Fimbria susanensis* Squires, 1990, left valve,  $\times 1$ , UCMP holotype 38568, UCMP loc. 7009. 58. *Venericardia (Pacifcor) calafia susanensis* Verastegui, 1953, right valve,  $\times 0.8$ , UCMP hypotype 37431, UCMP loc. 7009. 59. *Nemocardium linteum* (Conrad, 1855), ? right valve,  $\times 2.4$ , LACMIP hypotype 12698, LACMIP loc. 26611 [= CSUN loc. 965]. 60. *Saulella undulifera* (Gabb, 1869), latex peel of external mold, right valve,  $\times 2.1$ , LACMIP hypotype 12699, LACMIP loc. 26610 [= CSUN loc. 967]. 61. *Macoma rosa* Hanna, 1927, internal mold, left valve,  $\times 3.6$ , LACMIP hypotype 12700, CSUN loc. 1342. 62. *Pitar uvasana coquillensis* Turner, 1938, left valve,  $\times 2.4$ , LACMIP hypotype 12701, CSUN loc. 1344. 63. *Corbula (Caryocorbula) dickersoni*

*Nemocardium linteum* (Conrad). Stewart, 1930: 275–277, pl. 8, fig. 6; Turner, 1938:52, pl.10, fig. 10; Vokes, 1939:76–77, pl. 11, figs. 6, 9; Weaver, 1943:159–160, pl. 38, fig. 3; 1953:28; Stewart, 1946:pl. 11, fig. 19; Moore, 1968:30, pl. 13, fig. d; Zinsmeister, 1983a:pl. 2, fig. 7; Squires, 1984: 49–50, fig. 12c; 1987:65, 67, fig. 113; 1988b:19, fig. 51; Squires et al., 1992:pl. 1, fig. 33; Squires and Demetrio, 1992:42, fig. 121.

*Cardium* (*Nemocardium*) *lintheum* Conrad. Kleinpell and Weaver, 1963:202, pl. 34, fig. 4.

**PRIMARY TYPE MATERIAL.** USNM holotype 1834, Domingine Formation near Martinez, California.

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12248.

**MOLLUSCAN STAGE RANGE.** “Martinez” through “Tejon.”

**GEOGRAPHIC RANGE.** Eastern Laguna San Ignacio area, Baja California Sur, Mexico, to Pulali Point, Jefferson County, Washington.

**LOCAL OCCURRENCE.** CSUN locs. 965, 1553, 1553a, 1554, 1555.

**REMARKS.** Specimens are uncommon at CSUN locality 1553 and rare at the other localities.

Family Tellinidae Blainville, 1814

Genus *Saulella* Zinsmeister, 1983b

**TYPE SPECIES.** *Tellina undulifera* Gabb, 1869, by original designation; Paleocene, California.

*Saulella undulifera* (Gabb, 1869)

Figure 60

*Tellina undulifera* Gabb, 1869:183, pl. 3, fig. 74; Dickerson, 1914:pl. 11, fig. 7a–7c.

“*Tellina?*” *undulifera* Gabb. Stewart, 1930:204–205, pl. 7, fig. 8; Nelson, 1925:415, pl. 53, fig. 8a, 8b.

*Saulella undulifera* (Gabb). Zinsmeister, 1983b: 1288, fig. 11, J.

**PRIMARY TYPE MATERIAL.** ANSP holotype 4551, from just “west of Martinez,” California.

**MOLLUSCAN STAGE RANGE.** “Martinez” and “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** Northern Baja California, Mexico, to northern California.

**LOCAL OCCURRENCE.** CSUN loc. 967.

**REMARKS.** Two small specimens (up to 17 mm in height) were found, and both are external molds. They represent the first occurrence of this species

in “Meganos Stage” strata. *Saulella undulifera* has long been used as a guide fossil of the Paleocene of the Pacific coast of North America and is common throughout the “Martinez Stage” in California (Nelson, 1925).

Genus *Macoma* Leach, 1819

**TYPE SPECIES.** *Macoma tenera* Leach, 1819 [= *Tellina calcarea* Gmelin, 1791], by monotypy; Recent, Arctic.

*Macoma rosa* Hanna, 1927

Figure 61

*Macoma rosa* Hanna, 1927:292, pl. 41, figs. 2–5, 8; Clark, 1929:pl. 6, fig. 15; Squires, 1984:50, fig. 12e.

**PRIMARY TYPE MATERIAL.** UCMP holotype 31094, Ardath Shale, UCMP loc. 3993; UCMP paratype 31095, UCMP loc. 5089; UCMP paratypes 31096–31097, UCMP loc. 5085; all from the Ardath Shale, San Diego County, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” and “Domengine” (no specimens known from “Capay Stage”).

**GEOGRAPHIC DISTRIBUTION.** San Diego to Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN loc. 1342.

**REMARKS.** A single internal mold was found, and this specimen represents the first occurrence of this species in “Meganos Stage” strata.

Family Veneridae Rafinesque, 1815

Genus *Pitar* Römer, 1857

**TYPE SPECIES.** *Venus tumens* Gmelin, 1791, by monotypy; Recent, West Africa.

*Pitar uvasana coquillensis* Turner, 1938

Figure 62

*Pitar uvasana coquillensis* Turner, 1938:54, pl. 11, figs. 14–17.

**PRIMARY TYPE MATERIAL.** UCMP holotype 33076, UCMP loc. A-836; UCMP paratypes 33077–33078, UCMP loc. A-838; all from Middle Fork Coquille River, Coos County, Oregon.

**MOLLUSCAN STAGE RANGE.** “Meganos” and “Capay.”

**GEOGRAPHIC DISTRIBUTION.** Simi Valley, California, to Middle Fork Coquille River, Coos County, Oregon.

←

Weaver and Palmer, 1922, left valve,  $\times 4.5$ , LACMIP hypotype 12702, CSUN loc. 1344. 64. *Corbula* (*Caryocorbula*) *parilis* Gabb, 1864, left valve,  $\times 4.4$ , LACMIP hypotype 12703, CSUN loc. 958. 65. *Netastoma squiresi* Kennedy, 1993, external (concave) mold of left valve, specimen lighted to give the effect of being a convex right valve,  $\times 3.8$ , LACMIP holotype 8405, CSUN loc. 967. 66, 67. Crabs. 66. *Cyclocorystes alderoni* Squires, 1980, dorsal view,  $\times 4$ , LACMIP hypotype 12704, CSUN loc. 965. 67. *Zanthopsis* sp., aff. *Z. hendersoni* Rathbun, 1926, dorsal view,  $\times 1.1$ , LACMIP hypotype 12705, CSUN loc. 958. 68. *Spatangoid echinoid*. *Schizaster diabloensis* Kew, 1920, crushed internal mold, aboral view,  $\times 1.9$ , LACMIP hypotype 12706, LACMIP loc. 26610 [= CSUN loc. 967].

**LOCAL OCCURRENCE.** CSUN locs. 1344, 1346, 1348.

**REMARKS.** Specimens are rare to common and most common at CSUN locality 1344. All specimens are single valves and are mostly poorly preserved due to weathering. These specimens represent the first occurrence of this species in "Meganos Stage" strata and its first occurrence outside of southwestern Oregon.

Order Myoida Stoliczka, 1870

Family Corbulidae Lamarck, 1818

Genus *Corbula* Bruguière, 1797

**TYPE SPECIES.** *Corbula sulcata* Lamarck, 1801, by subsequent designation (Schmidt, 1818); Recent, West Africa.

Subgenus *Caryocorbula* Gardner, 1926

**TYPE SPECIES.** *Corbula alabamiensis* Lea, 1833, by original designation; Eocene, Alabama.

*Corbula* (*Caryocorbula*) *dickersoni* Weaver and Palmer, 1922

Figure 63

*Corbula dickersoni* Weaver and Palmer, 1922:24–25, pl. 9, figs. 9–10; Clark, 1938:700, pl. 1, fig. 17; Weaver, 1943:257–258, pl. 61, figs. 13, 16–17, 20; Deméré et al., 1979:pl. 2, fig. 11.

*Corbula* (*Caryocorbula*) *dickersoni* Weaver and Palmer. Vokes, 1939:98, pl. 16, figs. 1, 5, 9. Givens, 1974:57, pl. 4, fig. 7. Squires, 1984:53, fig. 12m; 1987:70–71, fig. 124.

**PRIMARY TYPE MATERIAL.** CAS holotype 7452, CAS paratypes 7452A–B, both from UW loc. 329, Cowlitz Formation, Lewis County, Washington.

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12249.

**MOLLUSCAN STAGE RANGE.** "Meganos" through "Tejon."

**GEOGRAPHIC RANGE.** San Diego, California, to Little River area, Grays Harbor County, Washington.

**LOCAL OCCURRENCE.** CSUN loc. 1344.

**REMARKS.** A single specimen was found, and it represents the first occurrence of this species in "Meganos Stage" strata.

*Corbula* (*Caryocorbula*) *parilis* Gabb, 1864

Figure 64

*Corbula parilis* Gabb, 1864:150, pl. 29, figs. 239, 239a; Arnold, 1910:106, pl. 2, fig. 2; Dickerson, 1915:84, pl. 4, fig. 8; 1916:pl. 40, fig. 10; Hanna, 1927:295, pl. 43, figs. 7–11, 13; Stewart, 1930:288–289, pl. 3, fig. 5; 1946:pl. 11, figs. 9, 10; Turner, 1938:65–66, pl. 8, figs. 11–14; Weaver, 1943:256, pl. 59, fig. 16.

*Corbula* (*Caryocorbula*) *parilis* Gabb. Vokes, 1939:

99, pl. 16, figs. 2–3, 6–7, 10; Givens, 1974:57, pl. 4, fig. 9; Squires, 1987:71, fig. 125.

**PRIMARY TYPE MATERIAL.** UCMP holotype 33151, Eocene strata, Martinez, California.

**MOLLUSCAN STAGE RANGE.** "Meganos" through "Transition."

**GEOGRAPHIC DISTRIBUTION.** San Diego, California, to southwestern Oregon.

**LOCAL OCCURRENCE.** CSUN locs. 958, 967.

**REMARKS.** Specimens are rare and are well-preserved single valves. These specimens represent the first occurrence of this species in "Meganos Stage" strata.

Family Pholadidae Lamarck, 1809

Genus *Netastoma* Carpenter, 1864

**TYPE SPECIES.** *Pholas darwinii* Sowerby, 1849, by monotypy; Recent, southeastern Pacific.

*Netastoma squiresi* Kennedy, 1993

Figure 65

*Netastoma squiresi* Kennedy, 1993:400, 402, fig. 2.9, 2.10.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 8405, CSUN loc. 967, upper 100 m of the Santa Susana Formation, north side of Simi Valley, California.

**MOLLUSCAN STAGE RANGE.** "Meganos."

**GEOGRAPHIC DISTRIBUTION.** North side of Simi Valley, California.

**LOCAL OCCURRENCE.** CSUN loc. 967.

**REMARKS.** Only the holotype is known for this species. It is an external mold of a juvenile left valve. *Netastoma squiresi* is the oldest known representative of the genus, whose geologic range was previously known as Pliocene to Recent (Kennedy, 1993).

Phylum Arthropoda Siebold and Stannius, 1848

Class Malacostraca Latreille, 1806

Order Decapoda Latreille, 1803

Family Xanthidae MacLeay, 1838

Genus *Cyclocorystes* Bell, 1858

**TYPE SPECIES.** *Cyclocorystes pulchellus* Bell, 1858, by original designation; early Eocene, England.

*Cyclocorystes aldersoni* Squires, 1980

Figure 66

*Cyclocorystes aldersoni* Squires, 1980:474–475, figs. 2, 3.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 5893; LACMIP paratypes 5864–5866; all from CSUN loc. 354, upper Santa Susana Forma-



tion, east-central Santa Monica Mountains, California.

**MOLLUSCAN STAGE RANGE.** “Martinez” and “Meganos.”

**GEOGRAPHIC DISTRIBUTION.** Garapito Creek, east-central Santa Monica Mountains, Los Angeles County, and south side of Simi Valley; both in southern California.

**LOCAL OCCURRENCE.** CSUN locs. 965, 966.

**REMARKS.** Specimens are rare, moderately well preserved, and missing their legs. These specimens represent the first occurrence of this species in “Meganos Stage” strata and its first occurrence outside of the Santa Monica Mountains.

Genus *Zanthopsis* M’Coy, 1849

**TYPE SPECIES.** *Cancer leachii* Desmarest, 1822, by original designation; early Eocene, England.

*Zanthopsis* sp., aff. *Z. hendersoni* Rathbun, 1926

Figure 67

**LOCAL OCCURRENCE.** CSUN loc. 958.

**REMARKS.** Two internal molds were found. They show close affinity with *Zanthopsis hendersoni* Rathbun, 1926, from Oligocene rocks in Oregon and from the upper part of the Santa Susana Formation on the north side of Simi Valley. The exact location of the type locality of *Z. hendersoni* is not known, but it is near Eugene in Lane County, Oregon. The specimens from CSUN locality 958 differ from *Z. hendersoni* Rathbun (1926: 53–54, pl. 10, figs. 5, 6) by having a frontal region that is much less produced and not dentate and by having a tubercle on each of the proto gastric areas. The frontal region on specimens from CSUN locality 958 is essentially straight and without teeth. It is possible that the material from the upper part of the Santa Susana Formation represents a new species. More specimens of *Z. hendersoni* are needed to determine the full range of morphologic variability of this species. Only then will it be possible to decide if the specimens of *Z. sp.*, aff. *Z. hendersoni* represent a new species.

The geologic range of genus *Zanthopsis* is Paleocene to Oligocene, with distribution in Europe, West Africa, West Indies, Panama, and North America (Glaessner, 1969).

Phylum Echinodermata Klein, 1734

Class Echinoidea Leske, 1778

Order Spatangoida Claus, 1876

Family Schizasteridae Lambert, 1905

Genus *Schizaster* Agassiz, 1836

**TYPE SPECIES.** *Schizaster studeri* Agassiz, 1836, by subsequent designation (ICZN, 1948:523–529, opin. 209); late Eocene, Italy and southern France.

*Schizaster diabloensis* Kew, 1920

Figure 68

*Schizaster diabloensis* Kew, 1920:150–151, pl. 41, fig. 5a–c; Clark and Woodford, 1927:123, pl. 22, fig. 14; Clark, 1929:pl. 4, fig. 13; Squires, 1984: 56, fig. 13d; 1994:pl. 3, fig. 8.

**PRIMARY TYPE MATERIAL.** UCMP holotype 11387, UCMP loc. 1427, Eocene strata, south side of Mount Diablo, California.

**MOLLUSCAN STAGE RANGE.** “Meganos” through middle part of “Tejon.”

**GEOGRAPHIC DISTRIBUTION.** Simi Valley, California, through Marysville Buttes, California.

**LOCAL OCCURRENCE.** LACMIP loc. 26610.

**REMARKS.** Three specimens were found. Two are badly crushed internal molds. The other specimen (Fig. 68) is a partial external mold.

Clark and Woodford (1927) and Clark (1929) reported *Schizaster diabloensis* as occurring in the “Meganos horizon” at various places throughout California, including Simi Valley, but they provided few stratigraphic details. The specimens from LACMIP locality 26610 confirm the presence of this species in “Meganos Stage” strata. Squires (1994) recently reported the youngest occurrence of *S. diabloensis* to be in the Coldwater Sandstone (middle part of the “Tejon Stage”) in upper Sespe Creek, Ventura County, California.

LOCALITIES

All base maps are U.S. Geological Survey, 7.5-minute (unless otherwise stated), topographic quadrangles.

CAS LOCALITIES

711. “On the east side of Grapevine Canyon near the point where the stream flows out upon the valley floor” (Anderson and Hanna, 1925:39). Grapevine quadrangle, Kern County, California.

30667. At elevation 800 m along crest of ridge on north side of Media Agua Creek, 442 m north and 183 m east of SW corner of section 27, T 28 S, R 19 E, La Yeguas Ranch quadrangle, 1959, Kern County, south-central California.

CSUN LOCALITIES

NORTH SIDE OF SIMI VALLEY

All are in the upper 100 m of the Santa Susana Formation (“Meganos Stage”) and, unless otherwise stated, in the Santa Susana quadrangle, 1951 (photorevised 1969), Ventura County, southern California. See Fig. 2 for stratigraphic position relative to the base and top of the upper 100 m of the Santa Susana Formation.

354. East bank of the south fork of Garapito Creek, 518 m S20°E from the intersection of the San Bernardino baseline and Los Angeles City boundary, Topanga quadrangle, 1952, Los Angeles County, southern California. Collected by R. Squires, 1979.

958. Bulldozer-generated exposure now under houses, at elevation of 346 m, just west of intersection of Chumash Street and Indian Hills Drive, 381 m south and 107

m east of section 5, T 2 N, R 17 W. Collected by R.L. Squires, Aug. 19, 1984.

959. At elevation of 347 m, 373 m east and 55 m south of NW corner of section 5, T 2 N, R 17 W. Collected by R.L. Squires, Aug. 24, 1984.

960. At elevation of 390 m, on south bank of Las Lajas Canyon, 594 m east and 579 m north of SW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, Aug. 24, 1984, and Feb. 28, 1986.

961. At elevation of 376 m, on north bank of Las Lajas Canyon, 693 m east and 739 m north of SW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, Aug. 24, 1984.

962. At elevation of 451 m, on east side of dirt road, 756 m east and 411 m south of NW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, February 28, 1986.

963. At elevation of 483 m, 735 m east and 305 m south of NW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, February 28, 1986.

964. [= LACMIP 21551]. At elevation of 509 m, in middle of dirt road, 792 m east and 171 m south of NW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, February 28, 1986.

965. [= LACMIP 16111]. At elevation of 527 m, on east side of dirt road, 792 m east and 94 m south of NW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, Feb. 28, 1986.

966. [= LACMIP 16893 and LACMIP 26609]. At elevation of 529 m, on east side of dirt road, 792 m east and 152 m south of NW corner of section 32, T 3 N, R 17 W. Collected by R.L. Squires, February 28, 1986.

967. [= LACMIP 12648 and LACMIP 26610]. At elevation of 533 m, just east of dirt road and on northeast side of small hill, 762 m east and 183 m north of SW corner of section 29, T 3 N, R 17 W. Collected by H. Seiden, 1951, and R.L. Squires, Feb. 28, 1986.

968. At elevation of 427 m, 457 m east and 308 m south of NW corner of section 32, T 3 N, R 17 W. This locality is about 3 m stratigraphically below base of Lajas Formation. Collected by R.L. Squires, Feb. 28, 1986.

969. [= LACMIP 16894]. At elevation of 381 m, on east side of Chivo Canyon, 343 m west and 107 m north of SE corner of section 30, T 3 N, R 17 W. Collected by R.L. Squires, March 1, 1986.

970. At elevation of 415 m, on north side of small tributary of east side of Chivo Canyon, 119 m west and 122 m north of SE corner of section 30, T 3 N, R 17 W. Collected by R.L. Squires, March 1, 1986.

971. At elevation of 401 m, on north side of small tributary of east side of Chivo Canyon, 21 m west and 107 m north of SE corner of section 30, T 3 N, R 17 W. Collected by R.L. Squires, March 1, 1986.

972. At elevation of 407 m, on north side of small tributary of east side of Chivo Canyon, 30 m west and 119 m north of SE corner of section 30, T 3 N, R 17 W. Collected by R.L. Squires, March 1, 1986.

973. [= LACMIP 16895]. At elevation of 412 m, near head of small tributary of east side of Chivo Canyon, 31 m west and 122 m north of SE corner of section 30, T 3 N, R 17 W.

## SOUTH SIDE OF SIMI VALLEY

All are in the upper 100 m of the Santa Susana Formation ("Meganos Stage") and, unless otherwise stated, in the Calabasas quadrangle, 1952 (photorevised 1967), Ventura County, southern California.

1342. Top of hill at elevation of 431 m, 38 m west and 762 m north of SE corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 14, 1989. This locality is in close proximity to CSUN loc. 1343 and 3 m stratigraphically below it.

1343. [= UCMP 3791]. On east side of hill at elevation of 427 m, 23 m west and 785 m north of SE corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 14, 1989. This locality is in close proximity to CSUN loc. 1342 and 3 m stratigraphically above it.

1344. In saddle at elevation of 419 m, 183 m west and 823 m north of SE corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 14, 1989.

1345. On west side of Runkle Canyon, at elevation of 355 m, 664 m east and 168 m south of NW corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 16, 1989.

1346. On west side of Runkle Canyon, at elevation of 335 m, 739 m east and 148 m south of NW corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 16, 1989.

1347. On west side of Runkle Canyon, at elevation of 353 m, 655 m east and 125 m south of NW corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 16, 1989.

1348. On west side of Runkle Canyon, at elevation of 325 m, 777 m east and 61 m south of NW corner of section 22, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 16, 1989.

1349. On east side of Runkle Canyon, at elevation of 317 m, 579 m west and 1579 m south of NE corner of section 14, T 2 N, R 18 W. Collected by R.L. Squires, Aug. 16, 1989.

1565. At elevation of 340 m, along west side of Bus Canyon, on north bank of an unnamed tributary that enters Bus Canyon from the west, 274 m south and 503 m west of NE corner of section 28, T 2 N, R 18 W, Thousand Oaks quadrangle, 1950 (photorevised 1967), Ventura County, southern California. Collected by A.J. Marro, 1985.

## LACMIP LOCALITIES

461-B. On the northern slope of a small canyon intersecting Las Lajas Canyon from the east, Santa Susana quadrangle, 1959 (photorevised 1961), Ventura County, southern California. Collected by J.A. Sutherland, circa early 1960s. This locality is 61 m (200 ft.) from the top of the Lajas Formation.

7124. At elevation of 343 m, 610 m S45°W of 1480 ft. hill, SW 1/4 of section 13, T 2 N, R 18 W, Calabasas quadrangle, 1952 (photorevised 1967), Ventura County, southern California. Collected by W.P. Popenoe and M. Sperling, July 4, 1929.

12648. See CSUN 967.

21551. See CSUN 964.

23173. [Exact stratigraphic position not known.] About 15 m downslope from top of east-west trending ridge, southwest of Runkle Canyon, approximately 884 m north and 427 m west of SE corner of section 27, T 2 N, R 18 W, Calabasas quadrangle, 1952 (photorevised 1967), Ventura County, southern California. Collected by J.H. Fantozzi, Oct. 3, 1953.

26609. See CSUN 966.

26610. See CSUN 967.

26111. See CSUN 965.

26615. At elevation of 466 m, 518 m east of NW corner of section 32, on section line between sections 29 and 32,



T 3 N, R 17 W, Santa Susana quadrangle, 1959 (photo-revised 1961), Ventura County, southern California. Collected by H. Seiden, 1952.

## UCMP LOCALITIES

672. South portion of crest of Parson's Peak, SE 1/4 of the NW 1/4 of section 24, T 18 S, R 14 E, Coalinga quadrangle, Fresno County, California.

1427. SW 1/4 of section 11, northeast of Wall Point, south side of Mount Diablo, northern California.

3157. On ridge top on north side of Deer Valley, 792 m south and 411 m west of NE corner of section 20, T 1 N, R 2 E, Antioch South quadrangle, 1980, Contra Costa County, northern California. Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark and Woodford (1927)]. Collected by B.L. Clark and A.O. Woodford, circa 1923.

3159. On same ridge top as UCMP loc. 3157, 1036 m south and 46 m west of NE corner of section 20, T 1 N, R 2 E, Antioch South quadrangle, 1980, Contra Costa County, northern California. Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark and Woodford (1927)]. Collected by B.L. Clark and A.O. Woodford, circa 1923.

3577. On ridge top 3399 m north and 610 m east of SW corner of Brentwood quadrangle, 1978, Contra Costa County, northern California. Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark and Woodford (1927)]. Collected by B.L. Clark and A.O. Woodford, circa 1923.

3791. [see CSUN 1343]. Collected by R.N. Nelson, circa early 1920s.

3792. [Exact stratigraphic position not known]. West of Runkle Canyon on same ridge as UCMP loc. 3791, NE1/4 SE1/4 of section 22, T 2 N, R 18 W, Calabasas quadrangle, 1952 (photorevised 1967), Ventura County, southern California. Collected by R.N. Nelson, circa early 1920s.

3796. [Exact stratigraphic position not known]. On ridge at elevation of 640 m, 1524 m N68°W of 2150 ft. hill, south 1/2, NE 1/4 of section 27, T 2 N, R 18 W, Calabasas quadrangle, 1952 (photorevised 1967), Ventura County, southern California. Collected by R.N. Nelson, circa early 1920s.

3993. In bottom of Rose Creek where creek makes a strong bend to west, .3 km (.2 mi.) south of Bench Mark 176, 3.2 km east of La Jolla, La Jolla quadrangle, San Diego County, California.

5062. In sea cliff south of mouth of Soledad Valley, due west of midpoint between "P" and "u" of "Pueblo," La Jolla quadrangle, San Diego County, California.

5085. 2.62 inches north of the top of the "S" of "Soledad Mountain," on the north side of the creek, on a small ridge formed by the creek and sea cliff, elevation 22 m, La Jolla quadrangle, San Diego, California.

5089. 91 m (300 ft.) north of the Scripps Institution pier, in the conglomerate above the mudstone. In the sea cliff, elevation 3 m, La Jolla quadrangle, San Diego County, California.

7000. [Exact location not known]. Las Lajas Canyon, in first canyon on north side of road, .4 km east of point where boundary line of Century Oil property crosses road, Santa Susana quadrangle, Ventura County, California.

7004. About 91 m east of locality 7003 in next small canyon that enters Lajas Canyon from the east just south of the most northerly extension of the 717-m (1500-ft.)

contour, Santa Susana quadrangle, Ventura County, California. Locality is equivalent to CSUN loc. 374.

7009. At elevation of 378 m in a small gully, in sandy shale about 100 m north of UCMP loc. 3759 [= 2134 m south of BM 961 at Santa Susana well, flank of 717-m (1500-ft.) hill] in sandy shale, 378 m elevation, Santa Susana quadrangle, Ventura County, California. Collected by R.B. Stewart.

A-836. About 3 km west of town of Remote, in bed of Middle Fork of Coquille River opposite Roseburg-Coos Bay Highway 42, White Rock quadrangle, Coos County, southwestern Oregon.

A-838. West of town of Remote, in bed of Middle Fork of Coquille River opposite Roseburg-Coos Bay Highway 42, White Rock quadrangle, Coos County, southwestern Oregon.

A-993. Second gully past Marrland Canyon (now known as Las Lajas Canyon) at second small falls up gully approximately 183 m, Santa Susana quadrangle, Ventura County, California.

A-994. About 69 to 91 m down the canyon from UCMP loc. A-993 on west side of canyon about 18 m from streambed, Santa Susana quadrangle, Ventura County, California.

## UW LOCALITY

329. On north bank of the Cowlitz River at bend 1.5 to 2.5 km east of Vader, section 28, T 1 N, R 2 W, Castle Rock quadrangle (15-minute), 1953, Lewis County, Washington.

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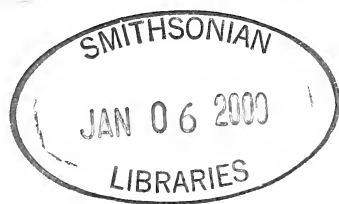
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# CONTRIBUTIONS IN SCIENCE

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MIDDLE EOCENE BRACKISH-MARINE  
MOLLUSKS FROM THE MATILJA SANDSTONE  
AT MATILJA HOT SPRINGS, VENTURA  
COUNTY, SOUTHERN CALIFORNIA

RICHARD L. SQUIRES



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# MIDDLE EOCENE BRACKISH-MARINE MOLLUSKS FROM THE MATILIJA SANDSTONE AT MATILIJA HOT SPRINGS, VENTURA COUNTY, SOUTHERN CALIFORNIA

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RICHARD L. SQUIRES<sup>1</sup>

**ABSTRACT.** This study is the first detailed account of within-habitat, brackish-marine Eocene mollusks in the Transverse Ranges of southern California. The fossils are from the lower middle Eocene ("Transition Stage") upper part of the Matilija Sandstone at Matilija Hot Springs, near Ojai, Ventura County, southern California. Sixteen species (eight gastropods and eight bivalves) were found, and three of these are new: a gastropod *Tympanotonos* (T.) *californicus* new species, and two bivalves *Neotrapezium californicum* new species and *Corbicula jestesi* new species. This is the first confirmed record of *Tympanotonos* in North America and the first record of *Neotrapezium* in North America. The megafauna contains the earliest known record of the gastropod "*Melanatria*" *markleyensis* and the latest known records of the bivalves *Barbatia* (B.) *morsei*, "*Tellina*" *joaquinensis*, and "*Tellina*" *domingenensis*.

The local brackish-marine section, which is approximately 55 m thick, was deposited on the upper part of a deltaic complex and consists of lagoonal mudstones and siltstones alternating with beach or barrier-bar sandstones. Within the lagoonal rocks are interbeds of coastal-sabkha limestone and gypsum, as well as subaerial? redbeds. Mollusks are abundant within the lagoonal rocks and represent parautochthonous assemblages that have undergone varying amounts of postmortem transport but were not moved out of their original lagoonal habitat of mud and silt. Other megafossils are rare. Some of the molluscan assemblages consist of up to 13 species of mollusks. All of the shells are unabraded, and many are complete. Other assemblages consist entirely of concentrations of either the bivalve *Pelecypora aequilateralis* or the bivalve *Cuneocorbula torreyensis*. Both types of concentrations consist of tightly packed, unabraded single valves. Within some of the beach and barrier-bar sandstones are fragments of the oyster *Acutostrea idriaensis idriaensis*, which were transported out of their muddy lagoonal habitat.

## INTRODUCTION

Brackish-marine rocks are uncommon in the rock record because they are highly susceptible to erosion. A local, 55-m-thick section of middle Eocene ("Transition Stage") brackish-marine rocks in the upper part of the Matilija Sandstone at Matilija Hot Springs, located 6.5 km northwest of the city of Ojai in Ventura County, southern California (Fig. 1A), was preserved because it underwent subsidence and was overlain by a protective cover of deeper marine deposits. Kerr and Schenck (1928) were the first to recognize the brackish-marine aspect of these rocks. They reported a "lignitic facies" with abundant specimens of mollusks near Matilija Hot Springs, but they believed that the facies was confined to a single bed. Jestes (1963) was the first to more fully recognize the extent of this brackish-marine paleoenvironment, which he documented by means of a preliminary study of the fossil mollusks. Link (1975) and Link and Welton (1982) did

sedimentological studies that confirmed Jestes' interpretation. They utilized Jestes' preliminary molluscan studies but did not elaborate on them. Molluscan fossils are abundant and, in many cases, well preserved in these rocks, but until this present study, they were not analyzed in detail. Squires (1991a, 1998) worked on two of the gastropod species from these rocks, namely *Potamides* (*Potamidopsis*) *californica* Squires, 1991a, and *Loxotrema turritum* Gabb, 1868. In recent years, I have become increasingly interested in brackish-marine Eocene rocks, and my students and I have returned on many occasions to the Matilija Hot Springs section to undertake more detailed studies. The goal of this present article is to fully document, for the first time, all the mollusks and to give the details of their stratigraphic distribution in the study area.

The molluscan stage terminology used here stems from Clark and Vokes (1936), who proposed five mollusk-based provincial Eocene stages: "Meganos" (uppermost Paleocene to lowermost Eocene), "Capay" (middle lower Eocene), "Domengine" (upper lower to lower middle Eocene), "Transition" (lower middle Eocene), and "Tejon" (middle middle Eocene to upper Eocene). Givens (1974) modified the use of the "Capay Stage." The stage names are

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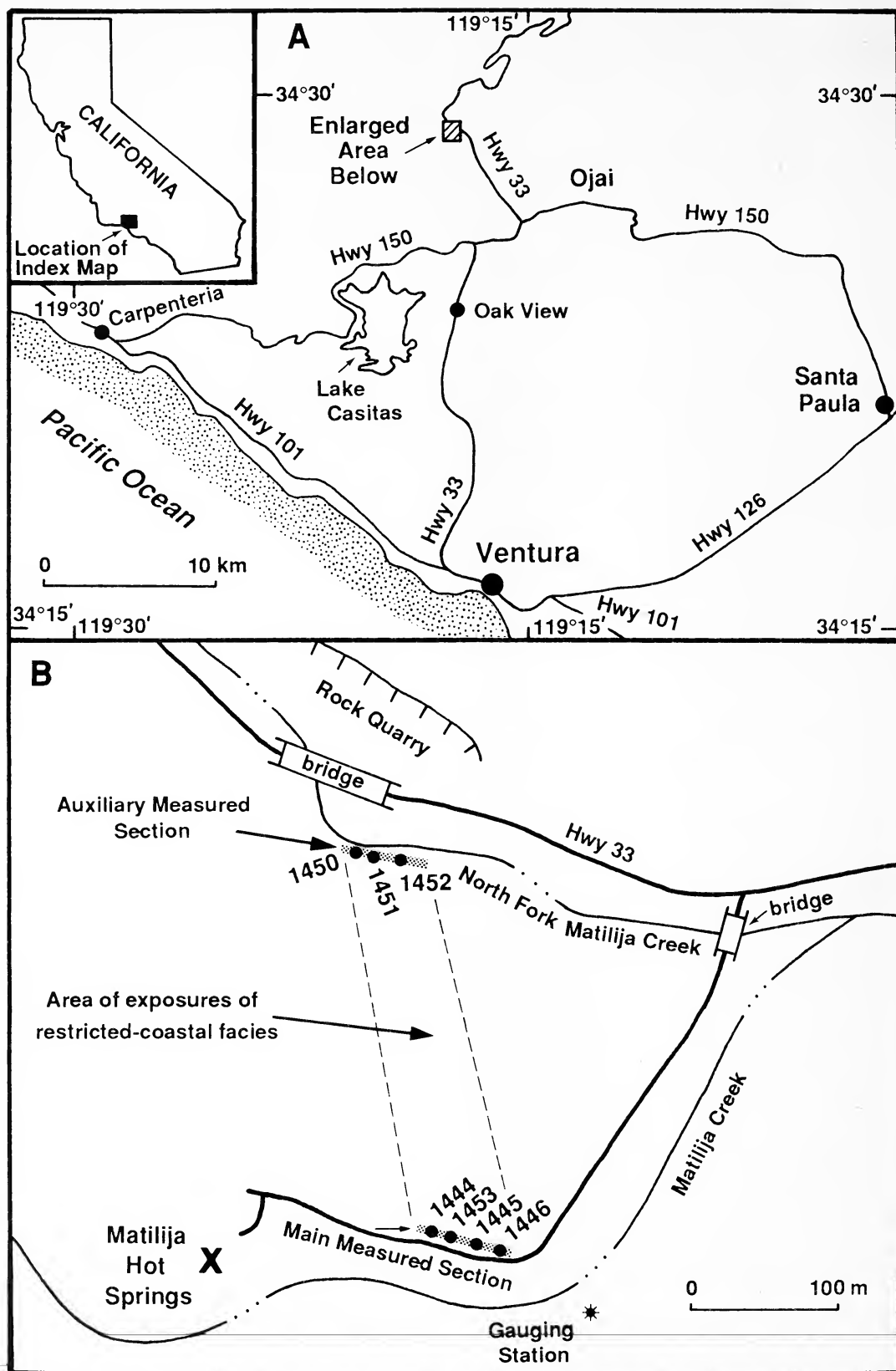


Figure 1. Index map showing (A) the generalized location and (B) the detailed location of Matilija Hot Springs, Ventura County, southern California. Part (B) also shows locations of the measured sections and of the CSUN megafossil localities.

in quotes because they are informal terms. Squires (in press) correlated all the stages, except the upper part of the "Tejon Stage," to the standard calcareous nannofossil zonation.

In this present article, the term "brackish marine" refers to restricted waters with salinities lower than those of normal ocean waters. Furthermore, the term "brackish marine" refers to waters landward of beaches or barrier bars but with some connection to the shallow-marine environment. The term "shallow marine" refers to unrestricted, nearshore waters of normal ocean salinity seaward of beaches or barrier bars.

The following institutional acronyms are used:

ANSP	Academy of Natural Sciences, Philadelphia
CSUN	California State University, Department of Geological Sciences, Northridge
LACM	Natural History Museum of Los Angeles County, Section of Malacology
LACMIP	Natural History Museum of Los Angeles County, Section of Invertebrate Paleontology
MCZ	Museum of Comparative Zoology, Harvard University
UCMP	University of California Museum of Paleontology, Berkeley
UCR	University of California, Riverside
USGS	United States Geological Survey, Reston, Virginia

## STRATIGRAPHY

The study area rocks are in the upper part of the Matilija Sandstone and crop out in a small area bounded on the south by a side road leading to the Matilija Hot Springs and on the north by the river bed of the North Fork Matilija Creek, a distance of 270 m (Fig. 1B). This general area is also the type section of the Matilija Sandstone, named by Kerr and Schenck (1928). The study area rocks consist of resistant beds of sandstone, 1 to 5 m thick, alternating with nonresistant, finer grained intervals, about 2 to 7 m thick. These alternating rock types will be referred to as the "restricted-coastal facies." The finer grained intervals consist of complexly interbedded mudstone, fossiliferous mudstone, siltstone, claystone, limestone, and gypsum, as well as stringers of sandstone. Although Link and Welton (1982: fig. 3, section 5) provided a columnar section of the restricted-coastal facies, they did not indicate which beds contain fossils. This present study revealed, for the first time, the stratigraphic distribution of these fossils (Figs. 2, 3).

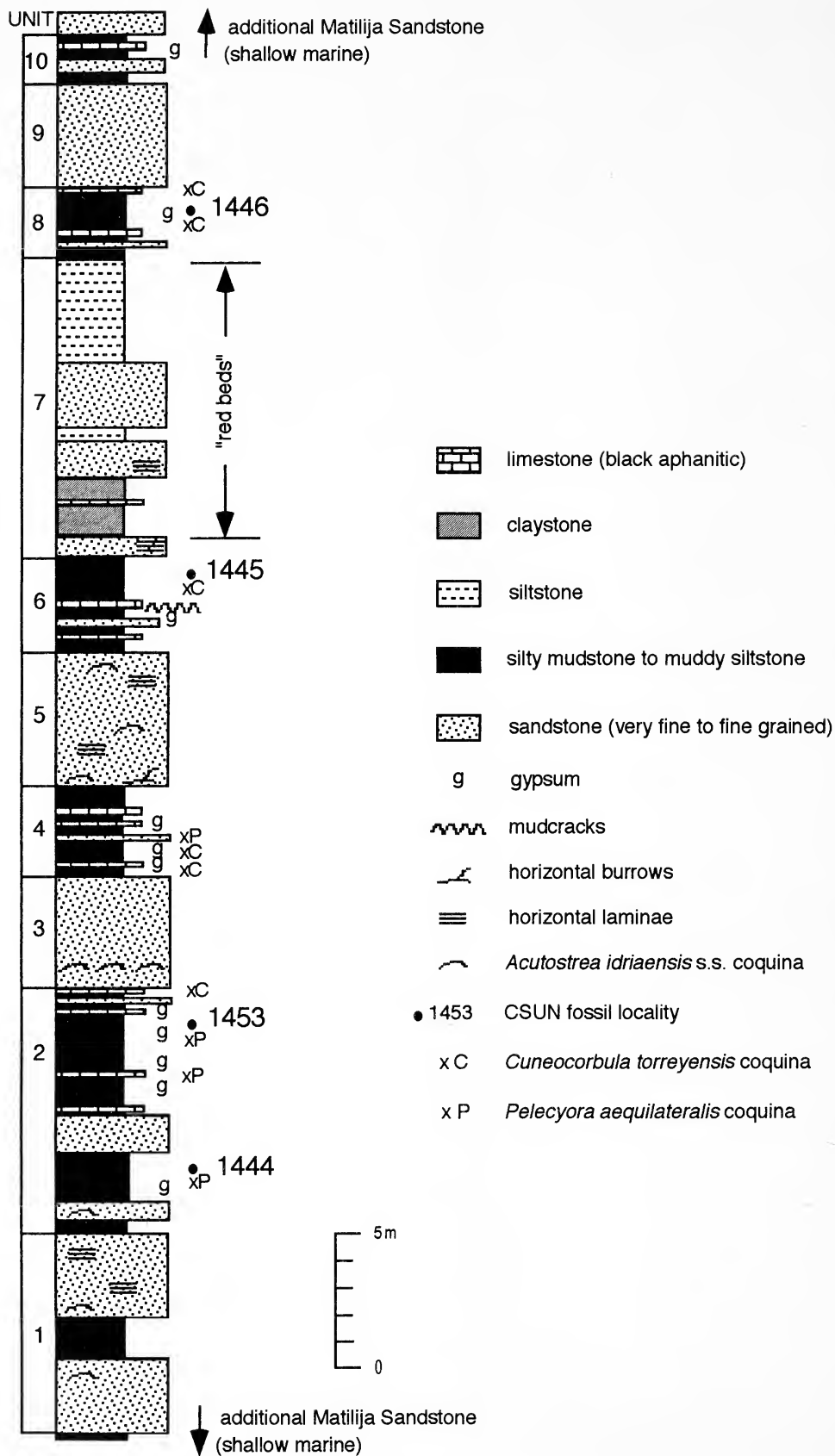
The most accessible and best exposed section of the restricted-coastal facies is in a roadcut along the north side of the side road leading to Matilija Hot

Springs (Fig. 1B). The roadcut exposes a continuous section of nearly vertical beds, and this is where Link and Welton (1982) and Jestes (1963) focused their studies. This is also where I measured my main section (Fig. 2). I did a microstratigraphic study and recorded every change in lithology and every place where fossils were found. The side of the roadcut is steep, and access to some of the beds is extremely limited.

An auxiliary section was measured along the south side of the riverbed of the North Fork of Matilija Creek (Figs. 1B, 3). The lower part of the section is accessible, but the middle part is along the cut-bank side of the creek. Access is difficult when there is considerable water flow in the creek. The upper part of the section is covered. Very steep slopes and dense brush prevent "walking out" of individual beds between the main and the auxiliary measured sections. Although individual beds could not be correlated between the two sections, six stratigraphic units are recognizable at both sections. These units, which are denoted on Figures 2 and 3 as units 1 through 6, consist of alternating sandstone and finer grained units that are similar in terms of lithology and overall fossil content. The finer grained units thin toward the auxiliary section. Additional complex stratigraphic units (7 through 10) are present at the main section, but at the auxiliary section only a single, very thick sandstone and an overlying thick covered interval correspond to units 7 through 10. Unit 7 at the main section is an interval of "red-beds" consisting of unfossiliferous sandstone, siltstone, and claystone beds. In addition to having some red color, rocks in this interval show much variation in color, with gray, maroon, bluish gray, and greenish gray also present.

A few meters of fossiliferous mudstone and interbedded sandstone were temporarily uncovered by recent bulldozing activity in an active rock quarry on the north side of the North Fork of Matilija Creek (Fig. 1B), but private property and safety restrictions make this area inaccessible. Extensive slope wash and dense brush prevent the detection of any more exposures of the study area rocks immediately south of the roadcut along the road to Matilija Hot Springs and immediately north of the rock quarry.

The sandstones in the restricted-coastal facies usually are fine grained, tabular units that are nearly structureless. Some of them are horizontally laminated, and a few have horizontal burrows near their lower contact. Most of the sandstones are not fossiliferous (Figs. 2, 3). The only fossils found in them are scarce fragments of the oyster *Acutostrea idriaensis idriaensis* (Gabb, 1869). The most abundant oyster fragments are in a 10-cm-thick limy sandstone interbed near the base of a 4-m-thick sandstone (unit 3) in the main measured section. In this interbed, the oysters form a coquina consisting of fragments of single valves, which are thick shelled and concave down.



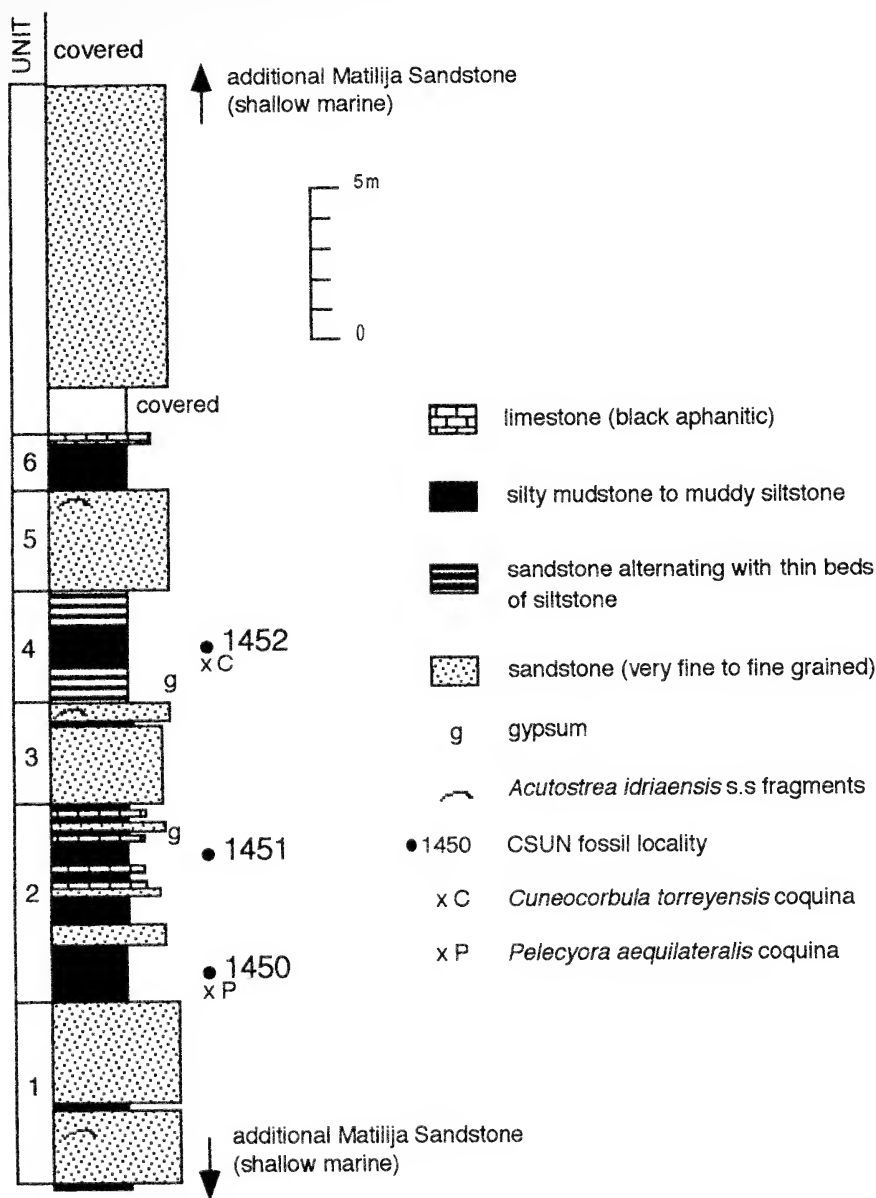


Figure 3. Stratigraphy and CSUN megafossil localities of the restricted-coastal facies in the upper part of the Matilija Sandstone along the auxiliary measured section in the Matilija Hot Springs area. See Figure 1 for location of this measured section.

The finer grained intervals in the restricted-coastal facies show much complexity and variation in the vertical sequence of rock types. It is not unusual to have 10 to 12 changes in lithology in just one meter of vertical section, especially where limestone

and gypsum are present. The best examples are in units 2 (upper half), 4, 6 (lower half), 8, and 10. In these units, aphanitic limestone and gypsum are complexly interbedded with mudstone, gypsiferous mudstone, limy sandstone, thin sandstone, and, in

Figure 2. Stratigraphy and CSUN megafossil localities of the restricted-coastal facies in the upper part of the Matilija Sandstone along the main measured section in the Matilija Hot Springs area. See Figure 1 for location of this measured section.

Table 1. Checklist and abundance of brackish-marine mollusks from CSUN localities in the restricted-coastal facies, upper part of the Matilija Sandstone at Matilija Hot Springs. Localities listed from left to right in ascending stratigraphic order. Localities 1450 and 1451 are 270 m (885 ft.) to the north of the other localities. A  $\geq$ 30 specimens, C = 10–29 specimens, UC = 5–9 specimens, R = 1–4 specimens, — = not found.

Taxa	Localities and abundance						
	1444	1450	1451	1452	1453	1445	1446
Gastropoda							
<i>Crepidula inornata</i>	R	C	—	—	—	C	R
<i>Crommium</i> sp. cf. <i>C. andersoni</i>	UC	R	—	—	—	—	—
<i>Loxotrema turritum</i>	C	A	R	R	—	C	R
“ <i>Melanatria</i> ” <i>markleyensis</i>	—	—	—	—	—	A	UC
<i>Neverita</i> ( <i>Neverita</i> ) <i>globosa</i>	R	R	R	—	—	—	—
<i>Potamides</i> ( <i>Potamidopsis</i> ) <i>californica</i>	A	A	C	—	C	UC	C
<i>Pyrgulfera</i> ( <i>P.</i> ) <i>lajollaensis</i>	—	UC	—	R	R	UC	R
<i>Typanotonos</i> ( <i>T.</i> ) <i>californicus</i> new species	C	A	C	—	A	—	—
Bivalvia							
<i>Acutostrea idriaensis idriaensis</i>	C	C	C	R	—	C	UC
<i>Barbatia</i> ( <i>Barbatia</i> ) <i>morsei</i>	R	C	R	—	—	—	—
<i>Corbicula jestesi</i> new species	—	—	—	R	—	A	—
<i>Cuneocorbula torreyensis</i>	—	—	—	A	—	A	—
<i>Neotrapezium californicum</i> new species	UC	A	R	—	UC	UC	R
<i>Pelecycora aequilateralis</i>	A	A	R	—	UC	C	A
“ <i>Tellina</i> ” <i>domingensis</i>	R	C	—	—	—	R	R
“ <i>Tellina</i> ” <i>joaquinensis</i>	UC	A	UC	UC	C	A	UC

some cases, fossiliferous mudstone. Fossils in the finer grained intervals are confined to mudstone and siltstone (Figs. 2, 3), but not every mudstone or siltstone contains fossils. Fossils in the finer grained intervals are found in either muddy, thin coquina beds or in less densely packed, muddy fossiliferous beds that immediately overlie most of the coquina beds. The latter contain huge numbers of bivalve specimens of either *Pelecycora aequilateralis* (Gabb, 1869) or *Cuneocorbula torreyensis* (Hanna, 1927), and the specimens are always stacked one upon the other and tightly packed. Although many of these specimens have been crushed by compaction, they are otherwise complete and unworn single valves, and, in these respects, differ from usual coquinas found in the rock record. In the less densely packed fossiliferous beds associated with nearly all of these coquina beds, fossils are abundant but more widely spaced. There is much more diversity, with up to 13 species present, and articulated bivalves are common, as well as nearly complete growth series of unworn bivalves and gastropods. Seven of these fossiliferous beds were found in the restricted-coastal facies and represent the localities shown on Figures 1B, 2, and 3 as CSUN localities 1444, 1445, 1446, 1450, 1451, 1452, and 1453. Each locality overlies a coquina bed, except locality 1451, which overlies a limestone bed. There is similarity in the taxonomic composition of the fossils at these localities, but the abundance of the species varies greatly from locality to locality (Table 1).

At CSUN locality 1453, the relationship between

the underlying coquina bed and the overlying fossil bed is especially clear-cut. The coquina bed consists of tightly packed and crushed specimens of *Pelecycora aequilateralis* in a sandy mudstone, and the coquina bed has a sharp contact with an overlying 10-cm-thick black mudstone containing abundant specimens of the gastropod *Tympanotonos* (*T.*) *californicus* new species. These gastropods, which possess sharp spines, are complete, and specimens range from just a few millimeters to 23 mm in length. There are small patches consisting of dense concentrations of only juveniles, some of which show a slight preferred orientation.

A coquina consisting entirely of unworn and unbroken single valves of *Cuneocorbula torreyensis* directly underlies CSUN locality 1445. Some specimens are concave up, some are concave down, and a few are vertical. This coquina bed is distinctive because the specimens of the bivalves form a “shell pavement” along the bedding planes. In the immediately overlying fossiliferous silty mudstone at CSUN locality 1445, there are other mollusks in addition to abundant specimens of *C. torreyensis*. Most notable is the bivalve *Corbicula jestesi* new species. Some shells of this species are articulated, and others are “butterflied,” (i.e., the opposing valves are open and lying adjacent to each other on the bedding plane). Many of the specimens of *Pelecycora aequilateralis*, “*Tellina*” *joaquinensis* Arnold, 1909, and *Neotrapezium californicum* new species in the fossiliferous mudstone are articulated individuals. There are also growth series of *P. aequilateralis* and “*T.*” *joaquinensis*.



At CSUN locality 1450, a *Pelecypora aequilateralis* coquina directly underlies a fossiliferous mudstone in which many specimens of “*Tellina*” *joaquinensis*, *Neotrapezium californicum*, as well as *P. aequilateralis*, were found articulated. Growth series of these three bivalves and of the gastropods *Crepidula inornata* Dickerson, 1916, and *Loxotremma turritum* were also found in this fossiliferous mudstone.

Link and Welton (1982:fig. 3, section 5) reported lignite in the restricted-coastal facies and graphically depicted several lignite beds scattered throughout their measured section, which is located along the same traverse as the main measured section of this present study. I was able to find carbonaceous material (rare, very small pieces of carbonized wood), although only at CSUN locality 1445 and near the top of unit 3 in the auxiliary section. Blackish, lignitic-looking stains are associated with some of the mudstones near CSUN locality 1446, but these stains are related to postdepositional processes. The mudstone at CSUN locality 1453 is black and superficially resembles coal.

## FAUNA

A total of about 1270 molluscan specimens identifiable to species were collected. Preservation of the fossils ranges from poor to moderately good, but many are in poor condition because of crushing, weathering, being coated with tightly adhering mud matrix, or a combination of all three factors. The bivalve specimens generally do not lend themselves for cleaning of the hinge, and, therefore, identification of some of the bivalves was particularly difficult. Many of the bivalves, especially “*Tellina*” *joaquinensis* and *Neotrapezium californicum*, are very fragile because the shells are particularly thin. The hinges are easily destroyed when attempts are made to remove tightly adhering mudstone.

Although I collected most of the studied specimens, I also used Jests’ (1963) collection, which is now stored at LACMIP. Diversity of the entire megafauna is low, with only 16 identifiable species, but some of the species are represented by extremely abundant specimens. Each locality has one to several dominant species, and these vary from locality to locality (Table 1).

Although Link and Welton (1982) reported turritellas and the freshwater bivalve *Unio*? from the study area, these taxa are not present. The so-called “turritellas” are the potamidid *Potamides* (*Potamidopsis*) *californica*, and the *Unio*? is *Neotrapezium californicum*.

The only other megafossils found in the restricted-coastal facies were a few, minute-sized fish scales (in mudstone at CSUN locality 1450) and rare specimens of encrusting bryozoans on oyster shells (at CSUN locality 1444).

## TAPHONOMY

Both Link (1975) and Link and Welton (1982) utilized the unpublished work of Jests (1963) in concluding that the coquinas are made up of brackish-water species that are essentially in place. Squires (1991a, 1998) studied two of the gastropod species from these coquinas and also reported them to have been brackish-water dwellers that have not undergone any significant postmortem transport.

Using the taphonomic terminology of Kidwell et al. (1986), the megafossil assemblages in the finer grained intervals represent parautochthonous assemblages. These are ones that underwent some postmortem transport but were deposited within their original habitat. The amount of postmortem transport is not the same, however, for all the mollusks in the finer grained intervals. Those at each of the seven collecting localities (Figs. 1–3) show little or no obvious evidence of any postmortem transport. They have unworn delicate sculpture, nearly complete growth series of the more abundant species, and are unbroken. There is also a high percentage of articulated and/or “butterflied” specimens, especially of *Pelecypora aequilateralis*, “*Tellina*” *joaquinensis*, and *Neotrapezium californicum*. These assemblages are closely analogous to paleocommunities, but they cannot be referred to as such because no specimens were found in life position. According to Kidwell et al. (1986), paleocommunities (autochthonous assemblages) are composed of specimens preserved in life position. Evidently, the megafossils found at each of the seven collecting localities experienced postmortem transport of a very short distance. At CSUN locality 1453, there is, in fact, some evidence of postmortem transport where localized concentrations of only juvenile *Tympanotonos* (*T.*) *californicus* are found. They show a low degree of preferred orientation. It is not uncommon to find adult shells lying next to each other, with their apices pointing in opposite directions. This is commonly associated with wave sorting of shells, but the amount of postmortem transport must have been slight because the very delicate apical tips are present on many specimens, and sharp projecting nodes are present on nearly every specimen. These localized concentrations grade into mudstone, containing other mollusks that show no obvious signs of postmortem transport.

Burial of all the mollusks must have been rapid because the shells show no clionid sponge boreholes, algal boreholes, or corrosion and only rare cases of epifaunal incrustations by bryozoans. The only boreholes found were on rare specimens of *Tympanotonos* (*T.*) *californicus*, *Pelecypora aequilateralis*, and “*Tellina*” *joaquinensis*. These boreholes most likely were made by the carnivorous gastropods *Crommium* sp. cf. *C. andersoni* (Dickerson, 1914) and *Neverita* (*N.*) *globosa* Gabb, 1869.

The fossils in the muddy coquinalike beds, which usually directly underlie the seven main collecting

localities, were more affected by postmortem transport, as evidenced by their concentration in large numbers of essentially one species (e.g., *Pelecypora aequilateralis* or *Cuneocorbula torreyensis*). Nevertheless, postmortem transport was within the original environment, based on the unworn and unbroken condition of the specimens and the presence of these same species in the immediately overlying assemblages that show little or no obvious signs of postmortem transport.

Using the taphonomic terminology of Kidwell et al. (1986), the fossils in the sandstones represent allochthonous assemblages transported out of their original habitat. These fossils consist only of scattered fragments of the oyster *Acutostrea idriaensis idriaensis* that were transported out of their nearby original muddy environment (see discussion below) and deposited in sand, which represented a foreign substratum. Their transported condition is based on their fragmented condition (mostly small-sized fragments). Only in the lower part of unit 3 in the main measured section are the fragments abundant enough to form an oyster hash. The source of the oysters was local, based on the presence of unworn, large single valves (up to 80 mm long) and a few articulated specimens of the oysters in the subjacent finer grained intervals. When the oysters were transported, they survived the high-energy processes to some degree because of their stout shells.

## DEPOSITIONAL ENVIRONMENT

In the region surrounding the study area, the Matilija Sandstone consists of deep-marine to shallow-marine deltaic facies associated with a major regressive event. In the lower part of the formation, sand-rich proximal turbidite deposition took place in outer neritic, bathyal depths, or both on the flanks of a prograding delta. As the delta prograded and filled the basin, the turbidites were covered by shallow-marine shelf deposits that grade upward into the restricted-coastal deposits, which formed at the delta top. These latter deposits are overlain, in turn, by shallow-marine shelf deposits that make up the uppermost part of the Matilija Sandstone. These uppermost beds are transitional with the deep-water Cozy Dell Shale and record a rapid basin deepening (Link, 1975; Link and Welton, 1982).

Link (1975) reported that the finer grained intervals in the restricted-coastal facies represent a low-energy lagoonal, bay, or estuarine environment. He also reported that the interbedded limestone and gypsum, in association with mudcracks and red beds suggest very shallow, quiet-water deposition in a high-evaporation environment. Furthermore, he reported that the sandstones formed in much higher energy conditions associated with narrow beaches or tidal channels. Link and Welton (1982) and Squires (in press) refined these interpretations and reported that the mudstone and coquina in the finer grained intervals represent a low-energy, la-

goonal environment where brackish-marine mollusks lived, and that the limestone, evaporites, and "red beds" formed in a sabkha environment along the margin of the lagoon. The "red beds" probably indicate subaerial exposure, and furthermore the well-sorted, horizontally laminated, very fine to fine-grained sandstones represent beach and barrier-bar washover deposits brought by storms into the lagoon. The limestone to gypsum evaporite sequences represent increasingly hypersaline conditions along the shoreline of the lagoon, and the complex alterations of these lithologies indicate rapidly fluctuating conditions. Squires (1998) reported that the formation of these evaporites coincided with a regional change of climate from humid subtropical or tropical to seasonal semiarid conditions.

The megafauna in the restricted-coastal rocks at Matilija Hot Springs is strongly indicative of brackish-water conditions. Some of the species are known elsewhere only from brackish-marine rocks and include: *Potamides* (*Potamidopsis*) *californica*, *Loxotrema turritum*, *Pyrgulifera* (*P.*) *lajollaensis* (Hanna, 1927), *Pelecypora aequilateralis*, *Cuneocorbula torreyensis*, and "Tellina" *joaquinensis*. Each of these species is discussed below.

*Potamides* (*Potamidopsis*) *californica* has been found elsewhere only in brackish-marine rocks in the Matilija Sandstone at Beartrap Creek of the Pine Mountain area, Ventura County, southern California (Squires, 1991a). The paleoenvironment of this species is consistent with modern analogues. Today, potamidids feed on surface detritus that accumulates on mud surfaces of enclosed intertidal flats in warm waters (Morton and Morton, 1983).

*Loxotrema turritum* is widespread and ranges from southern California to northwestern Kamchatka, Russia. Nearly all of the northeastern Pacific early Eocene specimens of this species underwent downslope postmortem transport, most likely from deltaic areas, into deeper waters and became mixed with shallow-marine mollusks. The northeastern Pacific middle Eocene specimens of this species lived in brackish-marine lagoons or bays within deltaic complexes (Squires, 1998). The northwestern Kamchatka middle Eocene specimens are found in coastal-marine rocks (Devyatilova and Volobueva, 1981).

*Pyrgulifera* (*P.*) *lajollaensis* is present in brackish-marine rocks in San Diego County, southern California (Hanna, 1927; Givens and Kennedy, 1979). In modern usage, these rocks are referred to as the Delmar Formation. This species is also known from one locality (UCR loc. 4747) in the Matilija Sandstone at Beartrap Creek (Givens, 1974). At this locality, the species is associated with *Loxotrema turritum*, *Potamides* (*P.?*) *carbonicola* Cooper, 1894, and the gastropod *Nerita* (*Theliostyla*) *triangulata* Gabb, 1869, as well as with the bivalve *Acutostrea idriaensis idriaensis*. These latter two species are common constituents of northeastern Pacific brackish-marine and very shallow-marine Eocene molluscan faunas (e.g., Vokes, 1939; Squires, 1984;

Squires, 1992). *Pyrgulifera*, long believed to be a freshwater genus, was reported by Bandel and Riedel (1994) to be a brackish-water genus that could tolerate freshwater inflow.

*Pelecypora aequilateralis* and *Cuneocorbula torreyensis* have been found elsewhere in three formations. One is the brackish-marine Delmar Formation near San Diego (Hanna, 1927; Givens and Kennedy, 1979). The second is a brackish-marine part of the Domengine Sandstone in the Vallecitos syncline near New Idria in central California, and some of these rocks contain *Loxotrema turritum* and *Potamides* (P.) *carbonicola*, as well as some coal beds (Vokes, 1939). The third is a section of rocks referred to by modern workers as the White-tail Ridge Formation near Glide in southwestern Oregon (Turner, 1938; Niem et al., 1992). Utilizing the work of Niem et al. (1992), Squires (1998) assigned these latter rocks to a deltaic (mixed fluvial and shallow marine) origin. *Cuneocorbula torreyensis* is also recorded from "Transition" age brackish-marine strata in the upper Juncal Formation in the Pine Mountain area in southern California (Givens, 1974).

"*Tellina*" *joaquinensis* has been found elsewhere with certainty only in localized brackish-marine rocks in Coalmine Canyon near Coalinga, central California (Arnold, 1909; Arnold and Anderson, 1910; Vokes, 1939). In modern usage, these rocks are referred to as the Domengine Formation. Two of the associated species in the Coalmine Canyon rocks are *Loxotrema turritum* and *Potamides* (P.) *carbonicola*.

*Crommium andersoni*, which is most likely present at Matilija Hot Springs, as well as *Neverita* (N.) *globosa*, *Acutostrea idriaensis idriaensis*, and *Barbatia* (B.) *morsei* Gabb, 1864, which are all present at Matilija Hot Springs, are similar in that they all have been found in brackish-marine strata, as well as in shallow-marine environments (Arnold, 1909; Vokes, 1939; Givens, 1974; Givens and Kennedy, 1976, 1979; Squires, 1987; Nesbitt, 1995). These species, which appear to have been euryhaline, indicate that the muddy and silty environs in the restricted-coastal facies probably had some connection to the open ocean. Nesbitt (1995) reported an *Acutostrea idriaensis idriaensis* paleocommunity from the upper middle Eocene Cowlitz Formation of southwestern Washington, and she inferred that this oyster "inhabited a shallow-water, soft-bottom embayment of a delta shore in which the water temperatures and salinities were seasonally very variable."

The gastropod *Crepidula inornata* and the bivalve "*Tellina*" *domingenensis* Vokes, 1939, are the only mollusks in the restricted-coastal facies at Matilija Hot Springs that have not been previously found in brackish-marine deposits. Possibly displaced (brackish-marine?) specimens of *C. inornata*, however, have been found in rocky shoreline deposits in the basal part of the Tejon Formation at the Edmonston Pumping Plant, Tehachapi Moun-

tains, south-central California (Lindberg and Squires, 1990). The numerous and well-preserved juvenile through adult, growth-stage specimens of this gastropod at Matilija Hot Springs strongly indicate that this species inhabited the brackish-marine environment. Like modern analogues, *C. inornata* would have been a hard-substrate-dwelling gastropod with a sedentary, epifaunal suspension (filter) feeding mode of life. Most *Crepidula* spp. are generalists with respect to temperature and salinity, and this has allowed them to be stable species in unstable environments (Hoagland, 1977), which would be the norm for brackish-marine conditions.

"*Melanatria*" *markleyensis* (Clark, 1938) was known previously only from the northeastern Pacific region at a single locality in the Markley Formation in northern California. This locality contains mostly shallow-marine mollusks in coarse-grained sandstone with lenses of conglomerate, but Clark (1938) reported that the megafauna has a brackish-water element, as shown by "*Melanatria*" *markleyensis* and species belonging to *Corbicula* and the gastropod *Elimia*. In the northwestern Kamchatka area, "*M.*" *markleyensis* has been found in middle Eocene coastal-marine rocks (Devyatilova and Volobueva, 1981). Today, *Melanatria* is found in rivers and streams in Madagascar (Starmühlner, 1969; Brown, 1980). The presence of "*M.*" *markleyensis* at the Matilija Hot Springs section could be explained in two ways: During the Eocene, either this species was a brackish-water dweller, or the specimens in the section were transported there from nearby freshwater sources. The former seems more likely because the specimens are unabraded.

The three new species found in the restricted-coastal facies at Matilija Hot Springs belong to genera that can be present in brackish-marine conditions. *Tympanotonos* is moderately common in Eocene and lower Oligocene strata of France, and Gitton et al. (1986) reported the genus from lower Oligocene lagoonal-marine strata in the Paris basin. The genus is found today in coastal-marine mangrove swamps (Bouchet, 1977; Plaziat, 1977). Modern species of *Neotrapezium* are commonly found attached by their byssus to hard substrates, and at least a few species (such as *Neotrapezium liratum*; Reeve, 1843) live in warm waters of low salinity (Kira, 1965; Morton, 1979; Morton and Morton, 1983). *Neotrapezium californicum* might have lived attached to the oyster *Acutostrea idriaensis idriaensis*. The byssate epifaunal bivalve *Barbatia* (B.) *morsei* and hard-substrate-dwelling gastropod *Crepidula inornata* could have done likewise.

Although fossil forms of *Corbicula* are found in brackish-marine, freshwater, and shallow-marine strata, modern forms are found only in brackish-marine and freshwater environments (Keen and Casey, 1969).

The depositional scenario of the restricted-coastal facies of the Matilija Sandstone at Matilija Hot

Springs agrees closely with what has been observed in modern lagoons that form behind barriers. As summarized by Boggs (1987), modern lagoons are typically low-energy environments, although tidal currents move into the lagoons through inlets between barriers, winds create some wind action along shorelines, and storms provide occasional periods of high-energy waves that can bring in wash-over deposits from the barrier beach. Interbedded sands are generally horizontally laminated. Faunas are highly variable and generally characterized by low diversity. The salinity conditions largely dictate the taxonomic composition of the faunas. Lagoons with normal salinity show faunas similar to those of the open ocean, whereas brackish-marine faunas dominate more restricted lagoons (Boggs, 1987). Huge numbers of specimens are commonly associated with these brackish-marine conditions (Bandel and Riedel, 1994). Carbonate deposition can prevail if somewhat hypersaline conditions are present, and if these conditions become very arid, then evaporites (mainly gypsum) form. Very hypersaline lagoons contain few organisms (Boggs, 1987).

#### AGE

Link and Welton (1982) reported a middle Eocene (P11 and P12 Zones of the standard planktonic zonation) age for the overlying Cozy Dell Formation in the Matilija Hot Springs area. The P11 Zone is equivalent to the CP13b and CP13c Zones of the standard calcareous nannoplankton zonation (Berggren et al., 1995). The restricted-coastal facies, therefore, are no younger than the CP13b or CP13c Zones. Squires (in press) assigned the restricted-coastal facies to the lower middle Eocene "Transition Stage," which is equivalent to the CP13a Zone.

#### SYSTEMATIC MATERIALS AND METHODS

Systematic arrangement of higher taxa of the gastropods generally follows Ponder and Warén (1988), and that of the bivalves follows Vokes (1980) and Coan and Scott (1997). The synonymies are selective. Usually, only works that include illustrations of the species are listed. In a few cases, however, works that only have faunal lists are included if they add significant geographic information about a species. The figured specimens used in this report, as well as the material collected by Jests (1963), are on deposit in the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section. Additional un-

figured specimens are on deposit in the Department of Geological Sciences Paleontology collection, California State University, Northridge.

#### SYSTEMATICS

Class Gastropoda Cuvier, 1797

Superorder Caenogastropoda Cox, 1959

Order Neotaenioglossa Haller, 1882

Superfamily Cerithioidea Férussac, 1819

Family Potamididae Adams and Adams, 1854

Genus *Potamides* Brongniart, 1810

**TYPE SPECIES.** *Potamides lamarcki* Brongniart, 1810, by monotypy; Oligocene, St. Michiel, France.

Subgenus *Potamidopsis* Munier-Chalmas, 1900

**TYPE SPECIES.** *Cerithium tricarinatus* Lamarck, 1804, by original designation; middle Eocene, Paris Basin, France.

*Potamides* (*Potamidopsis*) *californica*  
Squires, 1991a  
Figures 4, 5

*Potamides* sp. Jests, 1963:223.

*Potamides* aff. *P. tricarinata* (Lamarck). Jests, 1963:225.

*Potamides* (*Potamidopsis*) *californica* Squires, 1991a:356–358, figs. 2–5.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 11300, LACMIP paratypes 11301, 11302; all from the Matilija Sandstone, Beartrap Creek, Pine Mountain area, Ventura County, southern California, LACMIP loc. 7226.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 12440–12441.

**MOLLUSCAN STAGE RANGE.** "Transition" to lower part of "Tejon."

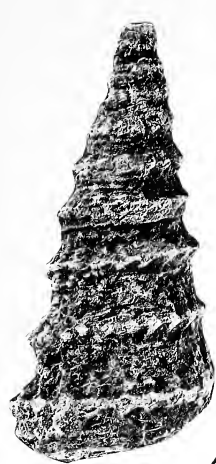
**GEOGRAPHIC DISTRIBUTION.** Matilija Hot Springs and Beartrap Creek, Ventura County, southern California.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1446, 1450, 1451, 1453.

**REMARKS.** This is the most ubiquitous gastropod in the restricted-coastal facies and is very abun-

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Figures 4–15. Gastropods from Matilija Hot Springs area upper part of the Matilija Sandstone. CSUN loc. 1453 unless otherwise indicated. All specimens coated with ammonium chloride. 4, 5. *Potamides* (*Potamidopsis*) *californica* Squires, 1991. 4. Abapertural view,  $\times 2.5$ , LACMIP hypotype 12440. 5. Apertural view,  $\times 2.6$ , LACMIP hypotype 12441. 6–13. *Tympanotonos* (*T.*) *californicus* new species. 6. Apertural view,  $\times 3.9$ , LACMIP paratype 12443. 7. Apertural view,  $\times 3.5$ , LACMIP paratype 12444. 8. Abapertural view,  $\times 3.8$ , LACMIP paratype 12445. 9. Apertural view,  $\times 3.7$ , LACMIP holotype 12442. 10. Abapertural view,  $\times 3$ , LACMIP paratype 12446. 11. Apertural view,  $\times 3.6$ , LACMIP paratype 12447. 12, 13. LACMIP paratype 12448. 12. Abapertural view,  $\times 3$ . 13. Oblique view of partial left side and anterior end,  $\times 3$ . 14. *Pyrgulifera* (*P.*) *lajollaensis* (Hanna, 1927), abapertural view,  $\times 2.4$ , LACMIP hypotype 12449, CSUN loc. 1445. 15. "*Melanatria*" *markleyensis* (Clark, 1938), abapertural view,  $\times 3.9$ , LACMIP hypotype 12450, CSUN loc. 1445.



4



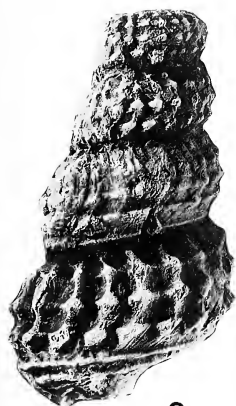
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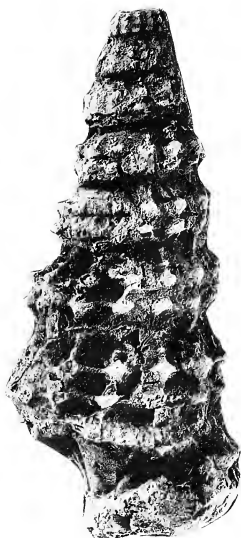
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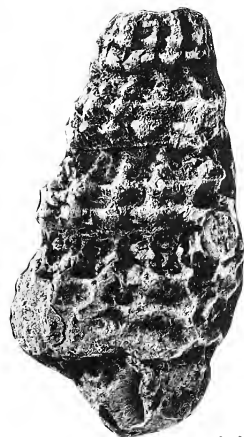
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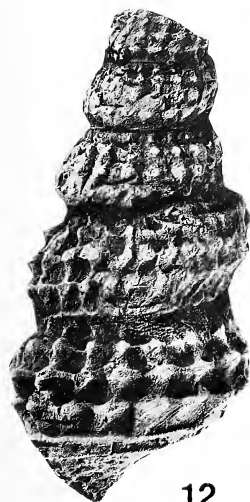
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11



12



13



14



15

dant at localities 1444 and 1450. At the other localities, between six and 12 specimens were found. Specimens are usually encased in brittle mudstone or silty mudstone, and extraction from the outcrop almost always results in loss of the uppermost spire and the aperture. Although no complete specimens were found, a few nearly complete specimens (up to 32 mm high) were recovered. This species is characterized by a turritelliform shape, concave whorls with reticulate sculpture, and a noded carina near the anterior suture. A sutural spiral rib immediately posterior to the suture can be strong on some specimens, such as the exceptionally well-preserved specimen illustrated in Figure 5. This same specimen also shows that the anterior half of the body whorl has three spiral ribs, all of which are noded. None of the specimens at any of the localities shows evidence of postmortem transport. The nodes on the carina are always sharp and unworn.

*Potamidopsis* is known only from upper Paleocene and middle Eocene brackish-marine strata in France and lower middle Eocene brackish-marine strata in southern California (Squires, 1991a). Saul and Squires (1998) reported a possible Early Cretaceous (Hauterivian Stage) species of *Potamidopsis* from the Ogo Member of the Budden Canyon Formation along the North Fork Cottonwood Creek, Shasta County, northern California. To date, *Potamides* (*Potamidopsis*) *californica* is known only from the Matilija Sandstone in Ventura County, southern California.

#### Genus *Tympanotonos* Schumacher, 1817

**TYPE SPECIES.** *Tympanotonos fluviatilis* Schumacher, 1817 [= *Murex fuscatus* Linnaeus, 1758], by monotypy; Recent, West Africa.

#### Subgenus *Tympanotonos* s.s.

*Tympanotonos* (*Tympanotonos*) *californicus* new species

Figures 6–13

**DIAGNOSIS.** A *Tympanotonos* s.s. in which the upper spire has rounded whorls with three equal spiral ribs showing small nodes and the lower spire has angulate whorls with cancellate sculpture consisting of two to three spiral ribs and numerous axial ribs.

**COMPARISON.** *Tympanotonos* (*T.*) *californicus* new species is most similar to *T.* (*T.*) *fuscatus radula*, which lives today in mangroves along the coast of West Africa. Some earlier workers, such as Thiele (1929–1935) considered *T.* (*T.*) *fuscatus radula* to be a distinct species, but modern workers such as Plaziat (1977) consider it a variety of *T.* (*T.*) *fuscatus*. Plaziat (1977) found both in the same general brackish-water habitat but reported that *radula* lives higher than *fuscatus* in the estuarine and deltaic mangrove swamps near Douala in Cameroon, Africa. A specimen of *T.* (*T.*) *radula* illustrated by Thiele (1929:fig. 202) and specimens of *T.* (*T.*) *fus-*

*catus radula* illustrated by Plaziat (1977:figs. 6a–6b, 7a–7c) are useful for comparative purposes with the new species, which differs by having slightly more rounded whorls on the lower spire. The new species is similar in the upper spire sculpture to *T.* (*T.*) *fuscatus fuscatus* from Liberia, Africa [LACM lot 51–4], but the new species differs by having much more subdued sculpture on the rest of the shell rather than having the large and projecting spines that characterize the carinate shoulder of the lower spire and body whorl of *T.* (*T.*) *fuscatus fuscatus*.

**DESCRIPTION.** Medium in size, up to 23 mm high (estimated), turreted-conical, approximately 15 whorls; high-spired with spire about two-thirds of shell height. Suture impressed, immediately anterior to a spiral riblet. Protoconch missing, apical area rapidly tapering (acicular), pleural angle approximately 20°. Whorl convexity changes with growth; earlier spire whorls rounded and gradational into angulate whorls on more mature spire and body whorl. Teleoconch sculpture consisting of spiral ribs crossed by numerous axial ribs. Sculpture changes with growth. Upper spire with three equal spiral ribs; beaded to noded where crossed by axial ribs. On middle and lower spires, posterior-most spiral rib weakens, with the other two spiral ribs becoming carinate, more strongly noded, and more prominent with growth. Sculpture cancellate with nodes projected somewhat; interareas between the two rows of nodes rather deep. On rare specimens, weak posterior-most spiral rib obsolete or nearly so. Mature whorls of very rare specimens with a fourth spiral rib, moderately prominent and noded, near the anterior suture. Posterior half of body whorl with three spiral ribs bearing strong nodes; posterior-most spiral rib weakest. Anterior half of body whorl flattish, with approximately six unnoded spiral ribs, strength decreasing anteriorly. Aperture somewhat roundish; inner lip smooth and twisted. Anterior end of aperture with a narrow but distinct notch. Outer lip not seen.

**HOLOTYPE DIMENSIONS.** 18.9 mm high, 7.5 mm wide.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 12442 (illustrated), LACMIP paratypes 12443 to 12448 (all illustrated); all from CSUN loc. 1453.

**TYPE LOCALITY.** CSUN loc. 1453.

**MOLLUSCAN STAGE RANGE.** “Transition.”

**GEOGRAPHIC DISTRIBUTION.** Matilija Hot Springs, southern California.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1450, 1451, 1453.

**REMARKS.** The new species is most abundant at CSUN locality 1453, where it forms coquinas. It is common at the other localities. Specimens range from 5 to 25 mm in height. Whether or not the largest specimens found represent fully mature individuals cannot be resolved, but it seems unlikely. On the bedding planes of some hand-specimens of rock, there are densely packed patches of mostly same-sized specimens less than 10 mm high. These



patches represent concentrations of juvenile specimens. These small specimens have rounded whorls with beaded sculpture on three equal spiral ribs and could easily be mistakenly identified as a separate species if more mature specimens (e.g., Figs. 8, 9, 12) showing a transition from rounded whorls with beaded sculpture to angulate whorls with cancellate sculpture were not present. It is uncommon to find specimens that show this transition in sculpture because nearly all the more mature specimens are missing their tips. This might be the result of breakage that occurred either during postmortem transport or during removal of the larger specimens from the rock. The mudstone containing the specimens of the new species is brittle and highly fractured. It easily falls apart, and removal of the larger specimens is extremely difficult. In addition, no specimens of the new species were found that show the outer lip, and only rare specimens show the outline of the aperture. Most likely these features were either crushed by postburial compaction or broken off when the rock was split to initially reveal the specimens. It is also possible that, at least in some cases, the more delicate parts of the shells were broken off prior to burial.

Wenz (1939) reported the geologic range of *Tympanotonos* to be Late Cretaceous (Turonian) to Recent. During the Eocene, the genus was relatively diverse in France, especially in the Paris Basin (Cossmann and Pissarro, 1910–1913; Le Renard and Pacaud, 1995). The French species belong to either subgenus *Eotympanotonus* Chavan, 1952, or to subgenus *Diptychochilus* Cossmann in Doncieux, 1908. The former is characterized by whorls whose posterior-most spiral rib develops spines, whereas the latter has a smooth but tabulate carina on the shoulder of the whorls. Neither subgenus is characterized by cancellate sculpture such as that seen on the new species.

The new species, which belongs to *Tympanotonos* s.s., is the only confirmed record of *Tympanotonos* in North America. Flynn et al. (1989:fig. 3 [1a–1b]) reported *Tympanotonos* sp. aff. *T. papalis* from lower Eocene (“Capay Stage”) strata of the Bateque? Formation near the village of “El Rosario” [i.e., Rosarito] in Baja California Sur, Mexico. Squires and Demetron (1992), however, reported that the northernmost exposures of the Bateque Formation are far south of the area studied by Flynn et al. (1989). The specimens of the so-called *Tympanotonos* sp. aff. *T. papalis* from the Rosarito area lack apertures and upper spires. These specimens are quite unlike those of *T. (Eotympanotonus) papalis* (Deshayes, 1833; Cossmann and Pissarro, 1910–1913:pl. 29, fig. 151bis–5), known from lower Eocene (Cuisian Stage) strata of the Paris Basin, France. The Mexican specimens have a lowly noded carina on the shoulder of the whorls, and the remaining parts of the whorls are smooth. The Mexican specimens are somewhat similar to Paris Basin species of *Tympanotonos* (*Eotympanotonus*), as well to certain species of the cerithiid genus *Ser-*

*ratocerithium* Vignal, 1897, but positive identification of the Mexican specimens awaits better preserved material.

**ETYMOLOGY.** The species is named for the state of California.

### Genus *Pyrgulifera* Meek, 1877

**TYPE SPECIES.** *Pyrgulifera humerosa* Meek, 1877, by monotypy; Upper Cretaceous (Cenomanian), Bear River Formation, near Bear River, southwestern Wyoming.

### Subgenus *Pyrgulifera* s.s. *Pyrgulifera* (*Pyrgulifera*) *lajollaensis* (Hanna, 1927)

Figure 14

*Trichotropis* (?) *lajollaensis* Hanna, 1927:311–312, pl. 48, figs. 4–6, 9, 11.

*Trichotropis*? *lajollaensis* Hanna. Clark, 1929:pl. 10, fig. 12.

*Trichotropis*(?) sp. Jests, 1963:226.

“*Trichotropis*” *lajollaensis* Hanna. Givens, 1974:70, pl. 6, fig. 18.

*Gyrineum* (?) sp. Jests, 1963:226.

*Pyrgulifera lajollaensis* (Hanna). Givens and Kennedy, 1979:95, table 2.

**PRIMARY TYPE MATERIAL.** UCMP holotype 30906, UCMP loc. 3992; UCMP paratype 30907, UCMP loc. 5084; UCMP paratype 30908, UCMP loc. 3992; all from the Delmar Formation, south of Del Mar, San Diego County, southern California.

**ILLUSTRATED SPECIMENS.** LACMIP hypotype 12449.

**MOLLUSCAN STAGE RANGE.** “Domengine” to lower part of “Tejon.”

**GEOGRAPHIC DISTRIBUTION.** San Diego and Matilija Hot Springs, southern California.

**LOCAL OCCURRENCE.** CSUN locs. 1445, 1446, 1450, 1452, 1453.

**REMARKS.** A total of 21 specimens were found. Eight were found at locality 1450, and they range from 13 to 28 mm in height. Seven specimens were found at locality 1445, and they range from 18 to 25 mm in height. At the other localities, only two or three specimens were found. Nearly all the collected specimens are poorly preserved. Some are only internal molds.

This species is characterized by a short, stout shell with angulate whorls, a wide ramp, numerous pointed axial nodes, and strong spiral ribs covering the entire shell. The axial nodes on the Matilija Hot Springs specimens are sharp and unworn, thereby indicating no signs of postmortem transport.

The familial assignment of *Pyrgulifera* is tenuous. Traditionally, it has been assigned to family Thiaridae, but Bandel and Riedel (1994) recently placed it in family Potamididae. Wenz (1939) reported that the geologic range of *Pyrgulifera* is Late Cretaceous (Cenomanian) to Eocene. Two species are known from estuarine rocks in the Upper Cre-

taceous (Cenomanian) Bear River Formation in southwestern Wyoming (White, 1895; Yen, 1954, 1958). Stephenson (1952) described two species of *Pyrgulifera* from the Cenomanian Woodbine Formation of Texas, but Bandel and Riedel (1994) considered the generic identification as doubtful. One of these Woodbine Formation species, *Pyrgulifera ornata* Stephenson (1952:157–158, pl. 37, figs. 9–13), however, does look much like a *Pyrgulifera*.

Givens (1974:70) reported *Pyrgulifera lajollaensis* from the *Ectinochilus canalifer* megafaunal biozone of the Matilija Sandstone at Beartrap Creek of the Pine Mountain area, Ventura County, southern California. Squires (in press) reported that the Matilija Sandstone in the Beartrap Creek area is early middle Eocene in age and equivalent to the lower part of the “Tejon Stage.”

## Family Thiaridae Troschel, 1857

### Genus *Melanatria* Bowdich, 1822

**TYPE SPECIES.** *Buccinum flumineum* Gmelin in Linnaeus, 1767, by original designation?; Recent, Madagascar, rivers and streams.

#### “*Melanatria*” *markleyensis* (Clark, 1938)

Figures 15–17

*Thiara* (*Melanoides*) *markleyensis* Clark, 1938: 706, pl. 3, figs. 24, 30; table 1.

*Cerithium* sp. Jests, 1963:222.

*Bittium* (?) *dumblei* (Dickerson). Jests, 1963:226.

*Melania markleyensis* (Clark). Devyatilova and Volobueva, 1981:114, pl. 9, figs. 16–18.

**PRIMARY TYPE MATERIAL.** UCMP holotype 30891; UCMP paratype 30892; both from the Markley Formation near Vacaville, Solano County, northern California, UCMP loc. A1297.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 12450 and 12451.

**MOLLUSCAN STAGE RANGE.** “Transition” to “Tejon.”

**GEOGRAPHIC DISTRIBUTION.** Matilija Hot Springs, southern California; Pleasant Creek near Vacaville, northern California; and northwestern Kamchatka, Russia.

**LOCAL OCCURRENCE.** CSUN locs. 1445, 1446.

**REMARKS.** A total of 45 specimens were found,

and 30 of these are from locality 1445. Although most specimens from locality 1445 are fragments, usually consisting of just the apices, a few represent nearly complete specimens that range from 11 to 26.5 mm in height. Jests, who must have picked up weathered-out material, collected these fragmentary specimens. I collected specimens from this same locality by removing rock from the outcrop, and these specimens are mostly complete, although the apertures are always poorly preserved. Only five specimens of this species were found at CSUN locality 1446. Two consist of moderately large fragments, and the other three are weathered tips.

The specimen that best shows the aperture is illustrated in Figure 16, but the outer lip and anterior end of the aperture are missing. This species is characterized by tabulate whorls on most of the spire and body whorl, by prominent axial nodes a short distance below the suture, and by beaded spiral sculpture. The apertural features are poorly known for this species, but the anterior end appears to be unnotched. Strength of the axial nodes is variable, as is their extent along the sides of the whorls.

I use quotation marks for the generic assignment of Clark's (1938) species, which cannot be assigned with certainty to any genus because apertural details are not fully known. I tentatively assign Clark's species to *Melanatria* rather than to *Thiara* Bolton in Röding, 1798 [= *Melania* Lamarck, 1799 fide Wenz (1939)], or *Melanoides* Olivier, 1804, because the species has more morphologic similarity to the type species of *Melanatria* than to the type species of the other two genera. Similar to *Melanatria fluminea*, which is the type species of *Melanatria*, Clark's species has a turreted-conical shape, whorls bearing prominent spiral ornament and axial ribs, and an apparently unnotched aperture. Although the type species of *Thiara*, which is *Thiara* (T.) *amarula* (Linnaeus, 1758), is somewhat similar to Clark's species, T. (T.) *amarula* has an oval-turreted shape, a row of backward-directed spines on the body whorl shoulder, smooth or fine spiral ornament, and a feebly notched anterior end of the aperture (Davies and Eames, 1971). The type species of *Melanoides*, which is M. (M.) *tuberculata* (Müller, 1774), differs significantly from Clark's species by having a fusiform shape, rounded whorls, and cancellate sculpture (especially on the spire).

→

Figures 16–28. Gastropods and bivalves from Matilija Hot Springs area upper part of the Matilija Sandstone. CSUN loc. 1450 unless otherwise indicated. All specimens coated with ammonium chloride. 16–26. Gastropods. 16, 17. “*Melanatria*” *markleyensis* (Clark, 1938), ×5.2, LACMIP hypotype 12451, CSUN loc. 1445. 16. Apertural view. 17. Abapertural view. 18, 19. *Loxotrema turritum* Gabb, 1868. 18. Apertural view, ×1.8, LACMIP hypotype 12452. 19. Abapertural view, ×2.6, LACMIP hypotype 6451, CSUN loc. 1446. 20, 21. *Crepidula inornata* Dickerson, 1916, ×2.3, LACMIP hypotype 12453. 20. Dorsal view. 21. Right-side view. 22, 23. *Crommium* sp. cf. *C. andersoni* (Dickerson, 1914), ×2.6, LACMIP hypotype 12454. 22. Apertural view. 23. Abapertural view. 24, 25. *Neverita* (*Neverita*) *globosa* Gabb, 1869, ×2.8, LACMIP hypotype 12455. 24. Apertural view. 25. Abapertural view. 26–28. Bivalves. 26. *Barbatia* (*Barbatia*) *morsei* Gabb, 1864, left valve, ×4.8, LACMIP hypotype 12456. 27, 28. *Acutostrea idriaensis idriaensis* (Gabb, 1869). 27. Left valve, ×1.7, LACMIP hypotype 12457. 28. Left valve, ×1.4, LACMIP hypotype 12458.





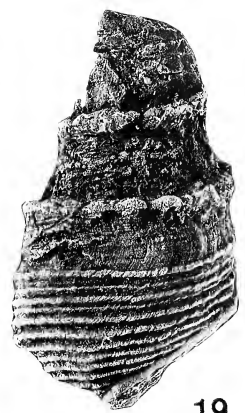
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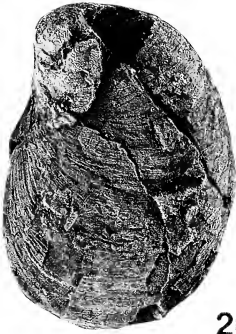
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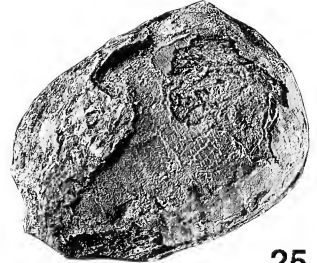
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28

"*Melanatria*" *markleyensis* resembles *Thiara* (*Melanoides*) *calafi* Clark (1938:706, pl. 3, figs. 24, 30). Both are from the same bed in the upper Eocene Markley Formation in northern California. "*Melanatria*" *markleyensis* differs from *T. (M.) calafi* by having whorls with a much stronger tabulate shoulder, coarser and fewer nodes on the shoulder, much closer proximity between the shoulder and the suture, and better development of beaded sculpture on the spiral ribs on the whorls. Clark (1938) reported that both of his species are closely related to *Potamides fettkei* Weaver (1912:36, pl. 2, figs. 23, 24; 1942 [1943]:379–380, pl. 75, figs. 18, 21, 22, 26) from the upper middle Eocene Cowlitz Formation in southwestern Washington. Givens and Kennedy (1976:964) reassigned "*Potamides*" *fettkei* to genus *Melanoides*. Although "*Melanatria*" *markleyensis* resembles *Melanoides fettkei*, especially in the prominent nodes on the shoulder, *T. (M.) calafi* is more like *Melanoides fettkei*. "*Melanatria*" *markleyensis* differs from *Melanoides fettkei* by having a much closer proximity of the tabulate shoulder and the suture, more closely spaced nodes on the shoulder, coarser beaded sculpture on the spiral ribs on the whorls, and no secondary spiral ribs.

Houbrick (1991) assigned *Melanatria* to the family Thiariidae. On the basis of a shared unique and unusual foliate gastric structure, he implied that the phylogenetic placement of *Melanatria* is close to the genera *Faunus* Montfort, 1810, and *Melanopsis* Férussac, 1807. He also reported that more work is needed to clarify their phylogenetic relationships.

Devyatilova and Volobueva (1981) reported this species from coastal-marine rocks of the middle Eocene Kamchik Formation along the shores of Penzhin Inlet at the head of the Sea of Okhotsk, northwestern Kamchatka. Their illustrated specimens are identical to those from the type locality in northern California. To date, there are no precise correlation data on how the Kamchatka Eocene rocks compare biostratigraphically with northeastern Pacific Eocene rocks. The presence of "*M.*" *markleyensis* in the Matilija Sandstone at Matilija Hot Springs, however, lowers the northeastern Pacific temporal range of this species into the "Transition Stage." The species previously was known only from the "Tejon Stage" in northern California.

Wenz (1939) reported the geologic range of *Melanatria* to be Paleocene?, Eocene to Recent, with all the confirmed fossil occurrences in Europe. If "*Melanatria*" *markleyensis* is proven eventually to belong to genus *Melanatria*, this species would extend the geographic range of this genus to the New World.

Family Melanopsidae Adams and Adams,  
1854

Genus *Loxotrema* Gabb, 1868

TYPE SPECIES. *Loxotrema turritum* Gabb, 1868, by original designation; early to middle Eo-

cene, California, Oregon, Washington, and Kamchatka.

*Loxotrema turritum* Gabb, 1868

Figures 18, 19

*Loxotrema turrita* Gabb, 1868:147, pl. 14, fig. 21; 1869:168, pl. 28, fig. 49; Arnold, 1909:14, pl. 4, fig. 17; Arnold and Anderson, 1910:71, pl. 26, fig. 17; Clark, 1929:pl. 10, fig. 3. Hanna, 1927:312, pl. 50, figs. 5–8; Vokes, 1939:159, pl. 20, figs. 15–19; Schenck and Keen, 1940:pl. 24, figs. 10–13; Weaver 1942 [1943]:374, pl. 75, figs. 1–3; pl. 103, fig. 18; Devyatilova and Volobueva, 1981:114–115, pl. 9, figs. 19–23.

*Struthiolaria* (*Loxotrema*) *turrita* (Gabb). Tryon, 1883:196, pl. 60, fig. 95.

*Loxotrema turritum* Gabb. Stewart, 1927:347–348, pl. 26, figs. 3, 4; Turner, 1938:tables 2, 4, 8, p. 81, pl. 17, figs. 12, 13; Moore, 1968:26, pl. 11, fig. d; Givens, 1974:70, pl. 6, fig. 17. Givens and Kennedy, 1976:963, pl. 1, figs. 5–8; Squires, 1998.

*Pachychilus* (*Loxotrema*) *turritum* (Gabb). Wenz, 1939:686, fig. 1968.

*Loxotrema* cf. *L. turritum* Gabb. Jestes, 1963:225. ?*Loxotrema turritum* Gabb. Squires, 1991b:table 1, pl. 1, fig. 16.

**PRIMARY TYPE MATERIAL.** Lectotype ANSP 4228, designated by Stewart (1927); "Tejon Group, 10 miles west of Griswold's, between San Juan and New Idria" (Gabb, 1869:168); Domingine Formation, Vallecitos syncline area, San Benito County, central California.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 6451 and 12452.

**MOLLUSCAN STAGE RANGE.** "Meganos" to lower part of "Tejon."

**GEOGRAPHIC DISTRIBUTION.** Southern to northern California; southwestern Oregon; Crescent Bay, Olympic Peninsula, southwestern Washington; and northwestern Kamchatka.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1446, 1450, 1451, 1452.

**REMARKS.** This species is abundant only at locality 1450, where specimens range from 18 to 30 mm in height. At the other localities, between 4 to 10 specimens were found. Specimens are usually encased in brittle mudstone, and extraction from the bedrock almost always results in loss of the uppermost spire and anterior end of the aperture. Many of the specimens have been crushed. This turreted species is characterized by tabulate whorls, a large cylindrical body whorl with strong spiral ribs, and a notched aperture. The small nodes on the tabulate body whorl are distinct on the Matilija Hot Springs specimens and show no signs of wear resulting from postmortem transport. Squires (1998) reported also that the specimens of *Loxotrema turritum* from Matilija Hot Springs show no evidence of postmortem transport. See Squires (1998) for a review of this species.

Devyatilova and Volobueva (1981) reported this species from middle Eocene coastal-marine rocks along the shores of Penzhin Inlet at the head of the Sea of Okhotsk, northwestern Kamchatka. These rocks are within the Kamchik Formation and the lower part of the Tkapravayam subformation. The specimens they illustrated are identical to those from the type locality in central California.

Superfamily Calyptraeidea Lamarck, 1809

Family Calyptraeidae Lamarck, 1809

Genus *Crepidula* Lamarck, 1799

**TYPE SPECIES.** *Patella fornicata* Linnaeus, 1758, by monotypy; Recent, eastern United States and northwestern Europe.

*Crepidula inornata* Dickerson, 1916

Figures 20, 21

*Crepidula inornata* Dickerson, 1916:489, pl. 38, figs. 5a, 5b; Lindberg and Squires, 1990:579.

*Crepidula (Spirocrypta) inornata* Dickerson. Vokes, 1939:165–166, pl. 21, figs. 10, 11.

*Crepidula* sp. Jests, 1963:223.

**PRIMARY TYPE MATERIAL.** UCMP holotype 11804, Domengine Formation near Coalinga, Fresno County, central California, UCMP loc. 672.

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12453.

**MOLLUSCAN STAGE RANGE.** “Domengine” to “Transition.”

**GEOGRAPHIC DISTRIBUTION.** Matilija Hot Springs, Ventura County, southern California; Edmonston Pumping Plant, near Grapevine, Kern County; and Coalinga area, Fresno County, central California.

**LOCAL OCCURRENCE.** LACMIP locs. 1444, 1445, 1446, 1450.

**REMARKS.** Specimens of this species are abundant at localities 1445 and 1450, where specimens range from 11 to 17 mm in length. Most are well preserved, but a few are crushed. Nearly all show delicate growth lines. At all the other localities, only single specimens were found.

Although some workers (e.g., Stewart, 1927; Turner, 1938; Hoagland, 1977) considered *Crepidula inornata* as conspecific with *C. pileum* (Gabb, 1864:137, pl. 29, figs. 233, 233a, 233b) from upper Eocene to middle Oligocene strata in California through Washington (Squires, 1987), other workers (e.g., Clark, 1938; Vokes, 1939; Kleinpell and Weaver, 1963) considered them to be separate species. *Crepidula inornata* is distinguished from *C. pileum* by having a smaller size, an elevated rather than a submarginal spire, and a bulbous penultimate whorl. The Matilija Hot Springs specimens have all the diagnostic characters of *C. inornata*. Lindberg and Squires (1990) reported this species from “Transition Stage” strata at the Edmonston Pumping Plant at the south end of the San Joaquin

Valley, central California. The presence of *C. inornata* at Matilija Hot Springs is the first record of this species from brackish-marine strata.

Superfamily Naticoidea Forbes, 1838

Family Naticidae Forbes, 1838

Genus *Crommium* Cossmann, 1888

**Type Species.** *Ampullaria willemetii* Deshayes, 1825, by original designation; Eocene, France.

*Crommium* sp. cf. *C. andersoni*  
(Dickerson, 1914)

Figures 22, 23

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12454.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1450.

**REMARKS.** Specimens are rare. Four specimens were found at locality 1444 and two at locality 1450. They range from 10 to 20 mm in height, and all are crushed internal molds. They resemble *Crommium andersoni* (Dickerson, 1914:120, pl. 12, figs. 2a, 2b) from lower to middle Eocene strata of California and southwestern Oregon. Marinovich (1977:225–227, pl. 18, figs. 3–7) also illustrated this species. The Matilija Hot Springs specimens, such as *C. andersoni*, have tabulated whorls, a smooth globose body whorl, and a lowly elevated spire. Whether or not the Matilija Hot Springs specimens have a narrow umbilical slit bounded by a narrow cordlike angulation, such as that found on *C. andersoni*, cannot be determined because the anterior end of the Matilija Hot Springs specimens are either incomplete or poorly preserved. If the Matilija Hot Springs specimens are *C. andersoni*, they would be the youngest record of this species.

Genus *Neverita* Risso, 1826

**TYPE SPECIES.** *Neverita josephina* Risso, 1826, by monotypy; Eocene to Recent, Europe.

*Neverita (Neverita) globosa* Gabb, 1869

Figures 24, 25

*Neverita globosa* Gabb, 1869:161, pl. 27, fig. 39; Dickerson, 1916:pl. 39, figs. 5a–b; Stewart, 1927:326–327, pl. 28, fig. 6; Clark and Woodford, 1927:121–122, pl. 22, figs. 5–10; Turner, 1938:89, pl. 19, figs. 6–7, 13–15; Vokes, 1939:169, pl. 21, figs. 9, 15–19; Schenck and Keen, 1940:pl. 24, figs. 2–5; Givens and Kennedy, 1979:tables 1–3.

*Neverita weaveri* Dickerson, 1915:57, pl. 4, figs. 10a–b.

*Neverita nomlandi* Dickerson, 1917:173–174, pl. 30, figs. 2a–b.

*Polinices weaveri* (Dickerson). Turner, 1938:86, pl. 20, figs. 14, 16.

*Neverita globosa reefensis* Vokes, 1939:169, pl. 21, figs. 24–25.

*Polinices (Neverita) globosa* (Gabb). Weaver, 1942 [1943]:339, pl. 68, figs. 21, 24; pl. 69, figs. 5–6; pl. 100, fig. 29.

*Polinices (Neverita) nomlandi* (Dickerson). Weaver, 1942 [1943]:340, pl. 69, figs. 8–9, 12.

*Neverita (Neverita) globosa* Gabb. Givens, 1974: 76; Marinovich, 1977:312–316, pl. 28, figs. 10–15; pl. 29, figs. 1–3; Squires, 1984:25, fig. 7g; 1987:37–38, fig. 47.

*Neverita (Glossaulax?) globosa* Gabb. Givens and Kennedy, 1976:965–966, pl. 2, figs. 5–14, 16, 18–19.

**PRIMARY TYPE MATERIAL.** MCZ holotype 27859, Domengine? Formation, 16 km west of Griswold's, on the road from San Juan to New Idria, and southeast of "Sheep Well," T 15 S, R 9 E, Priest Valley quadrangle, San Benito County, central California.

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12455.

**MOLLUSCAN STAGE RANGE.** "Meganos" through "Tejon."

**GEOGRAPHIC DISTRIBUTION.** San Diego, California, through southwestern Washington.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1450, and 1451.

**REMARKS.** A specimen was found at each locality. Collectively, they range from 11 to 17 mm in height. They are poorly preserved and are missing the outer lip.

Class Bivalvia Linnaeus, 1758

Subclass Pteriomorpha Beurlen, 1944

Order Arcoida Stoliczka, 1871

Superfamily Arcoidea Lamarck, 1809

Family Arcidae Lamarck, 1809

Genus *Barbatia* Gray, 1847

**TYPE SPECIES.** *Arca barbata* Linnaeus, 1758, by original designation; Recent, Mediterranean to northwestern Africa.

Subgenus *Barbatia* s.s.

*Barbatia (Barbatia) morsei* Gabb, 1864

Figure 26

*Barbatia morsei* Gabb, 1864:216, pl. 32, fig. 286; Arnold, 1909:13, 16, pl. 3, fig. 8; Arnold and Anderson, 1910:70, 73, pl. 25, fig. 8; Hanna, 1927:272, pl. 25, figs. 2, 10, 11, 13, 14. Clark, 1929:pl. 6, fig. 3; Stewart, 1930:87, pl. 8, fig. 7.

*Barbatia (Obliquarca) morsei* Gabb. Vokes, 1939: 49–50, pl. 1, figs. 25, 26, 28, 29; Reinhart, 1943: 30–32, pl. 1, fig. 4.

*Barbatia (Barbatia) morsei* Gabb. Moore, 1983:34, pl. 5, fig. 7.

**PRIMARY TYPE MATERIAL.** UCMP lectotype 11984, designated by Reinhart (1943); Eocene of

the San Diego region (exact locality unknown), San Diego County, southern California.

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12456.

**MOLLUSCAN STAGE RANGE.** "Domengine" to "Transition."

**GEOGRAPHIC DISTRIBUTION.** San Diego, Matilija Hot Springs, and Pine Mountain area, southern California; Coalmine Canyon near Coal- inga, central California.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1450.

**REMARKS.** Eleven specimens were found at locality 1450, and they range from 3 to 10.3 mm in height. Three specimens were found at locality 1444. Preservation at both localities is excellent to good, although most specimens have been slightly crushed. Both right and left valves are present, but no articulated specimens were found. The thinness of the valves makes them extremely fragile, and specimens usually break apart during extraction from the rock at the outcrop.

This species is characterized by the nearness of the beak to the anterior margin. The illustrated specimen (Fig. 26) shows the exterior sculpture better than any other known specimen of this species. It shows that there can be radial ribs on the posterodorsal area and that these ribs are the widest spaced of any on the shell. This specimen, which has a sharp angle where the posterior margin meets the hinge, shows no sign of any abrasion due to postmortem transport.

The Matilija Hot Springs specimens of this species are the geologically youngest known for this species.

Order Ostreoida Férussac, 1822

Superfamily Ostreoida Rafinesque, 1815

Family Ostreidae Rafinesque, 1815

Genus *Acutostrea* Vialov, 1936

**TYPE SPECIES.** *Ostrea acutirostris* Nilsson, 1827, by original designation; Upper Cretaceous, Europe and North America.

*Acutostrea idriaensis idriaensis* (Gabb, 1869)  
Figures 27, 28

*Ostrea idriaensis* Gabb, 1869:203, pl. 33, figs. 103b–d; pl. 34, figs. 103, 103a; Hanna, 1927: 276, pl. 30, figs. 1–2; pl. 31, figs. 3–4; Stewart, 1930:126–127, pl. 8, fig. 3; pl. 17, fig. 1; Vokes, 1935:291–304, pl. 22–24; Turner, 1938:46, pl. 6, fig. 9; Weaver, 1942 [1943]:78–79, pl. 15, fig. 5; Schenck and Keen, 1940:pl. 23, figs. 3, 4; Givens, 1974:44; Givens and Kennedy, 1979:tables 2, 4; Squires, 1984:45, fig. 101.

*Ostrea columbiana* Weaver and Palmer, 1922:13–14, pl. 8, figs. 15, 16.

*Ostrea oregonensis* Packard, 1923:4–6, pls. 1–4.

*Ostrea* sp. Jests, 1963:223, 225.

*Acutostrea idriaensis idriaensis* (Gabb). Moore, 1987:31–32, figs. 2, 3; pl. 14, fig. 6; pl. 16, fig. 3; pl. 29, figs. 3–5; Lindberg and Squires, 1990: 579.

Not *Ostrea idriaensis* Gabb. Devyatiliova and Volobueva, 1981:57, pl. 5, fig. 3.

**PRIMARY TYPE MATERIAL.** MCZ lectotype 15048, Domingine Formation, about 3 km east of New Idria, N 1/2 of section 15, T 17 S, R 12 E, Priest Valley quadrangle, San Benito County, central California.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 12457 and 12458.

**MOLLUSCAN STAGE RANGE.** “Capay” to “Tejon.”

**GEOGRAPHIC DISTRIBUTION.** San Diego, California, through southwestern Washington.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1446, 1450, 1451, 1453.

**REMARKS.** This species is one of the most ubiquitous bivalves in the restricted-coastal facies, and it is abundant in muddy rocks at all the localities, except at locality 1452 where it is rare. It is also present as a few scattered fragments in the beach and barrier-bar sandstones. At localities where it is abundant, specimens range from 25 to 75 mm in height. Preservation at all localities ranges from good to poor, and nearly all the specimens are disarticulated. They consist of only the left (lower) valve and are somewhat elongate, lowly arched, and usually have low radial ribs crossed by growth rugae. A few specimens are roundish and arched. Articulated specimens are rare.

Subclass Heterodonta Neumayr, 1884

Order Veneroida Adams and Adams, 1856

Superfamily Arcticoidea Newton, 1891

Family Trapezidae Lamy, 1920

Genus *Neotrapezium* Habe, 1951

**TYPE SPECIES.** *Cardita sublaevigata* Lamarck, 1819, by original designation; Recent, Indo-Pacific.

*Neotrapezium californicum* new species

Figures 29–33

*Unio*(?) *torreyensis* Hanna, 1963:224.

*Lithophaga* (?) sp. Jests, 1963:226.

**DIAGNOSIS.** A small-sized *Neotrapezium* with a moderately produced anterior end, usually straight posterior hinge-line area, and prominent growth lines.

**COMPARISON.** The new species is similar to the living *Neotrapezium liratum* (Reeve, 1843), an Indo-Pacific species introduced to various locations in the northeastern Pacific region (Bonnot, 1935 [as *Cypricardia lyrata*]; Solem, 1954; Hanna, 1966). Kira (1965:148, pl. 53, fig. 29) illustrated this species. The new species differs by having a slightly more produced anterior end.

The new species is similar to *Neotrapezium grignonensis* (Deshayes, 1824:64–65, pl. 9 figs. 18–19) from middle and upper Eocene (Lutetian and Bartonian stages) strata of the Paris Basin, France. Cossmann and Pissarro (1904–1906:pl. 15, figs. 63–1 through 63–10) figured this Paris Basin species, as well as seven other closely related “species” from the same region. Le Renard and Pacaud (1995) regarded *N. grignonensis* as conspecific with all of these seven other “species.” The new species is similar to *N. grignonensis* in that there is a range in morphology from elongate-ovate to subquadrate, but the new species differs by having an anterior end that is more produced, a posterior end that is never as produced, growth lines that are usually more accentuated, and a shell that never is as narrow or smooth as in some specimens of *N. grignonensis*.

**DESCRIPTION.** Small-sized (up to 13.2 mm high), thin-shelled, moderately elongate-ovate to subquadrate, equivalved, and inequilateral. Ligament external, opisthodontic. Beaks near anterior end, prosogyrous, and moderately elevated. Anterior margin slightly pointed; posterior hinge-line straight to slightly arched. Posterior margin steeply sloping. Very faint radial lirae rare on posterior area. Right valve with two cardinal teeth and long posterior lateral. Left valve with long posterior socket (cardinals unseen). Growth lines prominent, commonly clustered into bands; on a few specimens growth-line bands merge into very fine concentric ribs, strongest on posterior area and/or medial area. Growth rugae near ventral margin on some specimens. Irregular to distorted growth on some specimens.

**HOLOTYPE DIMENSIONS.** Height 7.7 mm, length 13.9 mm.

**PRIMARY TYPE MATERIAL.** LACMIP holotype 12459 (illustrated), LACMIP paratypes 12460 to 12463 (all illustrated); all from CSUN loc. 1450, except paratype 12462 (from CSUN loc. 1445).

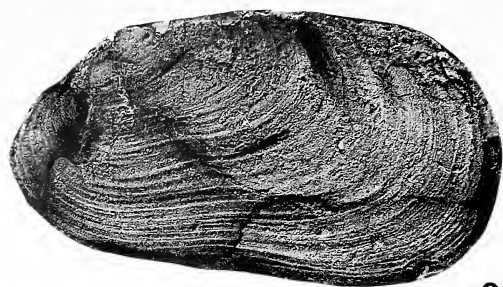
**TYPE LOCALITY.** LACMIP loc. 1450.

**MOLLUSCAN STAGE RANGE.** “Transition.”

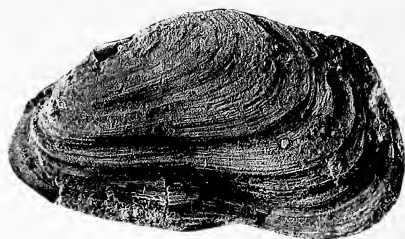
**GEOGRAPHIC DISTRIBUTION.** Upper part of Matilija Sandstone at Matilija Hot Springs area.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1446, 1450, 1451, 1453.

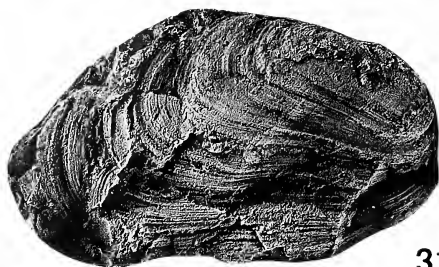
**REMARKS.** The new species is abundant at locality 1450, where specimens range from 1.3 to 13.2 mm in height. Specimens are uncommon to rare at the other localities. Preservation is generally good, and most are single valves. At locality 1450, however, about 13% of the specimens are articulated. Nearly all specimens are extensively crushed. The new species shows a considerable degree of variation in shape, based on 56 specimens preserved well enough to determine valve shape. Of these, 52 (93%) are elongate-ovate, and the other 4 (7%) are subquadrate. A few of the latter even show distorted (irregular or disjunct) growth, where the growth lines delineate a progression of different shapes on a valve. Consequently, the valve



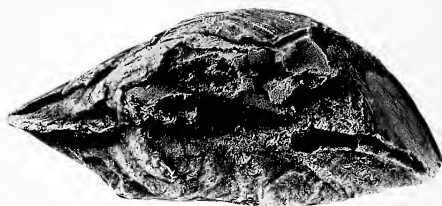
29



30



31



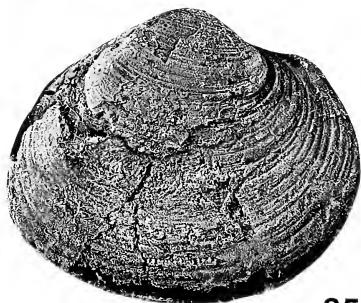
32



33



34



35



36



37



38



39



appears to be a composite of several individual valves, one on top of the other. An example is illustrated in Figure 31. Modern species of *Neotrapezium* are known to be nestlers or shallow infauna, and the nestling mode of life commonly causes distortion during growth (Kira, 1965; Morton, 1979). Of the 52 elongate-ovate specimens mentioned above, 25 have pronounced growth lines, 20 are somewhat smooth, and 7 have growth lines that are very accentuated posteriorly. Only the holotype of the new species shows any radial sculpture, and it is very faint. The subquadrate-shaped valves of the new species all have pronounced growth lines. The new species is the first record of *Neotrapezium* in the fossil record of North America. Although *Trapezium* (*Schedotrapezium*) *carinatum* Gabb (1864:170, pl. 23, fig. 150; Stewart, 1930:174–175, pl. 5, fig. 5; pl. 17, fig. 4) was reported from Upper Cretaceous (Campanian Stage fide LouElla Saul, personal communication, 1997) rocks in Placer County, northern California, this species is no longer considered to belong to the family Trapezidae and is now placed (Keen, 1969a) in *Schedotrapezium* Stewart, 1930, of the family Arcticiidae Newton, 1891.

A bivalve referred to as *Trapezium claibornense* Dall (1900a:1498, pl. 43, figs. 9, 10; Harris, 1919: 154, pl. 48, figs. 3, 4) was reported as a very rare species from middle Eocene (Claiborne Stage) strata of Alabama. Maestrati and Lozouet (1995), however, regarded Dall's species as probably being an astartid. The new species differs from Dall's species by having a lower height relative to the length of the valves, more variable concentric sculpture, a more rounded posterior end, and a posterior margin that is not obliquely angular.

The new species is also the first record of subgenus *Neotrapezium* in the fossil record of North America. This article follows Maestrati and Lozouet (1995) and Coan and Scott (1997) in regarding *Neotrapezium* as a distinct genus within the family Trapezidae.

**ETYMOLOGY.** The new species is named for the state of California.

Superfamily Corbiculoidea Gray, 1847

Family Corbiculidae Gray, 1847

Genus *Corbicula* Mergele von Mühlfeld, 1811

**TYPE SPECIES.** *Tellina fluminalis* Müller, 1774; Recent, Africa, Asia, Australia, and introduced into the United States of America (Brandt, 1974).

## *Corbicula jestesi* new species

Figures 34–39

*Corbicula williamsoni* Anderson and Hanna, 1925.

Jestes, 1963:223.

*Pitar* sp. Jestes, 1963:222.

*Macrocallista* sp. Jestes, 1963:223.

**DIAGNOSIS.** A *Corbicula* with circular-rounded shape, moderately inflated beaks, moderately strong concentric ribbing, and a very slight umbonal ridge.

**COMPARISON.** The new species was compared to all other fossil species of *Corbicula* known from the northern Pacific region (including Kamchatka). The new species is most similar to *C. williamsoni* Anderson and Hanna (1925:164–165, pl. 1, fig. 4; pl. 3, fig. 2) from the “Tejon Group” at Grapevine Canyon. Only a single specimen, a left valve, is known of this species. The new species differs from *C. williamsoni* by having concentric ribbing over the entire left valve (not just the anterior half of the valve), more closely spaced and weaker concentric ribbing, a much weaker umbonal ridge, and a less sloping anterior margin. The other northern Pacific Eocene *Corbicula* species differ from the new species by having much more produced beaks, usually more central beaks, and nearly obsolete sculpture.

**DESCRIPTION.** Medium sized (up to 27 mm high), equivalved, slightly inequilateral; circular-rounded shape, longer than high. Thick shelled. Beaks prosogyrous, slightly anterior of center, moderately inflated, and elevated above hinge line. Very slight posterior umbonal ridge. Anterior dorsal margin gently sloped and concave; posterodorsal margin straight. Anterior, ventral, and posterior margins broadly and regularly rounded. Posterior very slightly produced on some specimens. Three divergent cardinal teeth in each valve, middle tooth bifid in right valve. Left valve with a long anterior and a long posterior lateral tooth, the latter minutely serrated. Right valve with long anterior lateral socket; posterior part of hinge area unknown. Entire external surface of both valves with moderately strong, closely spaced concentric ribbing.

**HOLOTYPE DIMENSIONS.** Height 18.5 mm, length 22.6 mm (a “butterfly” specimen consisting of both valves).

**PRIMARY TYPE MATERIAL.** LACMIP holotype 12464 (illustrated), LACMIP paratypes 12465 to 12468 (all illustrated); all from CSUN loc. 1445.

**TYPE LOCALITY.** CSUN loc. 1445.

←

Figures 29–38. Bivalves from Matilija Hot Springs area upper part of Matilija Sandstone. All specimens coated with ammonium chloride. 29–33. *Neotrapezium californicum* new species, CSUN loc. 1450, unless otherwise indicated. 29. Left valve,  $\times 4.3$ , LACMIP holotype 12459. 30. Left valve,  $\times 3.6$ , LACMIP paratype 12460. 31. Right valve,  $\times 2.9$ , LACMIP hypotype 12461. 32. Dorsal view showing ligamental area, LACMIP paratype 12462,  $\times 2.4$ , CSUN loc. 1445. 33. Right-valve hinge,  $\times 6.3$ , LACMIP paratype 12463. 34–39. *Corbicula jestesi* new species, CSUN loc. 1445. 34. Left valve,  $\times 1.8$ , LACMIP paratype 12465. 35. Right valve,  $\times 2$ , LACMIP holotype 12464. 36. Left-valve hinge,  $\times 2.7$ , LACMIP paratype 12466. 37. Right-valve hinge,  $\times 3.2$ , LACMIP paratype 12467. 38, 39. Left-valve hinge, LACMIP paratype 12468. 38.  $\times 3$ . 39. Enlargement (of a portion of Figure 38) showing serrations,  $\times 10$ .

**MOLLUSCAN STAGE RANGE.** "Transition."

**GEOGRAPHIC DISTRIBUTION.** Upper part of Matilija Sandstone at Matilija Hot Springs.

**LOCAL OCCURRENCE.** CSUN locs. 1445, 1452.

**REMARKS.** Specimens are abundant at CSUN locality 1445, where they range from 12.5 to 27 mm in height. Most are single valves, but they are unbroken and unworn. Specimens are rare at CSUN loc. 1452.

Worldwide, the temporal range of *Corbicula* is Early Cretaceous to Recent (Keen and Casey, 1969). On the Pacific coast of North America, the only Cretaceous *Corbicula* are two Late Cretaceous species. One is Turonian in age and the other is Maastrichtian in age (Dailey and Popenoe, 1966). No Paleocene *Corbicula* species are known from this area. Only three species of northern Pacific Eocene *Corbicula* are known to be older than the new species. They are *C. oregonensis* Turner, 1938, from lower Eocene ("Capay Stage") rocks now assigned to the Whitetail Ridge Formation near Glide in southwestern Oregon; *C. triangula* Volobueva in Devyatilova and Volobueva, 1981, from lower Eocene rocks of the Central Amaam subformation in the Koryak Uplands north of Kamchatka; and *C. carlosensis* Vokes, 1939, from middle Eocene ("Domengine Stage") rocks within the Domengine Formation in central California. The highest number of northern Pacific Eocene *Corbicula* species are found in middle to upper Eocene rocks in Washington (Weaver, 1942 [1943]) and in middle Eocene rocks of northwestern Kamchatka (Devyatilova and Volobueva, 1981).

**ETYMOLOGY.** The species is named for Edward C. Jestes, who did the initial paleontological investigations of the restricted-coastal facies at Matilija Hot Springs and who found many of the specimens of this new species.

Superfamily Veneroidea Rafinesque, 1815

Family Veneridae Rafinesque, 1815

Genus *Pelecypora* Dall, 1902

**TYPE SPECIES.** *Cytherea hatchetigbeensis* Al-drich, 1886; Eocene, Wilcox, Alabama.

*Pelecypora aequilateralis* (Gabb, 1869)

Figures 40-41

*Venus aequilateralis* Gabb, 1869:184, pl. 30, fig. 76; Dickerson, 1916:pl. 37, figs. 2a, 2b.

*Pitaria aequilateralis* (Gabb). Hanna, 1927:288, pl. 39, figs. 1-5, 9, 12.

*Pelecypora aequilateralis* (Gabb). Stewart, 1930: 237-238, pl. 8, fig. 13; Vokes, 1939:87, pl. 14, figs. 4, 6, 7, 8, 11; Weaver, 1942 [1943]:194, pl. 45, fig. 9; pl. 46, figs. 3, 6; pl. 104, fig. 6; Givens and Kennedy, 1979:table 2.

*Pelecypora aequilateralis* (Gabb) var. Turner, 1938: 57, pl. 10, figs. 1-4.

*Spisula* (?) sp. Jestes, 1963:224, 226.

*Pitar* sp. Jestes, 1963:225.

*Thyasira* (?) sp. Jestes, 1963:226.

(?) *Venus* (*Antigona*) sp. Jestes, 1963:227.

**PRIMARY TYPE MATERIAL.** MCZ lectotype 15039, designated by Stewart (1930); Delmar? Formation, San Diego area (exact location unknown), San Diego County, southern California.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 12469 and 12470.

**MOLLUSCAN STAGE RANGE.** "Domengine" to "Transition."

**GEOGRAPHIC DISTRIBUTION.** San Diego, southern California, to southwestern Oregon.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1446, 1450, 1451, 1453, and scattered coquinas.

**REMARKS.** Specimens are extremely abundant at localities 1444, 1446, and 1450. At the first two localities, specimens range from 6 to 24 mm in height. At locality 1450, they range from 1.5 to 20 mm in height. Preservation at these three localities is excellent to good, although there are some internal molds. Many specimens are single valves, but articulated specimens are common. At the other main localities, *Pelecypora aequilateralis* is common to rare. Coquinas consisting almost entirely of this species are, however, scattered throughout the section. One of the best examples is the coquina bed immediately below locality 1453.

The specimens of *Pelecypora aequilateralis* in the study area show variation in overall shape of the valves, as well as in the strength of the concentric ribbing, but this species is characterized by such variation (Hanna, 1927; Turner, 1938; Vokes, 1939).

Superfamily Tellinoidea Blainville, 1814

Family Tellinidae Blainville, 1814

Genus *Tellina* Linnaeus, 1758

**TYPE SPECIES.** *Tellina radiata* Linnaeus, 1758, by subsequent designation, Children, 1823; Recent, Caribbean.

"*Tellina*" *joaquinensis* Arnold, 1909

Figures 42-43

*Tellina joaquinensis* Arnold, 1909:49, pl. 2, fig. 11; Arnold and Anderson, 1910:70, pl. 24, fig. 11.

Vokes, 1939:90, pl. 14, figs. 15, 19, 20.

*Tellina* sp. Jestes, 1963:222 (in part).

*Gari* sp. Jestes, 1963:226.

*Tellina* (?) sp. Jestes, 1963:225.

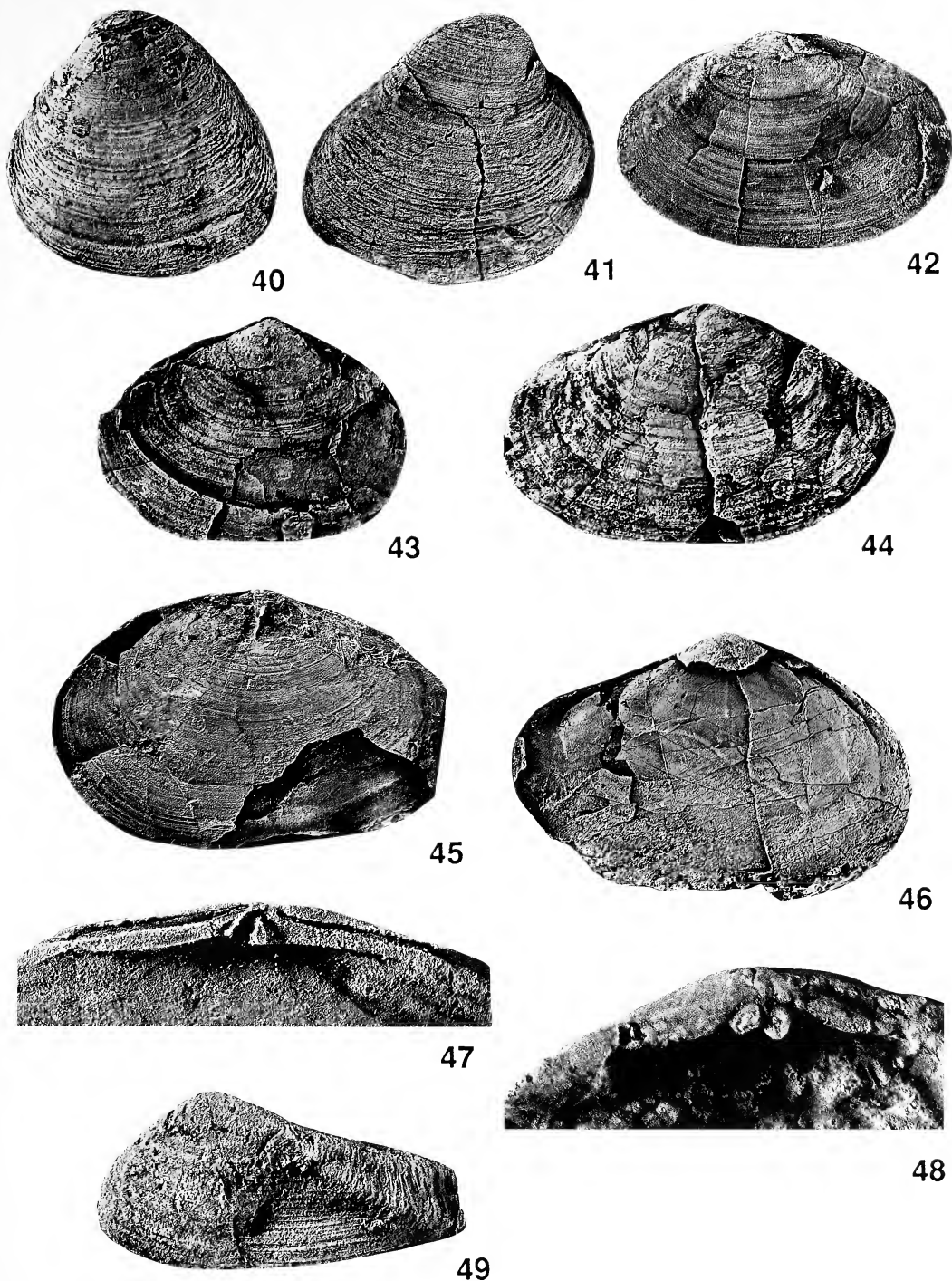
**PRIMARY TYPE MATERIAL.** USNM holotype 165619, Domengine Formation, Fresno County, central California, USGS loc. 4801.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 12471 and 12472.

**MOLLUSCAN STAGE RANGE.** "Domengine" through "Transition."

**GEOGRAPHIC DISTRIBUTION.** Matilija Hot





Figures 40–49. Bivalves from Matilija Hot Springs area upper part of Matilija Sandstone. All specimens coated with ammonium chloride. 40–41. *Pelecypora aequilateralis* (Gabb, 1869), CSUN 1450. 40. Left valve,  $\times 2.7$ , LACMIP hypotype 12469. 41. Right valve,  $\times 2.8$ , LACMIP hypotype 12470. 42–43. “*Tellina*” *joaquinensis* Arnold, 1909. 42. Left valve,  $\times 3$ , LACMIP hypotype 12471, CSUN loc. 1445. 43. Right valve,  $\times 2$ , LACMIP hypotype 12472, CSUN loc. 1445. 44–48. “*Tellina*” *domenginensis* Vokes, 1939. 44. Left valve,  $\times 1.5$ , LACMIP hypotype 12473, CSUN loc. 1445. 45. Left valve showing concentric ribs near umbo, posterior margin incomplete,  $\times 2.5$ , LACMIP hypotype 12474, CSUN loc. 1450. 46. Right valve, internal mold showing pallial sinus,  $\times 2.2$ , LACMIP hypotype 12475. 47. Latex peel of internal mold of left-valve hinge (incomplete),  $\times 3.6$ , LACMIP hypotype 12476, CSUN loc. 1450. 48. Right-valve hinge (incomplete),  $\times 6$ , LACMIP hypotype 12477, CUN loc. 1446. 49. *Cuneocorbula torreyensis* (Hanna, 1927), left valve,  $\times 5.1$ , LACMIP hypotype 12478, CSUN loc. 1445.

Springs, southern California; Coalmine Canyon, central California; and possibly Middle Fork of the Coquille River, southwestern Oregon.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1446, 1450, 1451, 1452, 1453.

**REMARKS.** This species is the only mollusk found at all of the six main localities in the restricted-coastal facies at Matilija Hot Springs. Specimens are abundant at localities 1445 and 1450 and common to uncommon at the other localities. At locality 1445, specimens range from 10 to 20 mm in height, and at locality 1450 they range from 13 to 22 mm in height. Preservation is usually poor. Nearly every specimen has been crushed. Articulated specimens are plentiful, especially at locality 1445. A specimen at this latter locality has a naticid borehole.

Arnold (1909) was somewhat contradictory in his description of this species. He stated that it is inequilateral, but in an accompanying paragraph he reported that it has approximate bilateral symmetry. The Matilija Hot Springs specimens confirm the latter. In fact, on some specimens, this bilateral symmetry makes it difficult to ascertain which is the left valve and which is the right valve.

I use quotation marks for the generic assignment of this tellinid. The species cannot be assigned with certainty to *Tellina* because the hinge is not known.

"*Tellina*" *joaquinensis* differs from "*T.*" *domenginensis* by having a much less elongate shape, less inflated and thinner valves, an absence of concentric ribs near the umbones, and a rounded rather than a pointed posterior.

Turner (1938:61, pl. 7, fig. 9) tentatively reported (as *Tellina* cf. *joaquinensis*) a single, poorly preserved specimen of this species in Eocene rocks along the Middle Fork Coquille River, Coos County, southwestern Oregon.

The presence of "*Tellina*" *joaquinensis* at Matilija Hot Springs is the youngest and southernmost record of this species.

#### "*Tellina*" *domenginensis* Vokes, 1939

Figures 44-48

*Tellina domenginensis* Vokes, 1939:91, pl. 14, figs. 12, 14, 16, 18.

*Tellina* sp. Jests, 1963:222 (in part).

*Gari* sp. Jests, 1963:223.

**PRIMARY TYPE MATERIAL.** UCMP holotype 15694, UCMP loc. 3315; UCMP paratypes 15695, 15696, both from UCMP loc. A-975; UCMP paratype 15697, UCMP loc. A-1220; all from the Domengine Formation, Fresno County, central California.

**ILLUSTRATED SPECIMENS.** LACMIP hypotypes 12473 to 12477.

**MOLLUSCAN STAGE RANGE.** "Domengine" through "Transition."

**GEOGRAPHIC DISTRIBUTION.** Matilija Hot Springs, southern California, and between Oil City

and Domengine Creek on west side of San Joaquin Valley, north of Coalinga, central California.

**LOCAL OCCURRENCE.** CSUN locs. 1444, 1445, 1450.

**REMARKS.** Specimens are common only at locality 1450, where they range from 12 to 20 mm high. A few specimens are articulated. Specimens are rare at the other two localities. Study area specimens reveal new information about this species' morphology, both exterior and interior. Fine concentric ribs are present near the umbones, although Vokes (1939) reported that the surface ornamentation consists only of coarse concentric growth lines. The pallial sinus of the right valve is revealed for the first time. It is broadly rounded, the dorsal margin ascends posteriorly, and the anterior margin is not close to the anterior adductor scar (Fig. 46). The relationship between the ventral margin of the right-valve pallial sinus and the pallial line is not clear, but they seem to be coalescent. The shape of the left-valve pallial sinus remains unknown. The cardinal teeth of both valves are also revealed for the first time. The left-valve cardinal teeth are divergent, with the anterior tooth strong and the posterior tooth very thin and lamellar (Fig. 47). The cardinal teeth on the right valve are both strong (Fig. 48), but whether or not these teeth are bifid cannot be determined. Unfortunately, poor preservation prevents study of the rest of the hingeline, where lateral teeth might be present. Until the presence of lateral teeth is confirmed, the species cannot be assigned with certainty to *Tellina*.

Among the tellinids, "*Tellina*" *domenginensis* has some important similarities to the extant *Peronidia albicans* (Gmelin, 1791; Afshar, 1969:84, pl. 35, figs. 1-5), which is the type species of *Peronidia* Dall, 1900b. Both have the following features: an ovate-trigonal shape with nearly central umbones; the posterior cardinal of the left valve is thin, lamellar, and mostly fused with the nymph; the posterior cardinal of the right valve is larger than the anterior one; and the pallial sinus is large and does not touch the anterior adductor scar.

There is also a close resemblance between "*Tellina*" *domenginensis* and the flat, almost equilateral *Peronidia nysti* (Deshayes, 1860; Báldi, 1973:225-226, pl. 21, figs. 1-2, 4) from upper Oligocene rocks in Hungary. Only the external features are known for *P. nysti*, and "*T.*" *domenginensis* differs from it by having concentric ribs near the umbones and a posterior margin that is rounded rather than slightly angular.

Better specimens of "*Tellina*" *domenginensis* are needed to determine whether or not this species is related to *Peronidia*. Additionally, there has been little agreement on the taxonomic position of *Peronidia*. It has been regarded as a subgenus of *Tellina* by some workers (Keen, 1969b; Coan, 1971; Coan and Scott, 1997); as a subgenus of *Macoma* by Afshar (1969); and as a subgenus of *Angulus* by Báldi (1973).

The presence of "*Tellina*" *domenginensis* at Ma-

Matilija Hot Springs is the youngest and the southernmost record of this species.

Subclass Asthenodonta Dall, 1895

Order Myoida Goldfuss, 1820

Suborder Myina Goldfuss, 1820

Superfamily Myoidea Lamarck, 1809

Family Corbulidae Lamarck, 1818

Genus *Cuneocorbula* Cossmann, 1886

**TYPE SPECIES.** *Corbula pelseneeri* Glibert and van de Poel, 1966 [= *Corbula biangulata* Deshayes, 1861]; upper Paleocene (Thanetian Stage), Paris Basin, France.

*Cuneocorbula torreyensis* (Hanna, 1927)

Figure 49

*Corbula torreyensis* Hanna, 1927:296–297, pl. 44, figs. 6–10, 15–16; Clark and Vokes, 1936:875, figs. 9, 11; Turner, 1938:66, pl. 8, figs. 6, 7; Weaver 1942 [1943]:259–260, pl. 61, fig. 12.

*Cuneocorbula torreyensis* (Hanna). Vokes, 1939: 101–102, pl. 16, figs. 16, 20, 21; Jestes, 1963: 222, 225; Givens and Kennedy, 1979:table 2.

*Corbula* (*Cuneocorbula*) *torreyensis* Hanna. Givens, 1974:58.

**PRIMARY TYPE MATERIAL.** UCMP holotype 31115; UCMP paratypes 31116–31119; all from Delmar Formation, San Diego area, San Diego County, southern California, UCMP loc. 3981.

**ILLUSTRATED SPECIMEN.** LACMIP hypotype 12478.

**MOLLUSCAN STAGE RANGE.** “Domengine” to “Transition.”

**GEOGRAPHIC RANGE.** San Diego and Matilija Hot Springs, southern California; Vallecitos Syncline, central California; and Glide, southwestern Oregon.

**LOCAL OCCURRENCE.** CSUN locs. 1445, 1452, and scattered coquinas.

**REMARKS.** Specimens are abundant at localities 1445 and 1452. At both localities, specimens range from 5 to 6 mm in height, and preservation is good. Specimens are unworn, unbroken, and mostly single valves. Articulated specimens are very rare. Throughout the section, specimens of *Cuneocorbula torreyensis* form coquinas consisting almost entirely of compacted specimens of this species.

## LOCALITIES

### CSUN LOCALITIES

All are in the upper part of the Matilija Sandstone (lower middle Eocene “Transition Stage”) in the NE 1/4 of the SE 1/4 of section 29, T 5 N, R 23 W, USGS topographic quadrangle, Matilija, California, 7.5 minute, 1952 (photorevised 1967), 1:24,000.

1444. [= LACMIP 16961]. Roadcut on north side of a short, paved road that leads from Highway 33 to Matilija

Hot Springs, about 48 m (157 ft.) west of sharp bend in this road, near bottom of restricted-coastal facies.

1445. [= LACMIP 24259]. Roadcut on north side of a short, paved road that leads from Highway 33 to Matilija Hot Springs, about 26 m (85 ft.) west of sharp bend in this road.

1446. [= LACMIP 24258]. Roadcut on north side of a short, paved road that leads from Highway 33 to Matilija Hot Springs, about 12 m (39 ft.) west of sharp bend in this road.

1450. [= LACMIP 16963]. On south bank of North Fork of Matilija Creek, near bottom of restricted-coastal rocks, about 260 m (852 ft.) west of junction of Highway 33 and a short, paved road that leads to Matilija Hot Springs.

1451. [= LACMIP 16964]. On south bank of North Fork of Matilija Creek, about 250 m (820 ft.) west of junction of Highway 33 and a short, paved road that leads to Matilija Hot Springs.

1452. [= LACMIP 16965]. On south bank of North Fork of Matilija Creek, about 230 m (754 ft.) west of junction of Highway 33 and a short, paved road that leads to Matilija Hot Springs.

1453. [= LACMIP 16962]. Roadcut on north side of a short, paved road that leads from Highway 33 to Matilija Hot Springs, about 43 m (141 ft.) west of sharp bend in this road.

### LACMIP LOCALITY

7226. In the vicinity of Beartrap Creek, just east of hill 4560 along an unmaintained trail and downslope for about 15 m (49 ft) from trail, at section line between sections 24 and 25, T 7 N, R 23 W, USGS topographic quadrangle, Reyes Peak, California, 7.5 minute, 1943, 1:24,000.

### UCMP LOCALITIES

672. SE 1/4 of the NW 1/4 of section 24, T 18 S, R 14 E, USGS topographic quadrangle, Joaquin Rocks, California, 7.5 minute, 1969, 1:24,000.

3315. Base of Domengine Formation, immediately south of Domengine Creek, USGS topographic quadrangle, Domengine Ranch, California, 7.5 minute, 1956 (photorevised 1979), 1:24,000.

3981. At 15 m (50 ft.) above high-tide level in a small gully .4 km (.24 mi.) south of mouth of Soledad Valley, USGS topographic quadrangle, Del Mar, California, 7.5 minute, 1967, 1:24,000.

3992. In sea cliff about .8 km (.5 mi.) south of the mouth of Soledad Valley at high-tide level, USGS topographic quadrangle, Del Mar, California, 7.5 minute, 1967, 1:24,000.

5084. At 2.55 inches due north of top of the “S” of Soledad Mountain, in sea cliff, elevation 3 m (10 ft.), fossils in the conglomerate above the mudstone, USGS topographic quadrangle, La Jolla, California, 7.5 minute, 1967, 1:24,000.

A-975. Second “reef” above base of Domengine Formation in draw across ridge to south of Big Tar Canyon, USGS topographic quadrangle, Garza Peak, California, 7.5 minute, 1953, 1:24,000.

A-1220. At base of Domengine Formation in small draw cutting long ridge, 53 m (175 ft.) north of line between sections 9 and 16, T 19 S, R 15 E, USGS topographic quadrangle, Domengine Ranch, California, 7.5 minute, 1956 (photorevised 1979), 1:24,000.

A-1297. From sandstone cliff on northeast bank of

Pleasants Creek opposite Brink ranch house about 1.2 km (.75 mi.) east of bench mark 258, and 3.2 km (2 mi.) south of Putah Creek, USGS topographic quadrangle, Mt. Vaca, California, 7.5 minute, 1951 (photorevised 1968), 1:24,000.

## UCR LOCALITY

4747. Just east of elevation 4072 on ridge south of mouth of Beartrap Creek, 594 m (1948 ft.) north and 457 m (1498 ft.) east of southwest corner of section 23, T 7 N, R 23 W, USGS topographic quadrangle, Reyes Peak, California, 7.5 minute, 1943, 1:24,000.

## USGS LOCALITY

4801. About 4.8 km (3 mi.) northwest of Coalinga, at Coalmine Canyon in NW 1/4 of section 26, T 20 S, R 14 E, USGS topographic quadrangle, Alcalde Hills, California, 7.5 minute, 1969, 1:24,000.

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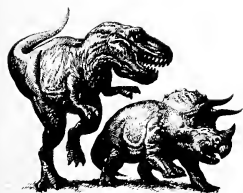
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# CONTRIBUTIONS IN SCIENCE

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A NEW HEMPHILLIAN (LATE MIOCENE)  
MAMMALIAN FAUNA FROM HOYE CANYON,  
WEST CENTRAL NEVADA

THOMAS S. KELLY



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# A NEW HEMPHILLIAN (LATE MIOCENE) MAMMALIAN FAUNA FROM HOYE CANYON, WEST CENTRAL NEVADA

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THOMAS S. KELLY<sup>1</sup>

**ABSTRACT.** A new late Hemphillian (late Miocene) fossil mammalian assemblage, the Hoye Canyon Local Fauna, is now recognized from an unnamed formation exposed along the western flanks of the Wellington Hills, Douglas County, Nevada. The fauna was recovered from the lower part of the unnamed formation and consists of the following taxa: Leporidae, *Pronotolagus nevadensis* n. sp.; Sciuridae, *Spermophilus wellingtonensis*; Sciuridae, *Marmota korthi* n. sp.; Geomyidae, *Parapliosacommys oregonensis*; Camelidae, *Hemiauchenia vera*; ?Antilocapridae, gen. and sp. indet.; Rhinocerotidae, gen. and sp. indet.; and Equidae, *Dinohippus* sp. indet. The middle and upper portions of the unnamed formation previously yielded late Blancan (late Pliocene) and early Irvingtonian (early Pleistocene) faunas. Discovery of the Hoye Canyon Local Fauna now indicates that the formation spans the late Hemphillian to the early Irvingtonian or about 7 to 1.8 million years before present.

## INTRODUCTION

Kelly (1997) documented the first records of fossil vertebrates from the Wellington Hills–Antelope Valley area of Douglas County, Nevada. The fossils were recovered from an unnamed formation exposed along the western flanks of the Wellington Hills from the vicinity of Hoye Canyon in the north to Risue Canyon in the south (Fig. 1). Kelly (1997) provisionally recognized two late Cenozoic mammalian faunas from the unnamed formation: the late Blancan Wellington Hills Local Fauna and the early Irvingtonian Topaz Lake Local Fauna. Kelly (1997) reported only one locality in the Hoye Canyon area, UCMP V-95013 (= LACM 6993), that did not yield any age-diagnostic fossils at the time. Because the northern outcrops of the unnamed formation in the Hoye Canyon area are isolated from the southern outcrops by foothills covered with Quaternary alluvium, Kelly (1997, fig. 3) only questionably correlated UCMP V-95013 with the late Blancan localities to the south.

Quarrying at LACM 6993 and the discovery of an additional locality, LACM 6994, that occurs slightly higher in the section above LACM 6993, has resulted in the recovery of age-diagnostic fossils. These new fossils indicate that the fauna from the Hoye Canyon localities is late Hemphillian (late Miocene) in age and, thus, considerably older than the fauna from the late Blancan (late Pliocene) localities of the southern outcrops. The assemblages from LACM 6993 and LACM 6994 are herein named the Hoye Canyon Local Fauna.

The purpose of this report is to document the new records of Hemphillian mammalian fossils from the Hoye Canyon area and reevaluate the biostratigraphy of the unnamed formation exposed along the western flanks of the Wellington Hills.

## METHODS

Larger mammal teeth and appendicular elements were measured with a vernier caliper to the nearest 0.1 mm and those of smaller mammals were measured with an optical micrometer disc to the nearest 0.01 mm. All teeth were measured along their greatest anteroposterior and transverse enamel dimensions. Metric abbreviations, dental terminology, and dental formulas follow standard usage. Measurements and calculations of the degree of deflection of the posterior external reentrants in the rabbit lower premolars follows those of White (1987, 1991). Specimens previously collected from the unnamed formation of the Wellington Hills–Antelope Valley area reported on by Kelly (1997) are housed in the University of California, Berkeley, Museum of Paleontology, whereas all new specimens recovered during this study have been deposited in the Vertebrate Paleontology Section of the Natural History Museum of Los Angeles County.

Abbreviations are as follows: AER, anterior external reentrant; AIR, anterior internal reentrant; ANT, anterior; A-P, greatest anteroposterior dimension; AR, anterior reentrant; d, deciduous; D-V, dorsoventral; L, left; Ma, million years before present; PER, posterior external reentrant; PIR, posterior internal reentrant; POST, posterior; R, right; s. s., *sensu stricto*; TR, greatest transverse dimension. Institutional acronyms are as follows: LACM, Natural History Museum of Los Angeles County; UCMP, University of California, Berkeley, Museum of Paleontology; V-, UCMP vertebrate fossil locality.

## GEOLOGY AND FOSSIL OCCURRENCES

Halsey (1953) first reported the occurrence of a thick deposit of Tertiary sediments along the west-

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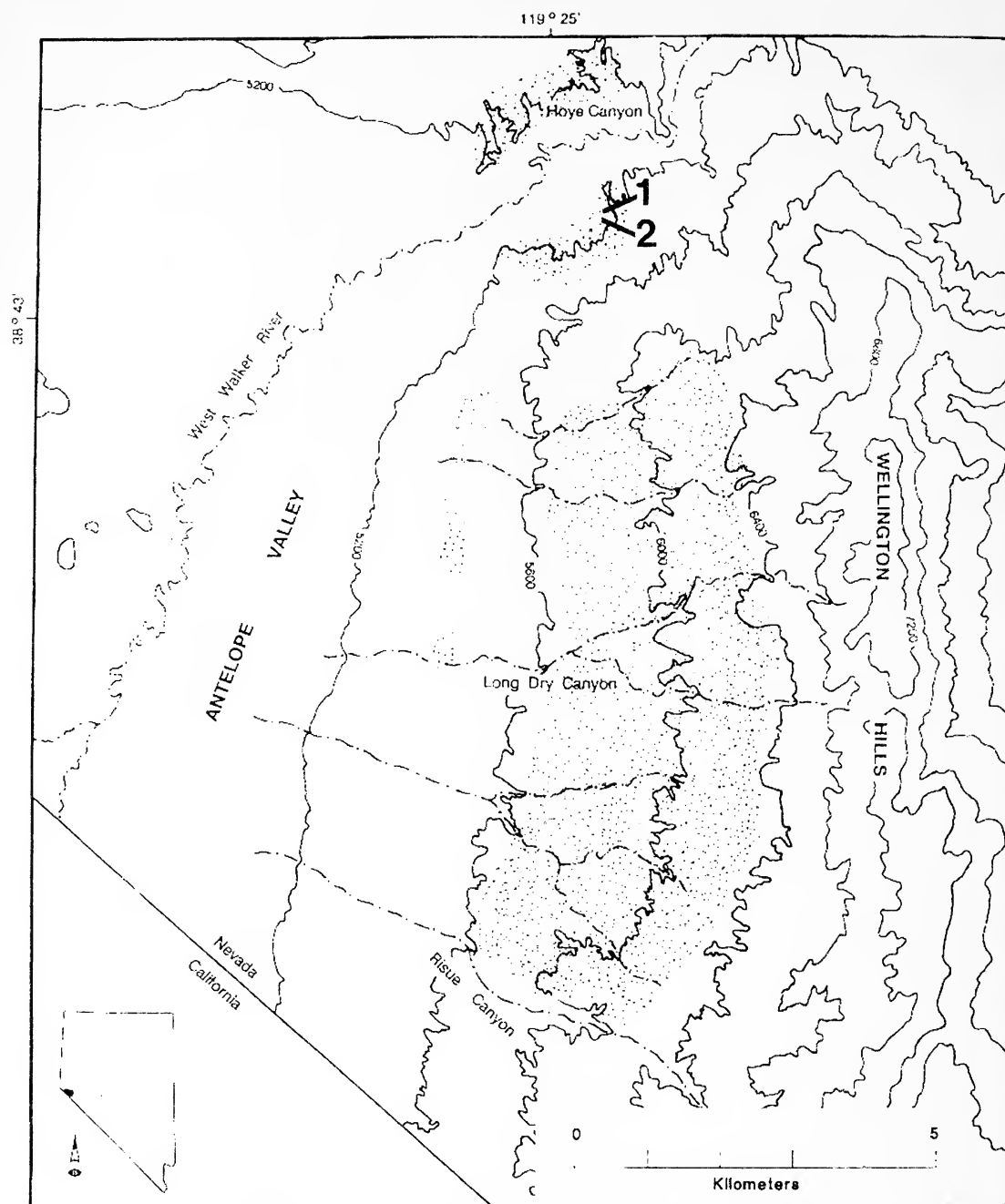


Figure 1. Map of Antelope Valley–Wellington Hills area showing geographic extent of unnamed formation (stippled areas) and locations of Hoye Canyon fossil localities (1 = LACM 6994, 2 = LACM 6993). Base map: U.S.G.S. 15 minute series, Desert Creek Peak, Nevada–California Quadrangle (scale = 1:62,000, contour interval = 400 ft).

ern flanks of the Wellington Hills from Risue Canyon northward to Hoye Canyon. Moore (1969) regarded these sediments as probably middle or early late Miocene (Barstovian or Clarendonian) in age. However, Kelly (1997) provided biostratigraphic evidence that these sediments are, in part, late Pliocene to early Pleistocene (late Blancan to early Ir-

vingtonian) in age. Kelly (1997) regarded these sediments as an unnamed formation because they are a single continuously deposited rock unit comprised of stream and lake deposits of relatively homogeneous lithologies.

The unnamed formation of the Wellington Hills area is comprised of alternating sequences of lacus-

trine, braided fluvial, and overbank sediments that are composed of tuffaceous mudstone, diatomaceous shale, siltstone, sandstone, and conglomerate (Kelly, 1997). In Hoyo Canyon, the unnamed formation unconformably overlies Miocene andesite interbedded with minor sedimentary deposits, probably a correlative of the Kate Peak Formation of Gianella (1936), and is unconformably overlain by Quaternary alluvium.

The mammalian fossils were recovered from lacustrine deposits exposed on the south side of Hoyo Canyon (detailed locality data on file at the LACM). Locality LACM 6993 occurs about 170 m above the contact with the Miocene andesite in a 1.6-m-thick sandstone bed that contains small mudstone clasts and thin lenses of conglomerate. The precise stratigraphic position of LACM 6993 relative to the base of the formation is difficult to determine because a small alluvium-filled valley separates the section that contains LACM 6993 from the lowermost portion of the formation. Locality LACM 6994 occurs near the top of a 3.9-m-thick bentonitic clay and mudstone bed, about 30 m stratigraphically higher in the section than LACM 6993.

## SYSTEMATIC PALEONTOLOGY

Order Lagomorpha Brandt, 1855

Family Leporidae Fischer de Waldheim,  
1817

Genus *Pronotolagus* White, 1991

*Pronotolagus nevadensis*, new species

Figure 2, Table 1

**HOLOTYPE.** Partial dentary with L  $P_3$ – $M_3$ , LACM 145952.

**TYPE LOCALITY.** LACM 6993.

**HYPODIGM.** From LACM 6993: partial dentary with L  $dP_{3-4}$ ,  $M_{1-3}$ , LACM 145953; partial dentary with L  $P_4$ – $M_3$ , LACM 145954; partial dentary with R  $P_4$ – $M_2$ , LACM 145955; R  $P_3$ , LACM 145956.

**DISTRIBUTION AND AGE.** Known only from the type locality, late Hemphillian.

**ETYMOLOGY.** Named for its occurrence in Nevada.

**DIAGNOSIS.** *Pronotolagus nevadensis* differs from *Pronotolagus albus* Voorhies and Timperley, 1997, by the following characteristics: (1) much smaller size (mean  $P_3$  A-P 62% smaller than that of *P. albus*); (2) better developed and deeper  $P_3$  AIR (depth averages 22.2% of TR occlusal dimension); (3) a distinct  $P_3$  PIR present and cement filled; (4) deeper  $P_3$  AER (depth averages 23% of TR occlusal dimension); and (5) shallower  $P_3$  PER (depth averages 44.2% of TR occlusal dimension). It differs from *Pronotolagus apachensis* (Gazin, 1930) by the following characteristics: (1) much smaller size (mean  $P_3$  A-P 50% smaller than that of *P. apachensis*); (2) deeper  $P_3$  AIR; (3) more distinct and

deeper  $P_3$  PIR (depth averages 8.5% of TR occlusal dimension). It differs from *Pronotolagus whitei* Korth, 1998, by the following characteristics: (1) much smaller size (mean  $P_3$  A-P 53% smaller than that of *P. whitei*); (2) deeper  $P_3$  AIR; (3) better developed  $P_3$  PIR; (4) deeper  $P_3$  AER; and (5) shallower  $P_3$  PER that is inclined posteriorly.

**DESCRIPTION.** Of the five specimens of *Pronotolagus nevadensis*, LACM 145953 retains  $dP_{3-4}$ , indicating that this specimen represents an immature individual, whereas  $P_3$ s of the holotype and the referred specimen (LACM 145956) are in early wear indicating that these specimens represent young adults. Although  $P_3$ s of LACM 145954 and LACM 145955 are missing, the remaining cheek teeth are in early wear and early moderate wear, respectively, indicating that they also represent young adults. The dentary is of typical leporid structure. The anterior margin of the masseteric fossa extends to a point below the middle of  $M_1$ . Numerous small foramina are present on the lateral side of the horizontal ramus below  $P_3$ .

$DP_3$  is molariform and rooted, with the trigonid and talonid being transversely expanded. An oval-shaped anterior conid is present that is connected to the middle of the anterior face of the trigonid by an isthmus. Likewise, the trigonid is connected to the middle of the anterior face of the talonid by an isthmus.  $DP_1$  also is molariform and rooted but differs from  $dP_3$  by having an anterior marginal crest along the anterior border of the trigonid instead of a distinct conid. Thin enamel bands are present along the posterolabial margins of the  $dP_{3-4}$  trigonids and talonids. Hypoconulids are lacking on both deciduous premolars.

$P_3$  of the holotype (LACM 145952, Fig. 2B) exhibits the following characteristics: (1) size small, as compared with other species of *Pronotolagus*; (2) an AIR and PIR are present with the AIR shallower than the PIR; (3) the AIR depth is 20.8% of the TR occlusal dimension; (4) the PIR depth is 8.3% of the TR occlusal dimension; (5) the AER depth is 25% of the TR occlusal dimension; (6) the PER is 45.8% of the TR occlusal dimension; (7) an AR is lacking; (8) the thick enamel of the PER is relatively straight with a slight posterior deflection (9.2 degrees); (9) the thin enamel of the PER is smooth, lacking crenulations; and (10) cement is present in the AIR, PIR, AER, and PER.  $P_3$  of the holotype was broken off 2.8 mm from the crown at the alveolar border during preparation that allowed examination of the enamel pattern farther down the crown. The enamel pattern (Fig. 2C) at this point is very similar to the occlusal enamel pattern, primarily differing by a slight increase in the depth of the AIR and PIR (21.2% and 10.2% of the TR occlusal dimension, respectively) and a slightly more posteriorly deflected PER (9.3 degrees). The  $P_3$  occlusal enamel pattern of LACM 145956 (Fig. 2D) is very similar to the holotype, primarily differing by having a slightly shallower

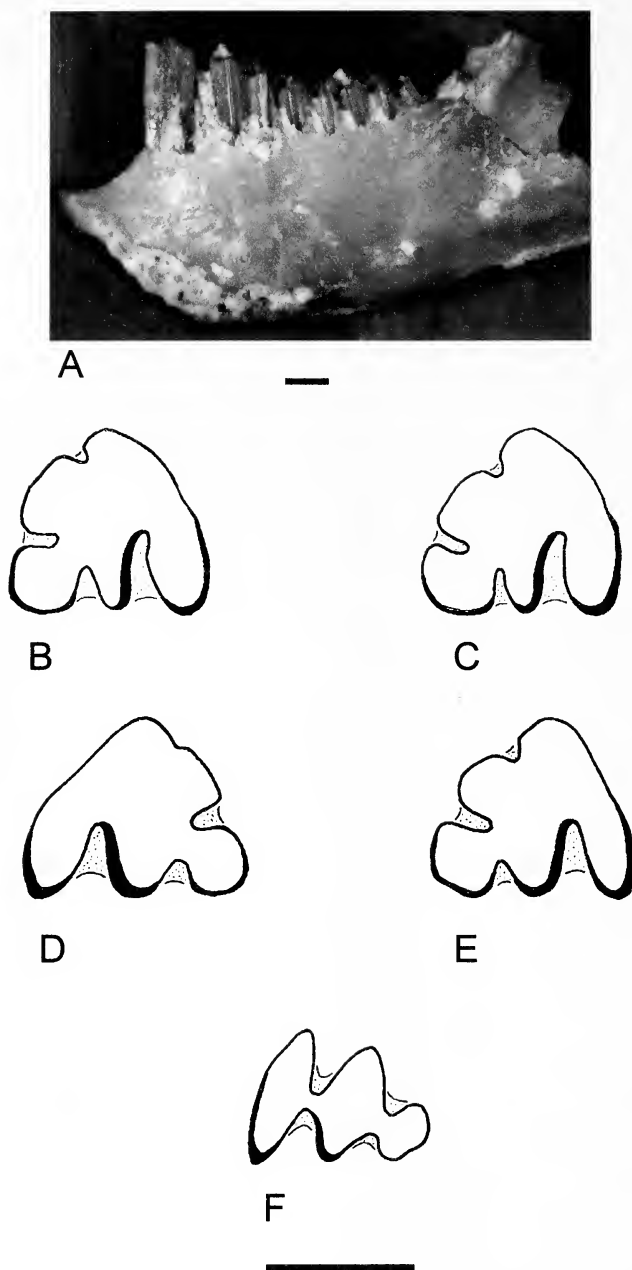


Figure 2. *Pronotolagus nevadensis* new species. A, partial dentary with L P<sub>3</sub>-M<sub>3</sub>, holotype, LACM 145952, lateral view. B, L P<sub>3</sub>, holotype, LACM 145952, occlusal view, anterior left. C, L P<sub>3</sub>, holotype, LACM 145952, cross-section 2.8 mm below crown, anterior left. D, R P<sub>3</sub>, LACM 145956, occlusal view, anterior right. E, R P<sub>3</sub>, LACM 145956, enamel pattern at base of tooth, anterior left. F, R dP<sub>3</sub>, LACM 145953, occlusal view, anterior right. Upper scale for A = 1 mm, lower scale for B-F = 1 mm.

PIR, AER, and PER. The reentrants at the occlusal surface of LACM 145956 exhibit the following characteristics: (1) the AIR is 20.9% of the TR occlusal dimension; (2) the PIR is 4.3% of the TR occlusal dimension; (3) the AER is 20.9% of the TR occlusal dimension; (4) the PER is 43% of the TR occlusal dimension; (5) the thick enamel of the

PER is almost straight with a slight posterior deflection (10 degrees); and (6) cement is present in the AIR, PIR, AER, and PER. The enamel pattern at the base of LACM 145956 (Fig. 2E) is similar to the occlusal enamel pattern, primarily differing by having a deeper AIR, PIR, AER, and PER (26.1%, 11.3%, 21.7%, and 43.5% of the TR di-

Table 1. Measurements (in mm) of specimens of *Pronotolagus nevadensis* new species from Hoye Canyon.

Tooth position/ dimension	Holotype				
	LACM 145953	LACM 145952	LACM 145954	LACM 145955	LACM 145956
dP <sub>3</sub> A-P	1.06				
ANT-TR	0.70				
POST-TR	1.01				
dP <sub>4</sub> A-P	1.00				
ANT-TR	1.05				
POST-TR	1.06				
P <sub>3</sub> A-P		1.20			1.19
TR		1.10			1.04
P <sub>4</sub> A-P		1.28	1.34	1.33	
ANT-TR		1.33	—	1.34	
POST-TR		1.21	1.55	1.31	
M <sub>1</sub> A-P	1.02	1.45	1.32	1.33	
ANT-TR	1.09	1.35	1.50	1.45	
POST-TR	1.10	1.30	1.45	1.44	
M <sub>2</sub> A-P	1.05	1.36	1.33	1.39	
ANT-TR	1.06	1.34	1.36	1.35	
POST-TR	1.04	1.23	1.33	1.34	
M <sub>3</sub> A-P	0.46	0.68	0.70		
TR	0.50	1.00	0.99		
dP <sub>3</sub> -M <sub>3</sub> alveolar A-P	5.25				
P <sub>3</sub> -M <sub>3</sub> alveolar A-P		6.31	6.61		
Depth of dentary below P <sub>4</sub>	3.98	5.05	4.91	5.09	

mension, respectively) and a less posteriorly deflected PER (9.7 degrees).

The lower molars are of typical leporid structure with oval-shaped trigonids and talonids that are connected by an isthmus, prominent anterior marginal crests along the anterior borders of the trigonids, and enamel along the posterolabial borders of the trigonids and talonids. In all of the partial dentaries, the molar crowns are well above their alveolar borders.

**DISCUSSION.** Species of rabbits are primarily differentiated by the morphologies of P<sup>2</sup> and P<sub>3</sub> (White, 1987, 1991). Recently, Voorhies and Timperley (1997) emended the diagnosis of *Pronotolagus*, wherein they listed the following diagnostic characteristics: (1) small- to medium-sized leporines; (2) an AR is lacking on P<sub>3</sub>; (3) the P<sub>3</sub> AIR is more deeply incised than the PIR when the latter is present; (4) the P<sub>3</sub> AER is shallow and wide; and (5) the P<sub>3</sub> PER ranges from 40 to 58% of the transverse occlusal surface. The Hoye Canyon rabbit specimens exhibit all of these diagnostic characters and can be assigned confidently to *Pronotolagus*.

Although only two P<sub>3</sub>s are known for *Pronotolagus nevadensis*, they both exhibit very similar occlusal enamel patterns. These enamel patterns also remain rather consistent down the crown as indicated by the cross-sectional pattern of the holotype 2.8 mm below the occlusal surface and by the enamel pattern at the base of LACM 145956 4.5

mm below the occlusal surface (Fig. 2B-E). Also, the A-P and TR dimensions vary little down the crowns. In the holotype, the P<sub>3</sub> A-P and TR dimensions vary from 1.20 mm and 1.10 mm at the occlusal surface to 1.23 mm and 1.12 mm at the alveolar border, respectively. In LACM 145956, the A-P and TR dimensions vary from 1.19 mm and 1.04 mm at the occlusal surface to 1.21 mm and 1.06 mm at the base of the crown, respectively. Thus, even though P<sub>3</sub>s are in early wear, their occlusal dimensions and enamel patterns would change little with additional wear. Dalquest (1979) noted that P<sub>3</sub> is diagnostic in almost all instances, even in immature rabbits where the occlusal surface is unworn by using the enamel pattern at the base of the tooth or cross-sectioned patterns.

The dimensions of rabbit cheek teeth vary with age, wherein P<sub>3</sub>s of immature individuals usually exhibit a marked increase in size from the occlusal surface to the base of the tooth (Dice and Dice, 1935, 1941; Wood, 1940; White, 1991). This is true especially for immature P<sub>3</sub>s that are unworn or just beginning to wear. For example, in an immature P<sub>3</sub> of *Nekrolagus progressus* (Hibbard, 1939), the A-P dimension at the base of the tooth is 38% larger than the occlusal dimension (Hibbard, 1963, fig. 1b-d). Similarly, in an immature P<sub>3</sub> of *Pratilepus kansasensis* Hibbard, 1939, the A-P dimension at the base of the tooth is 38% greater than the crown dimension (Hibbard, 1963, fig. 2a-a'). In an

unworn  $P_3$  of *Pronotolagus whitei*, the A-P crown dimension is about 22% smaller than the mean A-P dimension of adult  $P_3$ s (Korth, 1998, fig. 14D–G, table 14). In *Palaeolagus* Leidy, 1856, and *Lepus* Linnaeus, 1758, the  $P_3$  occlusal dimensions in early wear average about 18% and 10% smaller, respectively, than those of well-worn teeth (Dice and Dice, 1935; Wood, 1940; Hibbard, 1963). As noted above,  $P_3$ s of *Pronotolagus nevadensis* do not exhibit any significant differences in the A-P and TR dimensions from the occlusal surface to the base of the crowns. However, because of the small sample size, the possibility that older individuals could have larger  $P_3$ s cannot be ruled out. Even if the  $P_3$  A-P dimensions of more mature individuals of *P. nevadensis* were discovered to be 30% larger than those of the holotype and referred specimen, they would still be 45%, 40%, and 30% smaller than the means of those of *Pronotolagus albus*, *Pronotolagus whitei*, and *Pronotolagus apachensis*, respectively. Moreover, the fact that the A-P dimension of  $dP_4$  of *P. nevadensis* is 48% smaller than the mean  $dP_4$  A-P of *P. whitei* (Korth, 1998, table 14) further supports the conspicuous size difference between *P. nevadensis* and the other species of *Pronotolagus*.

Voorhies and Timperley (1997) noted the following evolutionary trends in *Pronotolagus* with decreasing geologic age: (1) a decrease in body size; (2) a deepening of the  $P_3$  AIR; (3) an increase in the amount of cement in the  $P_3$  AIR; and (4) a more distinct  $P_3$  PIR. At the time, only two species of *Pronotolagus* were known, *Pronotolagus albus* from the late Barstovian of Nebraska and *Pronotolagus apachensis* from the Clarendonian of California and the early Hemphillian of Nebraska. Subsequently, Korth (1998) described a third species, *Pronotolagus whitei* from late Clarendonian Pratt Quarry of the Merritt Dam Member of the Ash Hollow Formation, Nebraska. Although *P. whitei* is similar in size to *P. apachensis*, it differs from it by having a deeper  $P_3$  PER that is inclined anteriorly instead of posteriorly (Korth, 1998). Korth (1998) noted that the early Hemphillian specimens from the LeMoyne Quarry of Nebraska that White (1991) referred to *P. apachensis* differ from the topotypic Clarendonian sample of *P. apachensis* from California by having anteriorly inclined  $P_3$  PERs, like those of *P. whitei*. The  $P_3$  AIRs of the LeMoyne Quarry specimens are also deeper and more persistent than the topotypic samples of *P. apachensis* and *P. whitei* (White, 1991; Korth, 1998). Korth (1998) suggested that the LeMoyne Quarry sample might represent a distinct species more closely related to *P. whitei* than *P. apachensis*.  $P_3$ s of *P. nevadensis* differ from those of the early Hemphillian LeMoyne Quarry sample by having the following: (1) smaller size; (2) more persistent PIRs; and (3) shallower PERs that are inclined posteriorly rather than anteriorly.

*Pronotolagus nevadensis* is the smallest species of the genus and its  $P_3$  AIR and PIR are particularly well developed, as compared with those of *Prono-*

*tolagus albus*, *Pronotolagus whitei*, and *Pronotolagus apachensis* (White, 1991; Voorhies and Timperley, 1997; Korth, 1998). If the evolutionary trends noted by Voorhies and Timperley (1997) actually represent derived character transformations, then *P. nevadensis* is the most derived species of *Pronotolagus*. As noted above, the age of the Hoye Canyon Local Fauna is late Hemphillian and, therefore, *P. nevadensis* is also the youngest known species of *Pronotolagus*.

Order Rodentia Bowdich, 1821

Family Sciuridae Fischer de Waldheim, 1817

Genus *Spermophilus* Cuvier, 1825

*Spermophilus wellingtonensis* Kelly, 1997

Figure 3, Table 2

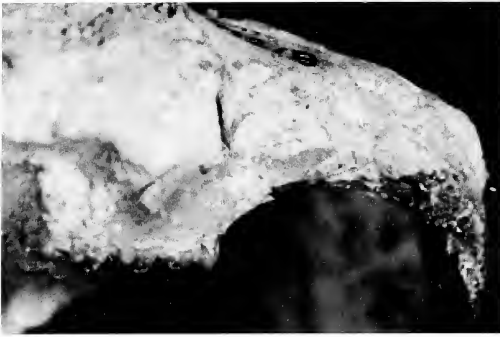
**SPECIMENS.** From LACM 6993: partial skull with L and R  $I^1$ – $M^3$  and associated appendicular elements, LACM 145957; partial dentary with R  $I_1$ , LACM 145958.

**DESCRIPTION.** The cranial morphology and upper dentition of *Spermophilus wellingtonensis* were previously unknown. The posterior portion of the partial skull is missing, being broken off dorsally across the parietals and ventrally across the palatines (Fig. 3A, B). The anterior tips of the nasals and premaxillaries and the zygomatic arches are also missing. Many small fractures are present, making it difficult to identify sutures and individual bones. The nasals taper posteriorly and the nasofrontal sutures form an obtuse angle with the apex pointing posteriorly. The partial parietals are slightly depressed, but the skull roof appears to have been relatively flat. The rostrum is elongate, tapering slightly anteriorly. The infraorbital foramen is an oval slit (2.3 mm D–V, 1.3 mm A–P) on the maxilla and positioned 1.4 mm anteriorly from the anterior margin of the  $P^3$  alveolus. The maxillary root

Table 2. Measurements (in mm) of upper dentition of *Spermophilus wellingtonensis* from Hoye Canyon.

Tooth position/ dimension		LACM 145957	
		Right	Left
$P^3$	A–P	1.28	1.29
	TR	1.25	1.27
$P^4$	A–P	2.36	2.28
	TR	2.74	2.79
$M^1$	A–P	2.59	2.71
	TR	3.17	3.20
$M^2$	A–P	2.64	2.63
	TR	3.34	3.42
$M^3$	A–P	3.11	3.13
	TR	3.17	3.16
$P^{3-4}$	A–P	3.23	3.32
$M^{1-3}$	A–P	8.09	8.12
$P^4$ – $M^3$	A–P	10.17	10.20
$P^3$ – $M^3$	A–P	10.77	11.35





A



B



C



**Figure 3.** *Sperophilus wellingtonensis*. A–C, partial skull, LACM 145957. A, right lateral view. B, palatal view. C, L P<sup>3</sup>–M<sup>3</sup>, occlusal view, anterior left. Upper scale for A, B = 10 mm; lower scale for C = 1 mm.

of the zygomatic arch extends from a point above the anterior portion of P<sup>4</sup> to one above the middle of M<sup>1</sup>. The palate is broad, and the tooth rows are nearly parallel. The anterior margin of the palatine–maxillary suture extends to a point below the middle of M<sup>1</sup>. The posterior palatine foramen is positioned below the middle of M<sup>2</sup>. The matrix within the orbits was not removed to allow the morphology of the foramina to be observed because of the fragile condition of the skull.

The teeth of LACM 145957 are well preserved and only moderately worn (Fig. 3C). P<sup>3</sup> is single-rooted and has an oval occlusal outline. A single prominent cusp is positioned anteriorly, and a well-developed posterior cingulum is present along the posterolingual border of the tooth.

P<sup>4</sup> is trapezoidal in occlusal outline and moderately reduced in size relative to M<sup>1–2</sup>. The P<sup>4</sup> anterior cingulum extends anterolabially from the anterior base of the protocone to the anterolabial corner of the tooth where a distinct, well-developed parastyle is present. The protoloph is complete, connecting the protocone and paracone. A small,

but distinct, mesostyle is present. The metaloph is almost complete, separated from the protocone by a very shallow notch that would disappear with slightly more wear. The protoloph and metaloph are separated by a deep valley and are distinctly taller than the anterior and posterior cingulae. The metaconule is well developed. The posterior cingulum extends from the posterolabial base of the protocone to the metacone with a narrow valley separating it from the metaloph.

M<sup>1</sup> has a trapezoidal occlusal outline. The anterior cingulum extends from the anterolabial base of the protocone to the anterolabial corner of the tooth, where a moderately well-developed parastyle is present. The protoloph and metaloph are complete, connecting the protocone to the paracone and the protocone to the metacone, respectively. The loph connecting the protocone to the metaconule is narrower than the loph that connects the protocone to the protoloph. A small, but distinct, mesostyle is present. A metaconule is developed as a distinct swelling on the metaloph. The metalophs and protolophs are considerably taller than the an-

terior and posterior cingulae. The posterior cingulum is similar in morphology to that of  $P^4$  with a narrow valley between it and the metaloph.  $M^2$  is very similar in structure to  $M^1$  but differs in having an anterior cingulum that is not as anteriorly expanded at its anterolabial margin and a narrower valley between the protoleph and metaloph.

$M^3$  is expanded anteroposteriorly, almost as long as it is wide. The anterior cingulum is very similar in structure to that of  $M^2$ , but the parastyle is not as prominent. The protoleph is complete. A small protoconule is developed as a slight swelling on the protoleph. A short metaloph is present and extends posterolabially from the protocone to a little more than a third of the way across the occlusal surface. The posterior cingulum extends posterolabially from the middle of the posterior base of the protocone to form a posterolabially expanded shelf and then curves anteriorly where it continues to the base of the paracone as a low loph. A metacone is lacking.

The partial dentary (LACM 145958) is damaged, with the posterior portion broken off at about the level of the  $M_2$  alveolus. The diastema between the lower incisor and  $P_4$  is 7.9 mm. Kelly (1997) already has described the morphology of the lower incisor of *Spermophilus wellingtonensis*.

**DISCUSSION.** Kelly (1997) described *Spermophilus wellingtonensis* from LACM 6993 (= UCMP V-95013) based on the holotype (a partial dentary with  $P_4$ - $M_3$ , UCMP 141314) and an additional partial dentary (UCMP 141341). The partial skull (LACM 145957) was recovered from the quarry at LACM 6993 within 0.5 m of where the holotype of *S. wellingtonensis* was discovered. Because both the holotype dentary and partial skull were recovered from the same locality and the size of their dentitions is compatible, the partial skull is referred to *S. wellingtonensis*.

Based on dental morphology, Kelly (1997) regarded *Spermophilus wellingtonensis* as most closely related to the late Hemphillian *Spermophilus shotwelli* (Black, 1963) of the McKay Reservoir Local Fauna of Oregon. Although similar in dental morphology, Kelly (1997) noted that *S. wellingtonensis* can be easily distinguished from *S. shotwelli* by the following characteristics: (1) the  $P_4$  anteroconid is well developed; (2) the  $P_4$  protoconid and metaconid are separated by a relatively deep notch or groove; (3) the  $M_{1-3}$  metalophids are less complete, with the trigonids open to the talonids at an earlier wear stage; and (4)  $M_3$  is larger relative to  $M_{1-2}$ . With the discovery of the upper dentition of *S. wellingtonensis*, the following additional characteristics can now be used to distinguish *S. wellingtonensis* from *S. shotwelli*: (1) much greater anterior expansion of the  $P^4$  anterior cingulum; (2) the presence of a well-developed  $P^4$  parastyle; (3) more complete  $M^{1-2}$  metalophs, attaching to the protocones at an earlier wear stage; and (4) slightly more prominent  $M^{1-2}$  mesostyles.

Genus *Marmota* Blumenbach, 1779

### *Marmota korthi* new species

Figures 4, 5, Table 3

*Marmota* or *Cynomys*, sp. indet.: Kelly, 1997:15.

**HOLOTYPE.** Associated partial maxilla with partial  $L P^4$ - $M^1$ , complete  $L M^{2-3}$ , and partial dentary with partial  $L I_1$ , complete  $L P_4$ - $M_2$ , and partial  $L M_3$ , LACM 145959.

**TYPE LOCALITY.** LACM 6993.

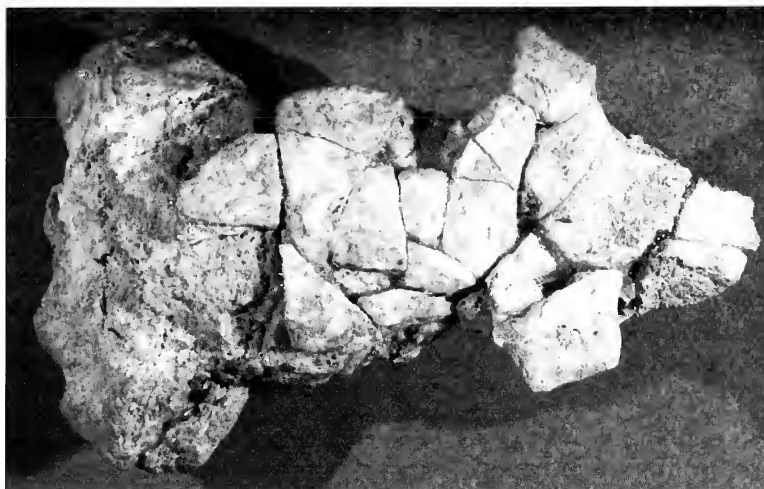
**HYPODIGM.** From LACM 6993: partial skull with  $L M^{1-3}$ , isolated  $R M^2$ , and associated partial skeleton, LACM 145961; partial maxilla with  $L P^4$ - $M^1$ , LACM 145960; partial dentary with broken  $R P_4$ - $M_3$ , UCMP 141313.

**DISTRIBUTION AND AGE.** Known only from the type locality, late Hemphillian.

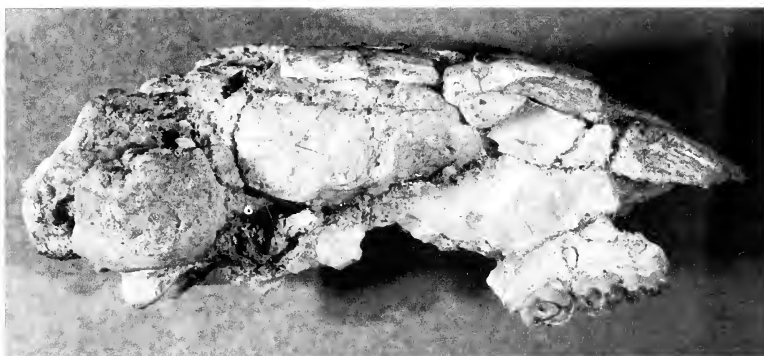
**ETYMOLOGY.** Named in honor of William W. Korth of the Rochester Institute of Vertebrate Paleontology in recognition of his many contributions to our understanding of rodent phylogeny.

**DIAGNOSIS.** *Marmota korthi* differs from *Marmota vetus* (Marsh, 1871) by the following characteristics: (1) size larger (mean  $P_4$  A-P 38% larger than that of *M. vetus*); (2)  $I$ - $P_4$  diastema relatively longer; (3) lower incisor lacking median groove; (4)  $P_4$  with incipient mesoconid present and more elongated anteroposteriorly relative to  $M_{1-2}$  anteroposterior lengths and wider transversely relative to  $M_{1-2}$  transverse widths; and (5)  $M_{1-2}$  metalophids more complete with better developed and deeper trigonid valleys that are completely closed off from talonids. It differs from *Marmota minor* (Kellogg, 1910) by the following characteristics: (1) size larger (mean  $P_4$  A-P 12% larger than that of *M. minor*); (2)  $P^4$  anterior cingulum less expanded anteriorly; (3)  $M^{1-3}$  metaconules better separated from protocones; (4)  $M^3$  metaloph better developed; (5)  $P_4$  trigonid open anteriorly and relatively narrower transversely; (6)  $P_4$  less elongated anteroposteriorly relative to  $M_{1-2}$  anteroposterior lengths and transverse width narrower relative to  $M_{1-2}$  transverse widths; (7)  $M_{1-2}$  metalophids more complete with trigonid valleys completely closed off from talonids; (8)  $M_{1-2}$  relatively less anteroposteriorly compressed; and (9)  $M_2$  anteroposterior length more elongated relative to  $M_1$  anteroposterior length. *Marmota korthi* can be easily distinguished from all other late Blancan to Recent species of *Marmota* by the following characteristics: (1) cheek teeth lower crowned; (2)  $M^{1-2}$  metalophs less complete and distinctly separated from protocone until late wear; (3)  $P_4$  less molariform, trigonid less transversely expanded, and less elongated anteroposteriorly relative to  $M_{1-2}$  anteroposterior lengths; and (4)  $M_{1-2}$  relatively less anteroposteriorly compressed.

**DESCRIPTION.** The partial skull (LACM 145961) of *Marmota korthi* is badly damaged (Fig. 4).  $L M^{1-3}$  of the skull are well worn. An isolated  $R M^2$  was found within the small block of matrix



A



B



C

**Figure 4.** *Marmota korthi* new species. A–C, partial skull, LACM 145961. A, dorsal view. B, right lateral view. C, ventral view. Scale = 10 mm and all have anterior right.



A



B



C



D



E

Figure 5. *Marmota korthi* new species. A, L P<sup>4</sup>-M<sup>1</sup>, LACM 145960, occlusal view. B, L P<sup>4</sup>, partial M<sup>1</sup>, M<sup>2-3</sup>, holotype, LACM 145959, occlusal view. C, L P<sub>3</sub>-M<sub>2</sub>, partial M<sub>3</sub>, holotype, LACM 145959, occlusal view. D, partial dentary, holotype, LACM 145959, lateral view. E, partial dentary, holotype, LACM 145959, occlusal view. Upper scale for A-C = 1 mm; lower scale for D, E = 10 mm, and all have anterior left.

Table 3. Measurements (in mm) of dentition of *Marmota korthi* new species from Hoye Canyon (e = estimated).

Tooth position/ dimension	Holotype			
	LACM	LACM	LACM	
	145959	145960	Right	Left
P <sup>4</sup>	A-P	4.30e	4.27	
	TR	4.68	4.64	
M <sup>1</sup>	A-P	4.55e	4.62	4.50
	TR	—	5.14	5.33
M <sup>2</sup>	A-P	4.99	4.87	4.86
	TR	5.34	5.48	5.49
M <sup>3</sup>	A-P	5.48		5.63
	TR	5.25		5.55
M <sup>1-3</sup>		14.64e		14.65
P <sup>4</sup> -M <sup>3</sup>		18.75e		
P <sub>4</sub>	A-P	4.87		
	ANT-TR	3.67		
	POST-TR	4.42		
M <sub>1</sub>	A-P	4.42		
	ANT-TR	4.81		
	POST-TR	4.94		
M <sub>2</sub>	A-P	4.83		
	ANT-TR	5.54		
	POST-TR	5.56		
M <sub>3</sub>	A-P	—		
	ANT-TR	—		
	POST-TR	—		
P <sub>4</sub> -M <sub>3</sub>	A-P	18.69e		

that yielded the skull. It is indistinguishable in wear and morphology from M<sup>2</sup> attached to the skull and is assumed to have broken off from the skull prior to or during burial. Because of the poor condition of the skull, it provides only limited information on the cranial morphology of *M. korthi*. The overall morphology of the partial skull appears to be very similar to those of Recent species of *Marmota*. The total A-P length of the specimen from the occipital condyles to the anterior edge of the broken nasals is 72.4 mm. The TR widths across the auditory bullae and the postorbital constriction of the frontals are 44.8 mm and 19.5 mm, respectively. Although broken off at the tips, the supraorbital processes of the frontals are well developed. Weakly developed frontal crests extend posteriorly from the supraorbital processes to converge with the sagittal crest. These crests appear to be slightly less developed than those of late Blancan to Recent species of *Marmota*. The auditory bullae are moderately inflated. The pterygoid processes are well developed.

P<sup>4</sup> of the holotype (Fig. 5B) is damaged with part of the anterior cingulum and paracone missing, whereas, in the referred specimen, P<sup>4</sup> is missing only a portion of the enamel along the lingual border. P<sup>4</sup> is molariform with a trapezoidal-shaped occlusal outline. The anterior cingulum extends anterolabially from the protocone to a distinct para-

style, which is separated from the paracone by a shallow notch. A deep valley is present between the protoloph and anterior cingulum. The well-developed protoloph extends labially from the large protocone to connect with the paracone. There is no indication of a protoconule on the protoloph. The protoloph is slightly lower in height than the metaloph. The metaloph is short and thick, connecting the well-developed metaconule to the metacone. The metaconule is well separated from the protocone by a distinct valley between the trigon and talon. A well-developed mesostyle is present between the paracone and metacone. The posterior cingulum is well developed and extends lingually from the protocone to connect with the posterior base of the metacone. The posterior cingulum is lower in height than the protoloph and metaloph.

In the holotype, M<sup>2-3</sup> are complete, but M<sup>1</sup> is damaged, with part of the paracone, metacone, and anterior cingulum broken off (Fig. 5B). In the referred specimens, M<sup>1</sup>s are complete (Figs. 4C, 5A). M<sup>1</sup> and M<sup>2</sup> are almost identical in structure, whereas M<sup>3</sup> differs from M<sup>1-2</sup> primarily by having an enlarged and posteriorly expanded posterior cingulum. All the upper molars exhibit the following characteristics: (1) the anterior cingulum is a low, complete crest that extends labially from the protocone to the paracone, forming a distinct valley between the anterior cingulum and the protoloph; (2) a parastyle is present as a small cusple on the anterior cingulum; (3) the well-developed protoloph extends from the large protocone to the paracone and is the tallest loph on the occlusal surface; (4) a protoconule is lacking; and (5) the well-developed metaconule is connected to the paracone by a thick metaloph but is separated from the protocone by a distinct valley until late wear. A small distinct mesostyle is present on M<sup>1-2</sup>, whereas, on M<sup>3</sup>, only a very small mesostyle is present. The M<sup>1-2</sup> posterior cingulae are low, complete crests that connect the protocones to the metacones. On M<sup>3</sup>, the posterior cingulum extends posterolabially from the protocone to about the middle of the tooth, where a slight notch occurs and after which the cingulum thickens and increases in height along its posterolabial border. The enlarged M<sup>3</sup> posterior cingulum is separated from the metaloph by a deep valley.

The dorsal surface of the dentary drops steeply anterior to P<sub>4</sub>, forming a sharply curved diastema (Fig. 5D). The anterior margin of the masseteric fossa is somewhat bulbous and ends anteriorly below the anterior margin of M<sub>1</sub>. The enamel band on the lower incisor extends laterally from the anteromedial edge to the dorsal lateral border, and its anterior surface is smooth, with no indication of a median groove.

P<sub>4</sub> is moderately enlarged relative to M<sub>1-2</sub> (Fig. 5C). A small, low anterior cingulid extends lingually from the base of the protoconid to the base of the metaconid, resulting in an anteriorly open trigonid. The protoconid and metaconid are the

tallest cusps and positioned relatively close to each other, resulting in a small trigonid. The metalophid is slightly damaged but appears to have been complete with a slight notch near its attachment to the metaconid. A small metastylid is present along the lingual border near the metaconid. The talonid is open lingually but closed off labially by a complete ectolophid between the protoconid and hypoconid. A shallow talonid trench is present just lingual to the ectolophid. A small, but distinct, mesoconid is present on the ectolophid between the protoconid and hypoconid. The hypoconid is well developed, whereas the entoconid is represented only by a very small cuspid on the posterior cingulid. The posterior cingulid is a continuous, low lophid that extends from the hypoconid to the entoconid. A very low lophid extends anteriorly from the entoconid toward the metastylid but is separated from the metastylid by a small notch.

$M_{1-2}$  have parallelogram-shaped occlusal outlines and are essentially identical in structure, except that  $M_2$  is larger than  $M_1$  (Fig. 5C). The metaconid is the tallest primary cusp, followed by, in decreasing height, the protoconid, hypoconid, and entoconid. The anterior cingulid is lower than the metalophid but is complete, connecting the protoconid to the metaconid and closing off the trigonid anteriorly. The metalophid is a high lophid connecting the metaconid to the protoconid, resulting in a deep and well-developed trigonid basin that is completely closed off from the talonid. A complete, well-developed ectolophid is present and positioned deep in from the labial border of the tooth. A mesoconid is lacking on the ectolophid. A shallow talonid trench is present along the ectolophid and metalophid margins. The posterior cingulid extends lingually as a low lophid from the well-developed hypoconid to the posterolingual corner of the tooth wherein it turns anteriorly and extends as a low lophid to a very small metastylid. Because of the low lophid along the lingual border, the talonid is open lingually. The entoconid is a relatively indistinct cuspid on the posterior cingulid near the posterolingual corner of the tooth.

$M_3$  is badly damaged, with only the anterior cingulid and part of the trigonid present. The trigonid appears to have been similar to those of  $M_{1-2}$  with a complete anterior cingulid and metalophid, resulting in a deep, completely enclosed trigonid valley.

**DISCUSSION.** Kelly (1997) referred a partial right dentary with badly damaged teeth (UCMP 141313) from LACM 6993 (= UCMP V-95013) to an indeterminate species of *Marmota* Blumenbach, 1779, or *Cynomys* Rafinesque, 1817. He could not make a definitive generic diagnosis because of the poor condition of the teeth. With the new marmot specimens reported here, UCMP 141313 can now be referred confidently to *Marmota korthi*.

*Marmota korthi* exhibits certain similarities to species of *Paenemarmota* Hibbard and Schultz (1948). Hibbard and Schultz (1948) described the

type species *Paenemarmota barbouri* from the Blancan Rexroad Formation of Kansas. In a detailed review of *P. barbouri*, Repenning (1962) synonymized *Marmota mexicanus* Wilson, 1949, with *P. barbouri*. Voorhies (1988) referred *Marmota sawrockensis* Hibbard, 1964, to *Paenemarmota* and provided a revised diagnosis of the genus. The following characteristics have been used previously to distinguish *Paenemarmota* from *Marmota* (Hibbard and Schultz, 1948; Repenning, 1962; Voorhies, 1988): (1) the cheek teeth are much larger; (2) the cheek teeth are relatively more hypsodont and have more inflated cusps; (3) the  $P^4$ - $M^2$  posterior cingulae are high crests that are separated from the metalophs by deep valleys; (4)  $P^4$  is larger than  $M^1$ ; (5) the  $P^4$  metaconule is slightly more developed; (6) the  $M^3$  metaloph is a distinct, high loph that is separated from the protocone until late wear; (7) the lower incisors have distinct longitudinal striations and their bases extend well behind  $M_3$ ; (8) the  $P_4$ - $M_3$  protoconids are large, equaling or exceeding the metaconids in height and basal area; (9)  $P_4$ - $M_3$  have deep talonid trenches present along the metalophid and ectolophid margins; and (10) the  $P_4$ - $M_3$  talonid basins have well-developed accessory ridges and cusps resulting in strongly rugose surfaces. *Marmota korthi* is similar to *P. sawrockensis* and *P. barbouri* by having a well-developed  $M^3$  metaloph that is separated from the protocone until late wear and lower cheek teeth with talonid trenches present. However, the talonid trenches of *M. korthi* are not as well developed as those of *P. sawrockensis* and *P. barbouri*. Talonid trenches are also present in species of *Cynomys* and *Spermophilus* Cuvier, 1825. *Marmota korthi* differs from *P. sawrockensis* and *P. barbouri* by the following characteristics: (1) the cheek teeth are much smaller; (2)  $P^4$  is smaller than  $M^1$ ; (3) the  $P^4$ - $M^2$  posterior cingulae are not as well developed and lack deep valleys between the cingulae and metalophs; (4) the lower incisors lack prominent longitudinal grooves; (5) the  $P_4$  protoconid and metaconid are less well separated; (6) the  $M_{1-3}$  metalophids are more complete; (7) the  $P_4$ - $M_3$  ectolophids are relatively deeper; and (8) the  $P_4$ - $M_3$  talonid basins lack heavy rugosity. It further differs from *P. barbouri* by having a much less molariform  $P_4$ . Except for the more complete  $M_{1-3}$  metalophids, all of the characters that distinguish *M. korthi* from *P. sawrockensis* and *P. barbouri* are also present in other species of *Marmota* and support its referral to the genus. Thus, well-developed  $M^3$  metalophs and  $P_4$ - $M_3$  talonid trenches no longer appear to represent valid diagnostic characters to differentiate *Paenemarmota* from *Marmota*.

Kellogg (1910) described *Marmota nevadensis* based on a partial dentary with  $P_4$ - $M_1$  from the middle Hemphillian Thousand Creek Formation of Nevada. Subsequent investigators (Hibbard and Schultz, 1948; Repenning, 1962; Black, 1963; Voorhies, 1988) have noted the following similari-



ties in the lower cheek teeth of *M. nevadensis* and species of *Paenemarmota*: (1) large size; (2) prominent longitudinal grooves on the lower incisors; (3) well-developed talonid trenches on  $P_4$ - $M_1$ ; and (4) heavy rugosity in the  $P_4$ - $M_1$  talonid basins. Voorhies (1988, p. 171) stated that, when better known, *M. nevadensis* "may eventually prove to represent *Paenemarmota* rather than *Marmota*." *Marmota nevadensis* differs from and appears less derived than *Paenemarmota sawrockensis* and *Paenemarmota barbouri* by its slightly smaller size and by having a less molariform  $P_4$  that is smaller relative to  $M_1$ . Until better known and following Korth (1994), it appears best to refer *M. nevadensis* to ?*Paenemarmota*. *Marmota korthi* differs from ?*P. nevadensis* by the following characteristics: (1) much smaller cheek teeth; (2) lack of prominent longitudinal grooves on the lower incisors; (3) lack of heavy rugosity in the  $P_4$ - $M_1$  talonid basins ( $M_{2-3}$  unknown for ?*P. nevadensis*); (4) a more complete  $M_1$  metalophid; (5) a relatively deeper  $M_1$  ectolophid; and (6) a less developed  $M_1$  posterior cingulum.

Pre-Pleistocene marmot fossils are rare (Black, 1963). *Marmota* first appears in the Clarendonian, where it is represented by a single species, *Marmota vetus* (Marsh, 1871; Black, 1963; Korth, 1994). Prior to this study, the only described species of *Marmota* from the Hemphillian was *Marmota minor* from the middle Hemphillian Thousand Creek Local Fauna of Nevada (Black, 1963). Hay (1921) described a third pre-Pleistocene species, *Marmota arizonae*, based on a partial skull from the late Blancan Anita Fauna of Arizona (Kurten and Anderson, 1980). Morphologically, *M. arizonae* is very similar to the late Rancholabrean to Recent *Marmota flaviventris* (Audubon and Bachman, 1841), differing only in the morphology of the snout (Kurten and Anderson, 1980). The only other North American species of *Marmota* recorded from the Pleistocene (late Irvingtonian to late Rancholabrean) is extant *Marmota monax* Linnaeus, 1758.

Black (1963) regarded the following dental transformations as derived for *Marmota* based on the Pleistocene to Recent species: (1) an increase in size; (2) an enlargement of  $P_4$  relative to the lower molars; (3) a reduction of the posterior portion of  $M_3$ ; and (4) further anteroposterior compression of  $M_{1-2}$ . Additionally, the Pleistocene to Recent species exhibit a moderate increase in crown height of the cheek teeth relative to the Clarendonian and Hemphillian species. Black (1963) regarded *Marmota minor* as having the following synapomorphies with Recent species of *Marmota*: (1)  $P_4$  is longer than  $M_{1-2}$ ; (2) the metalophids of  $M_{1-3}$  are reduced; (3) the posterior portion of  $M_3$  is reduced; and (4) the diastemal depression is deep anterior to  $P_4$ . *Marmota korthi* is derived relative to *Marmota vetus* by having the following characteristics: (1) increased size; (2) higher crowned cheek teeth; (3) greater enlargement of  $P_4$  relative to  $M_{1-2}$ ; and (4)

more complete  $M_{1-3}$  metalophids, with the trigonids completely separated from the talonids. *Marmota korthi* and *M. vetus* exhibit about the same degree of anteroposterior compression of  $M_{1-2}$ . *Marmota korthi* is derived relative to *M. minor* by the following characteristics: (1) increased size; and (2) more complete  $M_{1-2}$  metalophids with the trigonids completely separated from the talonids, resulting in deep, enclosed trigonid valleys. *Marmota korthi* further differs from *M. minor* by the following characteristics: (1) the  $P^4$  anterior cingulum is less expanded anteriorly; (2) the  $M^{1-3}$  metaconules are better separated from the protocones; (3) the  $M^3$  metaloph is better developed, forming a continuous crest from the metaconule to the metacone; (4) the ratio of the  $P_4$  anteroposterior length to the  $M_{1-2}$  anteroposterior lengths is slightly less (averaging 1.06 for *M. korthi* versus 1.14 for *M. minor*); (5) the ratio of the  $P_4$  transverse width relative to the  $M_{1-2}$  greatest transverse widths is slightly less (averaging 0.84 for *M. korthi* versus 0.93 for *M. minor*); and (6)  $M_{1-2}$  are slightly less anteroposteriorly compressed (the ratio of the  $M_{1-2}$  greatest transverse widths to the  $M_{1-2}$  anteroposterior lengths averaging 1.14 for *M. korthi* versus 1.26 for *M. minor*). *Marmota korthi* can be easily distinguished from all late Blancan to Recent species of *Marmota* by the following characteristics: (1) cheek teeth and body size slightly smaller; (2) cheek teeth lower crowned; (3) the  $M^{1-3}$  metalophs are well separated from the protocones by distinct valleys until late wear; (4)  $P_4$  is less enlarged relative to  $M_{1-2}$ ; and (5)  $M_{1-2}$  are less anteroposteriorly compressed.

## Family Geomyidae Bonaparte, 1845

### Genus *Parapliosacomys* Shotwell, 1967

#### *Parapliosacomys oregonensis*

Shotwell, 1967

Figure 6, Table 4

**SPECIMENS.** From LACM 6993: R  $P^4$ , LACM 145962; L  $M^{1 \text{ or } 2}$ , LACM 145963; partial dentary with L  $I_1$ ,  $dP_4$ - $M_3$ , LACM 145964; R  $dP_4$ , LACM 145965; partial dentary with R  $I_1$ - $P_4$ , LACM 145966; R  $P_4$ , LACM 145967; R  $P_4$ , LACM 145968; R  $P_4$ , LACM 145969; L  $P_4$ , LACM 145970; L  $P_4$ , LACM 145971; R  $M_1 \text{ or } 2$ , LACM 145972; R  $M_1 \text{ or } 2$ , LACM 145973.

**DISCUSSION.** The dental sample of *Parapliosacomys* from Hoyo Canyon (Fig. 6) is indistinguishable from the topotypic sample of *Parapliosacomys oregonensis* from McKay Reservoir, Oregon, and can be referred confidently to this species. Because Shotwell (1967) has already provided detailed descriptions of the dental morphology of *P. oregonensis*, a morphological description of the dental sample from Hoyo Canyon is not included here. It should be noted that the occlusal dimensions of the cheek teeth of *P. oregonensis* vary with

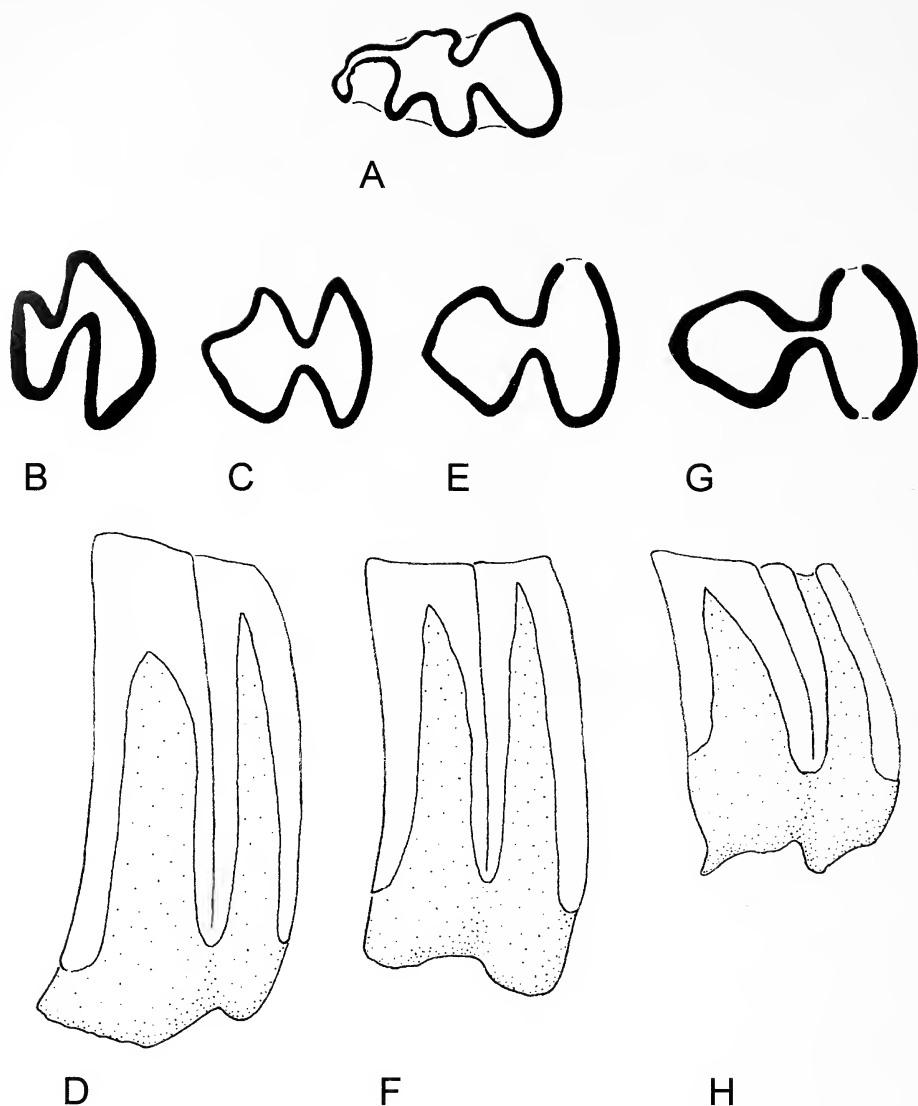


Figure 6. *Parapliosacomys oregonensis*. A, R dP<sub>4</sub>, LACM 145964, occlusal view, reversed, B, R P<sub>4</sub>, LACM 145962, C, D, L P<sub>4</sub>, LACM 145970. E, F, R P<sub>4</sub>, LACM 145968. G, H, R P<sub>4</sub>, LACM 145969. B, C, E, and G, occlusal views; D, labial view; F and H, lingual views, and all have anterior left. Scale = 1 mm.

wear, so that teeth in early wear have significantly smaller occlusal dimensions than those in late wear (Shotwell, 1967; Kelly and Lugaski, 1999).

Kelly (1997) questionably referred UCMP 141344 (L P<sub>4</sub>, well worn) and UCMP 141343 (L P<sub>4</sub>) from LACM 6993 (= UCMP V-95013) to ?*Nerterogeomys* sp. indet. and ?*Thomomys* sp. indet., respectively. With the discovery of the additional geomyid material from LACM 6993, these specimens can now be assigned confidently to *Parapliosacomys oregonensis*.

Three species have been assigned previously to *Parapliosacomys*: the type species, *Parapliosacco-*

*mys oregonensis*, from the late Hemphillian McKay Reservoir Fauna of Oregon and the late Hemphillian Churchill Butte Local Fauna of Nevada; *Parapliosacomys hibbardi* (Storer, 1973) from the Clarendonian WaKeeney Local Fauna of Kansas; and *Parapliosacomys annae* Korth, 1987, from the Barstovian Crookston Bridge Member of the Valentine Formation of Nebraska. However, Korth and Reynolds (1994) recently described the genus *Phelosacomys* and referred *P. hibbardi* and *P. annae* to their new genus. Thus, *Parapliosacomys* is a monotypic genus restricted to the late Hemphillian. The presence of *P. oregonensis* in the Hoye



Table 4. Measurements (in mm) of teeth of selected specimens of *Parapliosacomys oregonensis* from Hoye Canyon; all measurements taken at the occlusal surface (a = approximate, r = tooth just erupting).

Tooth position/ dimension		LACM 145962	LACM 145963	LACM 145964	LACM 145965	LACM 145968	LACM 145969	LACM 145970	LACM 145966	LACM 145967	LACM 145971
P <sup>4</sup>	A-P	1.44									
	ANT-TR	1.22									
	POST-TR	1.60									
M <sup>1 or 2</sup>	A-P		0.87								
	TR		1.66								
dP <sub>4</sub>	A-P			2.20	2.24						
	ANT-TR			1.10	1.07						
	POST-TR			1.26	1.35						
P <sub>4</sub>	A-P					1.93	2.47	1.71	1.39	1.73	1.50
	ANT-TR					1.23	1.15	1.25	1.30	1.46	1.26
	POST-TR					1.66	1.60	1.36	1.61	1.80	1.49
M <sub>1</sub>	A-P				1.09						
	TR				1.63a						
M <sub>2</sub>	A-P				1.10						
	TR				1.67						
M <sub>3</sub>	A-P				0.99r						
	TR				1.55r						

Canyon Local Fauna indicates the fauna is late Hemphillian in age.

Order Artiodactyla Owen, 1848

Family Camelidae Gray, 1821

Genus *Hemiauchenia* Gervais and Ameghino, 1880

*Hemiauchenia vera* (Matthew, 1909)  
Figure 7

**SPECIMENS.** From LACM 6993: partial dentary with partial L P<sub>3-4</sub>, complete M<sub>1</sub>, LACM 146521. From LACM 6994: partial first phalanx, LACM 145975; partial first phalanx, LACM 145976.

**DISCUSSION.** The partial dentary (LACM 146521) has the P<sub>3</sub> crown broken off at the alveolus, the anterior portion of the P<sub>4</sub> crown missing, and M<sub>1</sub> complete (Fig. 7). The partial dentary can be confidently referred to *Hemiauchenia vera* (Matthew, 1909, in Matthew and Osborn, 1909) because the teeth exhibit the following diagnostic characters (Webb, 1974; Kelly, 1998b): (1) relatively low-crowned and small in size, as compared with all other species of *Hemiauchenia*; (2) P<sub>3</sub> is two-rooted; (3) P<sub>4</sub> has a single posterior fossettid and appears to have had a simple triangular occlusal outline; (4) P<sub>4</sub> is anteroposteriorly compressed and indented into the anterior occlusal surface of M<sub>1</sub>; and (5) M<sub>1</sub> has very weak internal stylids and a small protostylid present. Measurements of the cheek teeth of LACM 146521 are as follows: P<sub>3</sub> alveolar A-P = 7.2 mm; P<sub>4</sub> A-P = 11.7 mm (estimated), TR = 6.6 mm; M<sub>1</sub> A-P = 20.3 mm, TR = 12.9 mm.

The partial first phalanges are characterized by their small size, as indicated by the following measurements: LACM 145975, distal condylar A-P = 10.5 mm, distal condylar TR = 12.6 mm; LACM 145976, distal condylar A-P = 11.5 mm, distal condylar TR = 11.8 mm, and midshaft A-P = 13.4 mm. The camel phalanges from Hoye Canyon are indistinguishable from those of *Hemiauchenia vera* (Kelly, 1998b). The presence of a dental specimen of *H. vera* in the Hoye Canyon Local Fauna strongly suggests that the phalanges also represent this species. For these reasons, the Hoye Canyon phalanges are provisionally referred to *H. vera*.

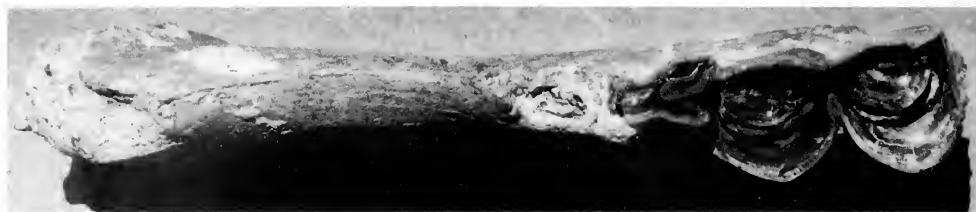
*Hemiauchenia vera* has been recorded previously from the type locality in Hemphillian deposits of the Ogallala Group of Long Island, Kansas, the late Hemphillian Yerington and Silver Springs local faunas of Nevada, the latest Hemphillian Buis Ranch Local Fauna of Oklahoma, and the late Hemphillian Upper Bone Valley Fauna of Florida (Webb, 1974; Tedford et al., 1987; Kelly, 1998b). The presence of *H. vera* in the Hoye Canyon Local Fauna indicates the fauna is Hemphillian in age, probably late Hemphillian.

Family Antilocapridae Gray, 1866

?Antilocapridae, gen. and sp. indet.

**SPECIMEN.** From LACM 6994: partial lower L I<sub>2 or 3</sub>, LACM 145977.

**DISCUSSION.** The partial lower incisor is complete, except that the tip of the root has been broken off. The root is robust relative to the crown, indicating that the tooth is not a deciduous incisor. The small, spatulate incisor is most similar to those of the Antilocapridae. The tooth differs from those



A



B

Figure 7. *Hemiauchenia vera*. A, B, partial dentary with partial L P<sub>3-4</sub>, M<sub>1</sub>, LACM 146521. A, occlusal view, anterior left. B, labial view, anterior left. Scale = 10 mm.

of the smallest Hemphillian camel, *Hemiauchenia vera*, by its smaller size and differs from those of the Tayassuidae by its smaller size and more spatulate shape. The lower incisor probably represents a member of the Antilocapridae, to which it is assigned very questionably.

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Owen, 1845

Rhinocerotidae, gen. and sp. indet.

Figure 8

**SPECIMEN.** From LACM 6994: associated partial L lower premolar, partial L M<sub>1-3</sub>, LACM 145978.

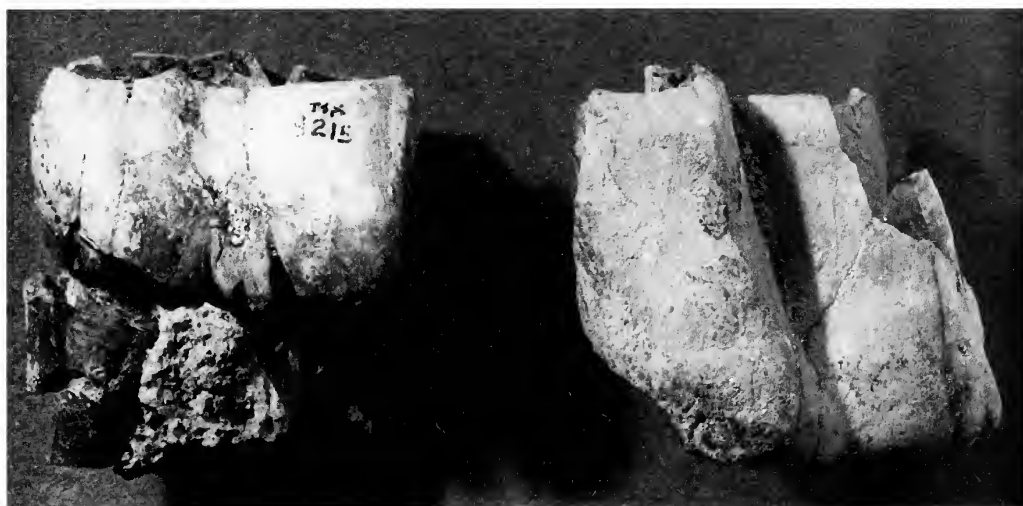
**DISCUSSION.** The teeth are badly damaged (Fig. 8). M<sub>1</sub> and M<sub>3</sub> are fairly complete, but the partial lower premolar only consists of a partial ectolophid and M<sub>2</sub> by only the posterior enamel wall. M<sub>1</sub> and M<sub>3</sub> exhibit the following characteristics: (1)

size small, as compared with other early to middle Hemphillian rhinos; (2) moderately hypsodont, considering their degree of wear; and (3) lingual cingulids lacking. Measurements of the lower molars are as follows: M<sub>1</sub> A-P = 50.2 mm, TR = 33.3 mm; M<sub>3</sub> A-P = 52.9 mm (broken), TR = 36.2 (broken).

The Hoyo Canyon rhino teeth are most similar in size and morphology to those from the late Hemphillian Washoe Local Fauna of Nevada that were referred to *Teleoceras* sp. indet. by Kelly (1997). A small species of *Teleoceras* Hatcher, 1894, also occurs in the late Hemphillian Silver Springs Local Fauna of Nevada (Kelly, 1998b). It appears that a dwarf species of *Teleoceras* occurred during the late Hemphillian in Nevada (Kelly, 1997, 1998b). Premolar and molar lingual cingulids are generally lacking in *Teleoceras* but commonly present in *Aphelops* Cope, 1873 (Osborn, 1904; Douglas, 1908; Matthew, 1932; Tanner, 1967, 1975). The Hoyo Canyon rhino teeth lack lingual cingulids,



A



B

Figure 8. Rhinocerotidae, gen. indet. A, B, L. M<sub>1</sub> and M<sub>3</sub>, LACM 145978. A, occlusal views, anterior left. B, labial views, anterior left. Scale = 10 mm.

suggesting that they might represent *Teleoceras*. It is possible that the Hoye Canyon rhino is conspecific with the small, late Hemphillian species of *Teleoceras*. However, a generic assignment cannot be made without determining if the Hoye Canyon rhino possessed upper incisors. As such, the Hoye Canyon rhino is referred to Rhinocerotidae, gen. and sp. indet.

Family Equidae Gray, 1821  
Genus *Dinohippus* Quinn, 1955

*Dinohippus* sp. indet.  
Figure 9, Table 5

**SPECIMEN.** From LACM 6993: associated partial L I<sub>1-2</sub>, P<sub>2</sub>-M<sub>3</sub>, LACM 145974.

**DISCUSSION.** The teeth are somewhat damaged, with most having some part of the base missing (Fig. 9). The crowns are complete in all respects but the following: (1) I<sub>2</sub> is missing a small portion of the enamel at the lateral edge of the tooth; (2) P<sub>3</sub> is missing a small portion of the anterior hypoconid; and (3) M<sub>1</sub> is missing part of the posterior half of the tooth, broken off 22.5 mm below the occlusal surface. P<sub>2-4</sub> and M<sub>3</sub> are unworn, and M<sub>1-2</sub> are in early wear, which, in the extant domestic horse, would indicate an age of about 2 years old.

The lower incisors are of typical equid structure, with well-defined central cusps, convex anterior enamel borders, and notable lateral tapering of the occlusal outlines. When placed together, the inci-



Figure 9. *Dinohippus* sp. indet. A, B, partial  $P_2$ - $M_3$ , LACM 145974. A, occlusal view, anterior left. B, labial view, anterior left. Scale = 10 mm.

sors appear to have formed a rounded dental arcade.

The cheek teeth of the Hoyo Canyon horse are characterized by having the following: (1) size large, estimated  $P_2$ - $M_3$  A-P about 170 mm; (2) hypsodont (mesostylar crown height of  $P_4$  = 64.6 mm, estimated crown height of  $M_1$  about 70 mm); (3) the cement layer is thick; (4) the  $P_{2-4}$  ectolophids do not penetrate the isthmuses between metaconids and metastylids; (5) the  $M_{1-2}$  occlusal enamel patterns are simple (the other teeth are unworn, but appear also to have simple enamel patterns, based on the cross-sectional patterns at the broken bases); (6) the  $M_{1-3}$  metaconids are notably smaller than

metastylids (especially evident about half way down the crowns from the occlusal surfaces and at the bases of the teeth); and (7) the  $M_{1-3}$  ectoflexids are deep, completely penetrating the isthmuses between the metaconids and metastylids.

The cheek teeth of the Hoyo Canyon horse are indistinguishable in size and morphology from those of the late Hemphillian "*Dinohippus*" *interpolatus* and *Dinohippus leidyianus*. These two species have very similar lower cheek teeth and are differentiated from each other primarily by the morphology of the facial fossae (Kelly, 1998a), which is unknown for the Hoyo Canyon horse. Previous investigators have suggested that these two species are conspecific, but their taxonomic status must await a complete revision of *Dinohippus* (Hulbert, 1993; Kelly, 1998a). The lower cheek teeth of the Hoyo Canyon horse differ from those of *Equus* Linnaeus, 1758, by having the  $M_{1-3}$  metastylids notably smaller than the metaconids. They differ from those of the Hipparionini Quinn, 1955, by having the following characteristics: (1) larger size; (2) lacking protostylids; (3) relatively smaller and less separated  $P_2$ - $M_3$  metaconids and metastylids with the  $M_{1-3}$  metastylids notably smaller than the metaconids; and (4) deeper  $M_{1-3}$  ectoflexids, completely penetrating the isthmuses between the metaconids and metastylids. They differ from those of the Protohippini Quinn, 1955, by having

Table 5. Measurements (in mm) of lower teeth of *Dinohippus* sp. indet. (LACM 145974) from Hoyo Canyon (a = approximate).

Tooth position	A-P	TR
$P_2$	31.8	17.2
$P_3$	29.2	15.1
$P_4$	30.7	15.9
$M_1$	27.6a	14.5
$M_2$	31.2	12.1
$M_3$	24.0	10.0

the following characteristics: (1) larger size; (2) more hypsodont; (3) protostylids lacking; and (4) the  $P_{3-4}$  metaconids and metastylids are about equal in size and position. The Hoyo Canyon horse appears to represent either "*D.*" *interpolatus* or *D. leidymanus*. However, a definitive specific assignment must await the discovery of more complete material.

## AGE OF FAUNA

The Hoyo Canyon Local Fauna consists of the following taxa: the rabbit *Pronotolagus nevadensis* n. sp.; the ground squirrel *Spermophilus wellingtonensis* Kelly, 1997; the marmot *Marmota korthi* n. sp.; the gopher *Parapliosacomys oregonensis* Shotwell, 1967; the camel *Hemiaucheria vera*; ?Antilocapridae, gen. and sp. indet.; Rhinocerotidae, gen. and sp. indet.; and the horse *Dinohippus* sp. indet.

The age of the Hoyo Canyon Local Fauna can be determined by the shared occurrences of certain taxa within the fauna. The geomyid, *Parapliosacomys oregonensis*, previously was known only from the late Hemphillian McKay Reservoir Fauna of Oregon and the late Hemphillian Churchill Butte Local Fauna from the Desert Mountains of west central Nevada (Shotwell, 1967; Kelly and Lugaski, 1999). *Marmota korthi* n. sp. is more derived than the only known Clarendonian species, *Marmota vetus* (Kellogg, 1910), but less derived than the Blancan to Recent marmot species. Similarly, *Pronotolagus nevadensis* n. sp. appears to be more derived than the Clarendonian to early Hemphillian *Pronotolagus apachensis* (Gazin, 1930). The camel, *Hemiaucheria vera*, is restricted to the Hemphillian (Webb, 1974). Most investigators generally regard the extinction of the Rhinocerotidae in North America as one of the events to mark the end of the Hemphillian (Tedford et al., 1987). However, Madden and Dalquest (1990) reported finding a single fragment of a rhinoceros tooth as a result of screen washing matrix from the Blancan Yellow Quarry, Scurry County, Texas (Beck Ranch Local Fauna). With the exception of this record, no other Blancan occurrence of the Rhinocerotidae is known (Prothero, 1998). *Dinohippus* sp. indet. from Hoyo Canyon appears to represent either "*Dinohippus*" *interpolatus* (Cope, 1893) or *Dinohippus leidymanus* (Osborn, 1918), both of which are known only from the late Hemphillian (Azzaroli, 1988; Hulbert, 1993; Kelly, 1998a). The combined presence of the Rhinocerotidae, *Pronotolagus nevadensis* n. sp., *Marmota korthi* n. sp., *Parapliosacomys oregonensis*, *Hemiaucheria vera*, and *Dinohippus* sp. (either "*D.*" *interpolatus* or *D. leidymanus*) indicates that the fauna is late Hemphillian (late Miocene) in age.

## CONCLUSIONS

An unnamed formation exposed along the western flanks of the Wellington Hills, Douglas County, Nevada, has previously yielded two mammalian fau-

nas: the late Blancan Wellington Hills Local Fauna and the early Irvingtonian Topaz Lake Local Fauna (Kelly, 1997). The northern outcrops of this unnamed unit occur in the Hoyo Canyon area, and the southern outcrops occur from Risue Canyon to about 3 km north of Long Dry Canyon (Kelly, 1997). Foothills covered with Quaternary alluvium separate the northern outcrops from the southern outcrops. Previously, only a single locality (LACM 6993 = UCMP V-95013) was known from the Hoyo Canyon area, and this locality did not produce any age-diagnostic fossils. Because the section containing LACM 6993 is isolated and cannot be traced laterally, Kelly (1997) only questionably correlated LACM 6993 with the late Blancan localities in the southern exposures. Quarrying at LACM 6993 and the discovery of an additional locality in the Hoyo Canyon area has now produced new specimens that indicate the assemblage from Hoyo Canyon is late Hemphillian and not Blancan in age. This assemblage is named the Hoyo Canyon Local Fauna.

The recognition of a late Hemphillian fauna from the Hoyo Canyon section allows a reevaluation of the geologic history and biostratigraphy of the unnamed formation of the Wellington Hills. Based on the faunas, the unnamed formation appears to have been deposited from at least the late Hemphillian (late Miocene) to the early Irvingtonian (early Pleistocene) or about 7 to 1.8 Ma. The Hoyo Canyon localities of the northern outcrops must occur stratigraphically below the late Blancan localities of the southern outcrops. This fact indicates that Kelly (1997) underestimated the total thickness of the unnamed formation by at least several hundred meters.

The unnamed formation of the Wellington Hills dips westward and, in the northern exposures, unconformably overlies uplifted Miocene andesitic rocks, while, in the southern exposures, it unconformably overlies uplifted Mesozoic granitic and metavolcanic basement rocks (Kelly, 1997). The steep escarpment along the eastern border of the Wellington Hills demarcates the position of a large northerly-trending normal fault zone that extends from the Stillwater Range in the south to the Virginia Range in the north (Gilbert and Reynolds, 1973). Gilbert and Reynolds (1973) proposed that Quaternary activity along the frontal fault zone resulted in the uplifting of the Wellington Hills. As the Wellington Hills were uplifted, so was the unnamed formation, as indicated by its westward tilting. Based on biostratigraphic and lithologic evidence, Kelly (1997) proposed that the major uplifting of the Wellington Hills could have occurred from sometime prior to the late Blancan, the age of the oldest known fauna at the time, to as late as or later than the early Irvingtonian, the age of the youngest fauna. With the recognition of a late Hemphillian fauna from the lower part of the unnamed formation of the Wellington Hills, it now appears that the major uplifting could have oc-

curred from the late Hemphillian to as late as or later than the early Irvingtonian.

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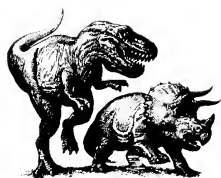
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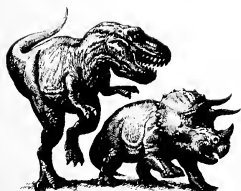
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# CONTRIBUTIONS IN SCIENCE

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REVISION OF THE "APOCEPHALUS MIRICAUDA-  
GROUP" OF ANT-PARASITIZING FLIES  
(DIPTERA: PHORIDAE)

BRIAN V. BROWN



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REVISION OF THE “APOCEPHALUS MIRICAUDA-GROUP”  
OF ANT-PARASITIZING FLIES  
(DIPTERA: PHORIDAE)

BRIAN V. BROWN<sup>1</sup>

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**ABSTRACT.** The “*Apocephalus miricauda*-group”, a paraphyletic assemblage, is revised and diagnosed. Seventy-three species are recognized, including the following 58 new to science: *A. acanthus*, *amplidiscus*, *annulatus*, *asyndetus*, *atrimarginatus*, *barbiventris*, *batillus*, *brevifrons*, *brochus*, *cardiacus*, *catholicus*, *comosus*, *conecitonis*, *conformalis*, *constrictus*, *contortiventris*, *contracticauda*, *crassilatus*, *curtinotus*, *cyclodiscus*, *deceptus*, *denotatus*, *dinoponerae*, *dracodermus*, *emargilatus*, *eurydomus*, *fenestratus*, *flexus*, *funditus*, *gigantivorus*, *glabriventris*, *globosus*, *incomptus*, *indeptus*, *indistinctus*, *inpalpabilis*, *intonsus*, *kungae*, *latinsulosus*, *lobicauda*, *maculosus*, *magnicauda*, *melinus*, *meniscus*, *orbiculus*, *pachycondylae*, *paldiae*, *petiolus*, *reticulatus*, *roeschardae*, *secus*, *spiculus*, *striativentris*, *strongylus*, *tanyurus*, *torulus*, *triangularis*, and

*trifidus*. The previously described species, all named by Borgmeier, are *A. densepilosus*, *digitalis*, *fuscipalpis*, *inimicus*, *lopesi*, *lyratus*, *minutus*, *miricauda*, *paraponerae*, *persecutor*, *piliventris*, *quadratus*, *spatulatus*, and *spatulicauda*. Additionally, a fossil species, *A. succineus* new species, is described from Dominican amber. The genus *Anaclinus* is considered a synonym of *Apocephalus*, and the one species, *A. lopesi*, is transferred to *Apocephalus* (new combination). The species *A. angularis* Borgmeier is considered a synonym of *A. minutus* (new synonym). Monophyletic groups within the *A. miricauda*-group include the *A. paraponerae*-subgroup, the *A. spatulatus*-subgroup, the *A. meniscus*-subgroup, the *A. miricauda*-subgroup, the *A. funditus*-subgroup, and the *A. spatulicauda*-subgroup. The “*A. miricauda*-group” is paraphyletic with respect to the *A. attophilus*-group. Most species are parasitoids of injured ponerine ants.

INTRODUCTION

The genus *Apocephalus* Coquillett is a large group of parasitoid phorid flies, including the original “ant-decapitating flies” of the New World. Traditionally, the group has been organized into two subgenera: *Apocephalus* s. s. and *Mesophora*. Subgenus *Mesophora* was treated previously (Brown, 1993, 1994, 1996, 1997a), but only one subsection of subgenus *Apocephalus* has been revised (Brown, 1997b).

In this paper I treat the “*A. miricauda*-group” of species, a paraphyletic group I proposed previously (Brown, 1997b; hereafter the quotation marks around the name of this group, which indicate non-monophyly, will be omitted). These flies are parasitoids, mostly of ponerine ants (Hymenoptera: Formicidae: Ponerinae), and mostly of injured or distressed individual workers.

METHODS AND MATERIALS

METHODS

Methods are the same as my previous works on *Apocephalus*, but a comment on species concepts is necessary. Some of the proposed new species in this revision are extremely similar to each other; for instance *A. flexus* new species and *A. orbiculus* new species differ mostly by the shape of a small internal sclerite (Figs. 51 and 53). Although these differences seem marginal and possibly insignificant, they are based on characters that are not known to differ significantly within species. Additionally, recent work in phorid taxonomy has used extremely narrow species definitions (e.g., Disney, 1989), and some evidence exists for cryptic species within otherwise well-defined taxa. In summary, the new species descriptions contained herein are proposals that can be reevaluated when additional specimens have been collected.

The female ovipositor is described in a similar manner as that of *A. attophilus*-group species (Brown, 1997b), but one additional structure is present in many *A. miricauda*-group species, namely the internal, sclerotized loop derived from sternite 9. In many species it is a round structure with a broad, moderately sclerotized process (Fig. 106), but in some others it is darkly sclerotized and of different structure (Figs. 107–109).

**PHYLOGENETIC ANALYSIS.** The character states of the *A. spatulatus*-subgroup (Table 1) were analyzed using the computer program HENNIG-86 (Farris, 1989). Other cladograms were constructed by hand.

**TERMS AND NAMES.** The nomenclature of ant species was checked against Bolton (1995). One notable change from normal use is that the more commonly used *Eciton* “*burchelli*” (Westwood) has been changed to the correct *E. burchellii*, following Bolton.

Geographical coordinates are quoted as decimal de-

grees, rather than degrees, minutes and seconds (e.g., 90.5°W, rather than 90°30'W; Crawford, 1983).

**BARCODES.** In addition to the usual insect labels recording locality information, specimens were labeled with barcoded insect labels (Thompson, 1994) and data were recorded in a database. All barcoded labels that begin with the abbreviation “LACM ENT,” indicate that the Natural History Museum of Los Angeles County (LACM) is the institution where the data are stored. Specimens with barcoded labels beginning “INBIO” have their data stored at LACM and the Instituto Nacional de Biodiversidad in Costa Rica. To make later recognition of holotypes easier, I list their individual barcode number in square brackets.

MATERIALS

This revision is based on adult female specimens. A few species are also known from males and immatures, but because of the highly incomplete record of these forms, they are not treated at this time.

Specimens belong to the following institutions (codens from Arnett et al., 1993; curator or collection manager names in parentheses):

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, U.S.A. (D. Grimaldi)
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DEBU	Department of Environmental Biology, University of Guelph, Guelph, ON, Canada N1G 2W1 (S. Marshall)
EMUS	Department of Biology, Utah State University, Logan, Utah 84322-5305, U.S.A. (W.J. Hanson)
INBC	Instituto Nacional de Biodiversidad, A.P. 22-3100, Santo Domingo, Heredia, Costa Rica (M. Zumbado)
INPA	Instituto Nacional de Pesquisas da Amazônia, Estrada do Aleixo, 1756, C.P. 478, 69.011 Manaus, Brazil (J. Rafael)
LACM	Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, U.S.A. (B. Brown)
LACM-IP	Invertebrate Paleontology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, U.S.A. (L. Groves)
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, U.S.A. (on indefinite loan to B. Brown)
MIUP	Museo de Invertebrados Graham B. Fairchild, Universidad de Panama, Estafeta Universitaria, Panama (D. Quintero)

MUCR	Museo de Insectos, Universidad de Costa Rica, San Pedro, San José, Costa Rica (P.S. Hanson)
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Av. Arenales 1267, Apartado 14-0434, Lima-14, Peru (G. Lamas)
MZSP	Museu de Zoologia, Universidade de São Paulo, Av. Nazaré 481, CP 7172, 01051 São Paulo, Brazil (F.C. do Val)
QCAZ	Quito Catholic Zoology Museum, Departamento de Biología, Pontificia Universidad Católica del Ecuador, 12 de Octubre y Carrion, Apto. 2184, Quito, Ecuador (G. Onore)
ROME	Department of Entomology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON, Canada M5S 2C6 (D.C. Darling)
TAMU	Department of Entomology, Texas A&M University, College Station, TX 77843, U.S.A. (R. Wharton)
UCMS	Department of Ecology and Evolutionary Biology, Box U-43, University of Connecticut, Storrs, CT 06269-3043 (J. O'Donnell)
UGGG	University of Guyana, Georgetown, Guyana (M. Tamessar)
UNCB	Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apto. 7495, Santa Fé de Bogotá, Colombia (E. Flores)
USNM	United States National Museum, Smithsonian Institution, Washington, DC 20560, U.S.A. (on indefinite loan to B. Brown)
USNM-IP	Department of Paleobiology, United States National Museum, Smithsonian Institution, Washington, DC 20560, U.S.A. (C. Labandeira)

Additionally, the abbreviation ALAS refers to the Arthropod Survey of La Selva Biological Station, Costa Rica.

## SYSTEMATICS

The monophyly of the many species groups of *Apocephalus* is still insufficiently established. In my previous work, I proposed that the *A. attophilus*-group was characterized by a separated apical sclerite (Brown, 1997b). Based on a more thorough knowledge of the *A. miricauda*-group, this character needs some refinement to allow it to diagnose the *A. attophilus*-group. Furthermore, as I previously suggested, there is no indication that the *A. miricauda*-group is monophyletic with respect to the *A. attophilus*-group. Instead, it appears to be a grade group relative to the *A. attophilus*-group.

There is some evidence that the *A. attophilus*-group and the *A. miricauda*-group together form a monophylum. Both have a distinctive ovipositor structure, in which most of the ovipositor is evenly, often lightly sclerotized, but apically there are darkened areas, particularly laterally. This condition is taken to represent the major synapomorphy of the species belonging to these two groups.

Another character state shared by the species of the two groups is that the cercus is straight in males, in contrast to the curved cercus found in many other species of the genus. The outgroup condition for this character is a straight cercus; there-

fore this is probably a plesiomorphic character state.

## PHYLOGENETIC HYPOTHESIS

The following character states were analyzed to provide an explanation of the relationships within the *A. miricauda*-group and the *A. attophilus*-group (Fig. 119):

1. Ovipositor with apical, lateral darkening (primitive state: without darkenings or darkening not lateral).
2. Ovipositor elongate (primitive state: ovipositor relatively short).
3. Dufour's mechanism elongate, with relatively large cells (primitive state: short, rounded Dufour's mechanism; cells small in center).

This character state is found in some members of the *A. miricauda*-group and all the *A. attophilus*-group species I have examined, such as *A. pseudocercus* Brown and *A. dichromatus* Brown (Figs. 114–115). Within the *A. miricauda*-group, the primitive state is found in the *A. paraponerae* (Fig. 117), *A. spatulatus*, and *A. miricauda*-subgroups. The outgroup condition is found in other *Apocephalus*, such as species of the *A. grandipalpis*-group (Fig. 116) and subgenus *Mesophora*.

4. Venter of ovipositor with separate apical sclerite (primitive state: venter not separated apically).

Some *A. miricauda*-group species look superficially like they should be placed in the *A. attophilus*-group, based on the structure of the dorsum of the ovipositor. Ventrally, however, these species have sternite 7 completely contiguous and unaffected by the separation of the apical sclerite from the ovipositor.

5. Apical sclerite with sclerotized connection to ovipositor restricted to thin, medial strip (primitive state: connection more extensive).
6. Anterior section of v-shaped darkening fused into a single process (primitive state: anterior section parallel, joining only at apex).

## HOST-PARASITOID RELATIONSHIPS

Most species of the *A. miricauda*-group are parasitoids of injured ants of the subfamily Ponerinae. In contrast, species of the *A. attophilus*-group attack healthy (noninjured) ants of the tribe Attini, subfamily Myrmecinae. Therefore, within the *A. attophilus*-group (including the *A. miricauda*-group), parasitism of ponerines is a plesiomorphic character state.

The hypothesized phylogenetic relationships among the phorid flies considered herein reflect similar ideas about ant phylogeny. Ponerines and myrmecines have been considered closely related in the past, but more recent reviews have discounted this relationship (e.g., Baroni Urbani et al., 1992). Ward (1994), however, has cast doubt upon confidence in the monophyly of Ponerinae and thus the

rejection of a sister-group relationship between ponerines and myrmecines.

If the Ponerinae is indeed paraphyletic relative to the Myrmecinae, it would lend support to the idea that host ants and parasitoid flies have coevolved, at least on a broad scale. This scenario would match the phylogeny in Fig. 119, in which parasites of the ponerines are paraphyletic with respect to parasitoids of the myrmecines. Many details need to be worked out, however, before this correlation between host and parasite phylogenies can be accepted as significant. For instance, although the *A. attophilus*-group species attack myrmecine ants, they attack only one small group, species of the fungus-growing ant genera *Acromyrmex* and *Atta*, although I have suggested that at least one species of the closely related *Trachymyrmex* probably is also attacked (Brown, 1997b). If coevolution of the groups was prevalent, then one would expect further myrmecines to be hosts. Because most species of the *A. attophilus*-group have unknown hosts, such a scenario of wider host range is still possible.

KEY TO GROUPS OF SUBGENUS  
*APOCEPHALUS*

- 1 Tergite 6 enlarged, wider than tergite 5, extended laterally on segment 6, often with greatly enlarged lateral setae . . . . . *A. pergandei*-group
- Tergite 6 of normal size, usually smaller and narrower than tergite 5, usually without greatly enlarged lateral setae . . . . . 2
- 2 Ovipositor dorsally concave, spatulate, with upturned apices (Figs. 37, 45) . . . . . *A. miricauda*-group (in part)
- Ovipositor dorsally flat or convex . . . . . 3
- 3 Ovipositor with apical section of ovipositor well differentiated from proximal section with clearly demarked narrowing at junction between the two, both dorsally and ventrally; sections articulating by at most a thin, median, sclerotized strip; v-shaped darkening usually anteriorly fused to form a long, single process; parasitoids of attine ants . . . . . *A. attophilus*-group
- Ovipositor with apical section not concurrently differentiated ventrally and dorsally; usually not differentiated into proximal and apical sections ventrally; anterior apex of v-shaped darkening not fused to form long, forward-directed, single process . . . . . 4
- 4 Ovipositor usually blunt-ending dorsally, often subparallel throughout length, with separated or differentiated proximal and apical sections dorsally; apical section often with lateral darkenings; some species with pointed, elongate ventral postapical sclerite on ovipositor that contrasts strongly with shape of dorsal apex; mostly parasitoids of injured ponerine ants . . . . . *A. miricauda*-group (in part)
- Ovipositor usually pointed dorsoapically, usually tapered posteriorly, not differentiated into separate anterior and posterior sections; if not pointed apically, then without lateral darkenings; ovi-

positor ventrally without pointed, postapical sclerite that contrasts strongly with shape of dorsal apex . . . . . other *Apocephalus*

*Apocephalus* Coquillett

- Apocephalus* Coquillett, 1901:501, fig. 1. Type species: *A. pergandei* Coquillett, by original designation. Gender masculine (Ride et al., 1985: Article 30a iii).
- Pseudoplastophora* Schmitz, 1915:327, figs. 6, 7. Type species: *P. caudataria* Schmitz, by monotypy. Synonymized by Borgmeier, 1968.
- Pleurophorina* Borgmeier, 1969:66, figs. 40-42. Type species: *P. turgida* Borgmeier, by original designation. Synonymized by Brown, 1997b.
- Zyziphora* Peterson and Robinson, 1976:119, figs. 1-5. Type species: *Z. hirtifrons* Peterson and Robinson, by original designation. Synonymized by Brown, 1992.
- Anaclinusa* Borgmeier, 1969:63-64, figs. 35-37. Type species: *Anaclinusa lopesi* Borgmeier, by original designation. New synonymy.

The genus *Anaclinusa* is here considered a synonym of *Apocephalus*, based on the single, unusual species *A. lopesi* (below).

*Apocephalus miricauda*-group

This is not a monophyletic group. It is here recognized in an informal sense to allow discussion of a group of species of a similar evolutionary grade. Almost all are parasitoids of injured ponerine ants, in contrast to their hypothesized relatives, the *A. attophilus*-group, which are parasitoids of healthy, uninjured attine ants.

*Apocephalus paraponerae*-subgroup

**DIAGNOSIS.** Ovipositor with ventral postapical sclerite that is usually apically pointed and triangular in shape (two species have apex truncate). Lateral, medially directed bars of sclerotization present at apex ventrally.

**FOSSIL RECORD.** There are seven pieces of Dominican amber (Oligocene-Miocene) that contain fossil phorids closely resembling *A. paraponerae* Borgmeier or *A. deceptus* new species. One of these pieces contains four specimens; another contains two. These are the oldest known fossils of this genus (Brown, 1999) and are treated in detail below.

**PHYLOGENETIC RELATIONSHIPS.** Species of this subgroup are apparently the most basal taxa in the *A. attophilus*-group.

Within the *A. paraponerae*-subgroup, three further divisions are apparent, based on the following characters (see also Fig. 120):

- 1. Dorsal, paired, preapical sclerites present on ovipositor (primitive state: no separate sclerites). This character state defines a group, herein called the *A. paraponerae*-series, containing *A. paraponerae*, *A. deceptus*, *A. strongylus* new species, *A. melinus* new species, and possibly *A.*

*roeschardae* new species (see discussion in species treatment of *A. roeschardae*). The highly aberrant *A. tanyurus* new species (see below) might also belong here.

2. Apex of ventral postapical sclerite truncate (primitive state: apex pointed).

This character state is shared by *A. melinus* and *A. roeschardae*.

3. Sternite 7 with anterior process (primitive state: sternite 7 broad).

This character state is shared by a number of species, herein called the *A. conecitonis*-series: *A. conecitonis*, *A. constrictus*, *A. crassilatus*, *A. dracodermus*, *A. indeptus*, *A. inpalpabilis*, and *A. reticulatus* (all new species).

### *Apocephalus paraponerae*-series

#### *Apocephalus paraponerae* Borgmeier (Figs. 1–2, 117)

*Apocephalus paraponerae* Borgmeier, 1958:324, figs. 8, 15.

**HOLOTYPE.** ♀, PANAMA: Barro Colorado Island, 19.vi.1956, C.W. & M.E. Rettenmeyer, *Paraponera clavata* nest entrance (University of Kansas; not examined).

**SPECIES RECOGNITION.** The ovipositor of this species is distinctive, with its long, thin, parallel lateral darkenings. The similar *A. deceptus*, below, has thicker lateral darkenings, smaller, thinner preapical sclerites, and usually more ventral setae on segment 6.

**DESCRIPTION.** Body length 1.4–2.1 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair to subequal in size to upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.57 wing length; range 0.53–0.59. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting usually of single median pair but sometimes up to four setae present. Ovipositor (Figs. 1–2) straight in lateral view, slightly sclerotized, but with small pair of darker preapical sclerites. Lateral darkening thin, subparallel, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Dufour's mechanism

round (Fig. 117). Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Widespread in lowland rain forest throughout the Neotropical Region.

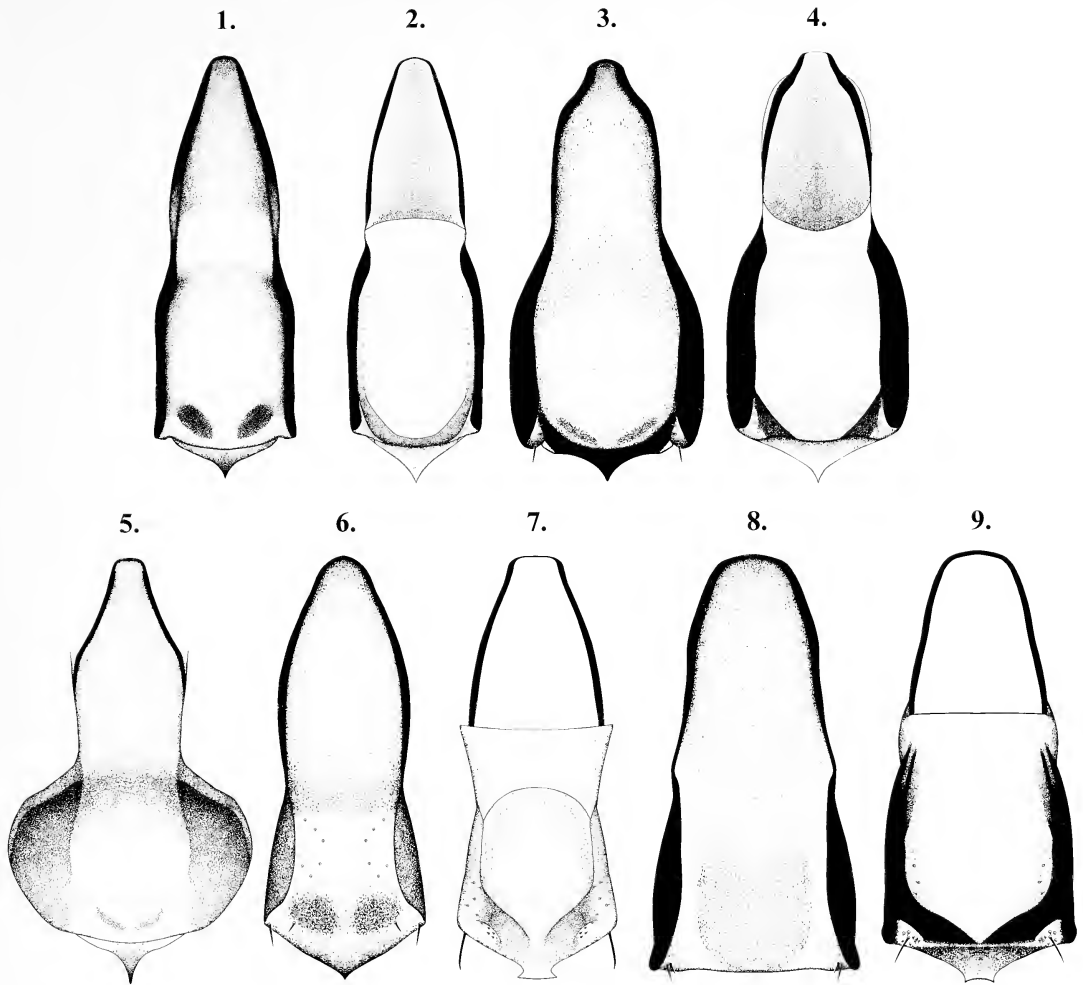
**WAY OF LIFE.** The life history of this species was studied by Brown and Feener (1991a, 1991b) and Feener et al. (1996). It is a parasitoid of injured and dying workers of *Paraponera clavata* but also attacks other ponerine ants such as *Ectatomma tuberculatum* (Olivier) and *Pachycondyla* spp. At least on the Osa Peninsula in Costa Rica, *A. paraponerae* must subsist entirely on *E. tuberculatum*, because *P. clavata* does not occur there (D. Feener, personal communication). No flies have been reared to adulthood from any host except *P. clavata*, but I have reared larvae from *Pachycondyla villosa* (Fabricius) and *E. tuberculatum*.

Females of *A. paraponerae* seem to adjust their clutch size to the size of the available host. When ovipositing in the much larger workers of *P. clavata*, females laid an average of 2.09 eggs/host ( $n = 11$ ,  $sd = 1.14$ ), whereas they laid an average of only 1.13 eggs on the smaller *E. tuberculatum* ( $n = 5$ ), *P. apicalis* ( $n = 1$ ; 1 egg), and *P. villosa* ( $n = 2$ ); the difference between the number of eggs laid on *P. clavata* versus the pooled mean for the smaller ant species was statistically significant (95%;  $T = 2.65$ ,  $p = 0.021$ ,  $df = 12$ ). As with other species in the *A. miricauda*-group, individual flies may be egg-layers or feeders (see Behavioral Aspects, below).

Based on behavioral characteristics and body size, Morehead and Feener (1997) have proposed that what is currently recognized as *A. paraponerae* may be a group of at least two races that are undergoing sympatric speciation. Specifically, they have proposed that individuals attacking *P. clavata* and *E. tuberculatum* are of different races. If this is true, then differences in the average clutch size of ovipositing females might be a characteristic of each race, not of individual choice by females. I have been unable to find consistent structural characters that separate females attacking *P. clavata* from those attacking other hosts.

**MATERIAL EXAMINED.** BRAZIL: Amazonas: Manaus, Reserva Ducke, 3.13°S, 60.02°W, 2♀, 8–15.iv.1992, J. Vidal, Arm. Cola. 1-B-1m (INPA); Rio de Janeiro, near Desengano State Park, site #2, 21.92°S, 41.80°W, 11♀, 10.v.1999, B. Brown, injured *Pachycondyla apicalis*, 200 m (LACM, MZSP), near Desengano State Park, site #3, 21.96°S, 41.81°W, 1♀, 7.v.1999, B. Brown, injured *Ectatomma tuberculatum*, 200 m (LACM), 2♀, 7.v.1999, B. Brown, injured *Ectatomma lugens*, 200 m (LACM), 6♀, 7.v.1999, B. Brown, injured *Pachycondyla villosa*, 200 m (LACM); Rondonia: 62 km SE Ariquemes, Fazenda Rancho Grande, 10.35°S, 62.80°W, 5♀, 14–25.ix.1993, B. Harris, 165 m, injured *Paraponera clavata* (LACM). COLOMBIA: Amazonas: Amacayacu National Park,





Figures 1–9. Ovipositors. Figures 1–2. *Apocephalus paraponerae* Borgmeier. 1. Dorsal. 2. Ventral. Figures 3–4. *Apocephalus deceptus* new species. 3. Dorsal. 4. Ventral. 5. *Apocephalus strongylus* new species, dorsal. Figures 6–7. *Apocephalus melinus* new species. 6. Dorsal. 7. Ventral. Figures 8–9. *Apocephalus roeschardae* new species. 8. Dorsal. 9. Ventral.

3.82°S, 70.26°W, 17♀, 30.viii.1997, B. Brown, G. Kung, injured *Paraponera clavata* (LACM), 2♀, 2.ix.1997, B. Brown, G. Kung, injured *Pachycondyla apicalis* (LACM), 8♀, 3.ix.1997, B. Brown, G. Kung, injured *Paraponera clavata* (LACM, UNCB), 1♀, 3.ix.1997, B. Brown, G. Kung, injured *Pachycondyla villosa* (LACM), 1♀, 5.ix.1997, B. Brown, G. Kung, injured *Dolichoderus attelaboides* (LACM), 7 km W Leticia, 4.13°S, 69.9°W, 1♀, 26.viii.1997, B. Brown, G. Kung, injured *Pachycondyla crassinoda* (LACM), 4♀, 26.viii.1997, B. Brown, G. Kung, injured *Pachycondyla apicalis* (LACM), 22 km NW Leticia, 4.04°S, 69.99°W, 1♀, 6.ix.1997, 5♀, 7.ix.1997, B. Brown, G. Kung, injured *Pachycondyla apicalis* (LACM); Valle: Rio Raposo, 3.67°N, 77.08°W, 2♀, x.1964, 1♀, vi.1965, V.H. Lee, light trap (LACM). COSTA RICA: Guanacaste: Finca Posmompá, near Pitilla, 11.05°N, 85.43°W, 8♀, 5–6.vii.1997, B. Brown, in-

jured *Pachycondyla villosa* (LACM), 26♀, 5–6.vii.1997, B. Brown, J. Paldi, injured *Paraponera clavata* (LACM); Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 23♂, 27♀, 19–26.v.1988, B. Brown, injured *Paraponera clavata* (LACM, MCZC), 2♀, 23–26.v.1988, B. Brown, Malaise trap SSO 50 (LACM) 3♂, 3♀, 22.iv.1989, B. Brown, D. Feener, on *Paraponera clavata* (LACM), 1♀, 8–15.v.1989, B. Brown, D. Feener, Malaise trap SOR@SHO (LACM), 20♀, 24.vi.1993, attracted to injured *Ectatomma tuberculatum* (LACM), 1♀, 24.vi.1993, B. Brown, injured *Pachycondyla apicalis* (LACM), 1♀, 26.vi–1.vii.1993, B. Brown and D. Feener, Malaise trap #3 (LACM), 1♀, 27.vi.1993, B. Brown, injured *Pachycondyla villosa* (LACM), 51♀, 27.vi.1993, D. Feener, *Paraponera* experiment vouchers (LACM), 4♀, 28.vi.1993, B. Brown, ovipositing on *Ectatomma tuberculatum* (LACM), 3♀, 2.vii.1993, B. Brown,

injured *Pachycondyla impressa*, 18♀, 2.vii.1993, D.H. Feener, attracted to injured *Ectatomma tuberculatum* (LACM), 1♀, 1–15.iii.1993, Malaise trap M/10/41, 1♀, 15.iv–1.v.1993, Malaise trap M/10/89, 2♀, 1–15.v.1993, Malaise trap M/10/104, 2♀, 18.v.1993, ALAS, Malaise trap, M/01/96, M/02/97 (INBC), 1♀, 15.v–1.vi.1993, Malaise trap M/08/114, 1♀, 15.v–1.vi.1993, Malaise trap M/10/116, 2♀, 1–15.vi.1993, Malaise trap M/10/132, 1♀, 15.vi–1.vii.1993, Malaise trap M/08/142, 1♀, 15.vi–1.vii.1993, ALAS, Malaise trap M/10/144 (INBC), 9♀, 15.vi–1.vii.1993, ALAS, Malaise trap M/12/146 (INBC), 1♀, 15.vi–1.vii.1993, ALAS, Malaise trap M/06/151 (INBC), 1♀, 15.vii.1993, ALAS, Malaise trap M/12/162 (INBC), 4♀, 3.viii.1993, ALAS, Malaise trap M/01/164, M/12/174 (INBC), 1♀, 16.ix.1993, ALAS, Malaise trap M/08/214 (INBC), 1♀, 15.x.1993, ALAS, Malaise trap M/12/246 (INBC), 1♀, 1.xii.1993, ALAS, Malaise trap M/01/276 (INBC), 1♀, 17.vii.1995, ALAS, Malaise trap M/10/407 (INBC), 1♀, 16.x.1995, ALAS, Malaise trap M/07/476 (INBC), 6♀, 25.vi.1997, B. Brown, J. Paldi, injured *Ectatomma tuberculatum* (LACM), 2♀, 7.vii.1998, ALAS, light L/18/415 (INBC), 1♀, 15.i.1998, ALAS, light L/??/274 (INBC), 1♀, 9.vii.1998, ALAS, light L/09/418 (INBC), 2♀, 22.vii.1998, ALAS, light L/17/426 (INBC), 1♀, 15.x.1998, ALAS, light L/08/489, Rara Avis, 10.28°N, 84.04°W, 1♀, 18–23.i.1989, D.A. Grimaldi (AMNH), 2♀, 10.vii.1993, B. Brown, attracted to injured *Paraponera clavata* (LACM), Estación Magsasay, Parque Nacional Braulio Carrillo, 1♀, iii.1991, A. Fernandez (INBC); Puntarenas: Coopemarti, 8 km S puente de Rio Rincon, 8.63°N, 83.47°W, 1♀, ii.1991, P. Hanson, Malaise trap, 30 m, primary rainforest (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 1♀, xii.1991, P. Hanson, Malaise trap (LACM), 5 km SW Rincon, 8.7°N, 83.51°W, 10♀, 4.vi.1998, B. Brown, injured *Pachycondyla apicalis* (LACM), Sirena, 8.48°N, 83.60°W, 16♀, 9.vii.1993, D. Feener, injured *Ectatomma tuberculatum* (LACM). ECUADOR: Napo: Yasuni Biological Research Station, 0.67°S, 76.39°W, 1♂, 3♀, 23.v.1996, B. Brown, injured *Paraponera clavata* (LACM), 1♀, 26.v.1996, J. Röschar, injured *Pachycondyla apicalis* (LACM); Pichincha: Rio Palenque Science Center, 0.60°S, 79.35°W, 1♀, 25.iv–6.vi.1996, P. Hibbs, Malaise trap, 200 m (LACM); Sucumbios: Añaña, 0.48°S, 76.38°W, 16♀, 10.ix.1997, P. DeVries, injured *Paraponera clavata* (LACM), Limoncocha, 0.40°S, 76.58°W, 3♂, 10♀, 27.vii.1970, C. Rettenmeyer, *Paraponera clavata*, #4606 (LACM), Sacha Lodge, 0.50°S, 76.50°W, 1♀, 22.ii–4.iii.1994, 3♀, 13–23.vi.1994, 1♀, 13–25.vii.1994, 1♀, 10–21.xi.1994, P. Hibbs, Malaise trap (LACM, QCAZ). GUYANA: Berbice: Dubulay Ranch, 5.68°N, 57.86°W, 8♀, 18.i.1999, B. Brown, injured *Paraponera clavata* (LACM, UGGG), Warniabo Creek, Dubulay Ranch, 5.66°N, 57.88°W, 16–20.i.1999, B. Brown, M. Sharkey, Malaise trap #9

(LACM). PANAMA: Canal Zone: Barro Colorado Island, 9.17°N, 79.83°W, 1♀ [no collector or date], associated with *Ectatomma tuberculatum* (LACM), 3♀, 27.vi.1956, C. and M. Rettenmeyer, *Paraponera clavata* (LACM), 1♀, vii.1967, W.W. Wirth, light trap (USNM), 1♂, 5♀, 10.i.1985, D.H. Feener, on *Paraponera*, #0873 (LACM), 1♀, 10–17.iii.1993, J. Pickering, Malaise trap #957 (LACM), 6♂, 6♀, 23.vi.1996, S. Morehead, injured *Paraponera clavata* (LACM); Darien: Cruce de Mono, 7.92°N, 77.62°W, 1♀, 6.ii–4.iii.1993, R. Cambra, J. Coronado, Malaise trap (MIUP); San Blas: Nusagandi Reserve, 9.33°N, 79°W, 1♀, 16–23.iv.1994, J. Pickering, Malaise trap #2862 (LACM). PERU: Madre de Dios: Pakitzta, 11.94°S, 71.28°W, 9♀, 13.ii.1992, 6♀, 14.ii.1992, B. Brown, D. Feener, injured *Paraponera clavata* (LACM, MUSM, USNM), 4♀, 27.ii.1992, B. Brown, D. Feener, injured *Pachycondyla crassinoda* (LACM), 2♀, 28.ii–4.iii.1992, B. Brown, D. Feener, Malaise trap #1 (LACM). VENEZUELA: Amazonas: Rio Mavaca Camp, 2.03°N, 65.10°W, 1♀, 16–27.iii.1989, D.A. Grimaldi (AMNH).

### *Apocephalus deceptus* new species (Figs. 3–4)

**SPECIES RECOGNITION.** This species most closely resembles *A. paraponerae* but has thicker lateral darkenings and more ventral setae on segment 6.

**DESCRIPTION.** Body length 1.5–1.8 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax yellow; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.53 wing length; range 0.53–0.54. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly and posteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Figs. 3–4) straight in lateral view, slightly sclerotized, but with small pair of darker preapical sclerites. Lateral darkening thin, subparallel (but slightly broader than those of *A. paraponerae*), margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** This species is known only from Amazonian Ecuador.

**WAY OF LIFE.** Females of this species are attracted to injured workers of *Pachycondyla commutata* (Roger), the presumed host.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for deceive, referring to the deceptive similarity of this species to *A. paraponerae*.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Añagu, 0.48°S, 76.38°W, 11.ix.1997, P. DeVries, injured *Pachycondyla commutata* [LACM ENT 024208] (LACM).

**PARATYPES.** ECUADOR: Napo: Cuyabeno, 0.2°S, 76.3°W, 1 ♀, 14.vi.1996, J. Röschard, injured *Pachycondyla commutata* (LACM); 1 ♀, same data as holotype (LACM).

### *Apocephalus strongylus* new species

(Fig. 5)

**SPECIES RECOGNITION.** The combination of broad lateral darkenings and the pair of preapical, dorsal sclerites of the ovipositor serve to distinguish this species from its closest relatives.

**DESCRIPTION.** Body length 1.4 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair subequal in size to upper pair. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.5 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 5) straight in lateral view, slightly sclerotized, but with small pair of darker preapical sclerites. Lateral darkening broadened, rounded laterally, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Brazil.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Greek *strongylos* for round, referring to the rounded apical portion of the ovipositor.

**HOLOTYPE.** ♀, BRAZIL: Pará: Tucuruí, 3.83°S, 49.67°W, 20.vii–8.viii.1982, J. Vidal, CDC trap [LACM ENT 038362] (INPA).

### *Apocephalus melinus* new species

(Figs. 6–7)

**SPECIES RECOGNITION.** This species can be recognized by the brown-colored lateral darkenings and the large, black, round preapical sclerites of the ovipositor.

**DESCRIPTION.** Body length 1.0–1.5 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.54 wing length; range 0.51–0.6. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of four long setae emanating from a small sternite. Ovipositor (Figs. 6–7) straight in lateral view, slightly sclerotized, but with small pair of darker preapical sclerites. Lateral darkening thin, subparallel, margin yellowish brown, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor ventrally with apically truncate postapical sclerite. Sternite 7 broad, lightly sclerotized. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens.

**GEOGRAPHICAL DISTRIBUTION.** Known from Amazonian Ecuador and Colombia.

**WAY OF LIFE.** Males and females were attracted to injured workers of *Dolichoderus attelaboides* (Fabricius), and in one instance, *D. decollatus* Smith. Larvae were reared from *D. attelaboides*.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for honey-colored, referring to the yellowish-brown color of the ovipositor's lateral darkenings.

**HOLOTYPE.** ♀, ECUADOR: Napo: Yasuni Biological Research Station, 20.v.1996, B. Brown, injured *Dolichoderus attelaboides* [LACM ENT 053807] (LACM).

**PARATYPES.** COLOMBIA: Amazonas: Amacayacu National Park, 3.82°S, 70.26°W, 1 ♀, 31.viii.1997, B. Brown, G. Kung, injured *Dolichoderus decollatus* (LACM), 1 ♂, 9 ♀, 5.ix.1997, B. Brown, G. Kung, injured *D. attelaboides* (LACM, UNCB), 22 km NW Leticia, 4.04°S, 69.99°W, 1 ♀,

28.viii.1997, B. Brown, G. Kung, injured *Pachycondyla commutata* (LACM). ECUADOR: 5♂, 12♀, same data as holotype (LACM, MCZC, QCAZ, USNM).

### *Apocephalus roeschardae* new species

(Figs. 8–9)

**SPECIES RECOGNITION.** This species can be recognized by the truncate apex of the ventral postapical sclerite, its dark overall color, and the large, medial sclerotization instead of paired sclerites dorsally.

**DESCRIPTION.** Body length 1.4–2.0 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax yellow; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur of even color anteriorly. Mean costal length 0.52 wing length; range 0.49–0.55. Wing vein  $R_{2+3}$  present. Halter mostly yellow but with dark brown spot on knob. Abdominal tergites dark brown. Venter of abdomen dark gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae emanating from a small sternite. Ovipositor (Figs. 8–9) straight in lateral view, with broad median sclerite. Lateral darkening thin, subparallel, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor ventrally with apically truncate postapical sclerite. Sternite 7 round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

**GEOGRAPHICAL DISTRIBUTION.** Known from Atlantic coastal Brazil, Ecuador, and Colombia.

**WAY OF LIFE.** Adult females are attracted to injured workers of the myrmicine ant, *Cephalotes atratus* (Linnaeus). I observed one female ovipositing in the abdomen of the host.

**PHYLOGENETIC RELATIONSHIPS.** It is possible that *A. roeschardae* is the sister-species of *A. melinus*, although this is only one of the most parsimonious conclusions from the data presented above. The relationship is supported by the peculiarly truncate ventral postapical sclerite in these two species. It is contradicted by the lack of paired sclerites in *A. roeschardae*. The abdomen of *A. roeschardae* is unusually colored, being completely dark brown, in contrast to that in other *A. miricauda*-group species, which have at least the ventral membrane yellow. Also, the sclerotized portions of the ovipositor are unusually robust. Such changes might have modified the “missing” character states

to states unrecognizable as homologous with those found in *A. melinus*.

**DERIVATION OF SPECIFIC EPITHET.** This species is dedicated to Ms. Jacqueline Röschar, who helped with field work in Ecuador and independently collected many new parasitic phorid flies.

**HOLOTYPE.** ♀, COLOMBIA: Amazonas: Amacayacu National Park, 3.82°S, 70.26°W, 31.viii.1997, B. Brown, G. Kung, injured *Cephalotes atratus* [LACM ENT 093613] (UNCB).

**PARATYPES.** BRAZIL: Rio de Janeiro: near Desengano State Park, site #1, 21.87°S, 41.80°W, 2♀, 5.v.1999, 6♀, 9.v.1999, B. Brown, injured *Cephalotes atratus*, 200 m (LACM, MZSP). COLOMBIA: Amazonas: Leticia, 4.19°S, 69.93°W, 1♀, 25.viii.1997, 1♀, 8.ix.1997, B. Brown, G. Kung, injured *C. atratus* (LACM), 22 km NW Leticia, 4.04°S, 69.99°W, 3♀, 28.viii.1997, injured *C. atratus* (LACM, UNCB). ECUADOR: Napo: Jatun Sacha, 1.07°S, 77.6°W, 1♀, 16.ix.1996, J. Röschar, injured *C. atratus* (LACM), Yasuni Biological Research Station, 0.67°S, 76.39°W, 1♀, 21.v.1996, 1♀, 22.v.1996, B. Brown, injured *C. atratus*, 220 m (LACM, QCAZ). PERU: Madre de Dios: Pakitza, 11.94°S, 71.28°W, 1♀, 4.ix.1991, T. Erwin, M. Pogue, fog tree #184 (USNM).

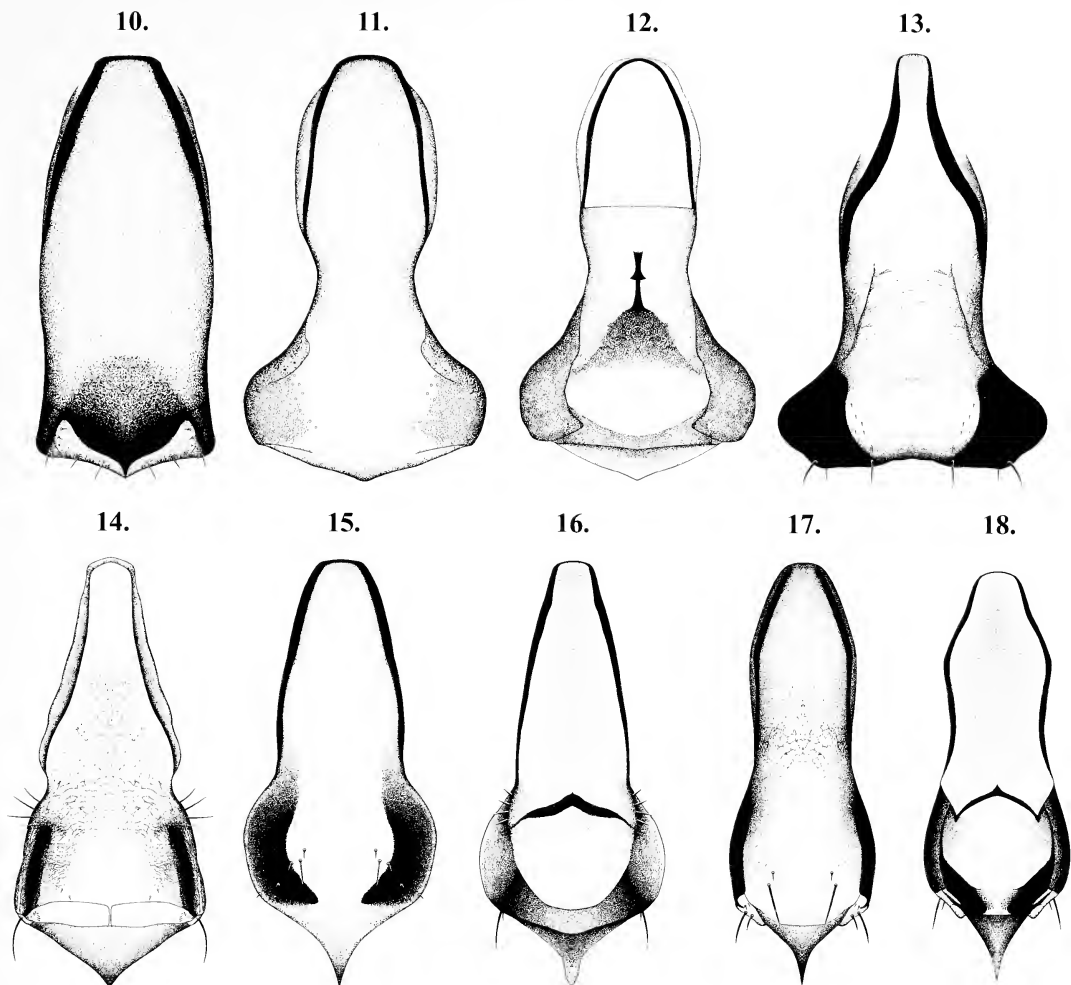
### *Apocephalus conecitonis*-series

#### *Apocephalus conecitonis* new species

(Fig. 10)

**SPECIES RECOGNITION.** Although similar to *A. secus*, this species differs by the shape of the ovipositor and setation of the venter, as outlined in the key. The apex of the ovipositor also is markedly downturned in this species.

**DESCRIPTION.** Body length 1.0–1.5 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur of even color anteriorly. Mean costal length 0.46 wing length; range 0.46–0.48. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 4–5 with row of setae on posterior margin. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Fig. 10) downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening short, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor pointed. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 short, narrow. Dufour’s mechanism not



Figures 10–18. Ovipositors. 10. *Apocephalus conecitonis* new species, dorsal. Figures 11–12. *Apocephalus constrictus* new species. 11. Dorsal. 12. Ventral. 13. *Apocephalus crassilatus* new species, dorsal. 14. *Apocephalus dracodermus* new species, dorsal. Figures 15–16. *Apocephalus indeptus* new species. 15. Dorsal. 16. Ventral. Figures 17–18. *Apocephalus palpabilis* new species. 17. Dorsal. 18. Ventral.

seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from the area of La Selva, Costa Rica.

**WAY OF LIFE.** Females of this species are associated with army ant raids, but it is not clear which ants they parasitize. It is possible that they are associated with army ants as a means to procure their actual hosts (Brown and Feener, 1998). On one occasion I collected these flies in association with a raid of *Eciton lucanoides* Emery on *Pachycondyla obscuricornis* (Emery), a ponerine ant and possible host; however, the army ants also were attacking *Paratrechina longicornis* (Latreille) and *Aphaenogaster araneoides* Emery.

**DERIVATION OF SPECIFIC EPITHET.** The name is from the Latin word *con*, for “with,” and

*eciton*, the name of army ants, referring to the association of these flies with ants of the genus *Eciton* Latreille.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 2♀, 11.v.1989, B. Brown, *Eciton burchellii* raid [LACM ENT 012251] (LACM).

**PARATYPES.** COSTA RICA: Heredia: Chila-mate, 10.45°N, 84.08°W, 2♀, v.1989, 1♀, iv–vi.1990, P. Hanson, Malaise trap (LACM), La Selva Biological Station, 10.43°N, 84.02°W, 2♀, 25.iv.1989, 44♀, 11.v.1989, 26♀, 13.v.1989, 1♀, 14.v.1989, 24♀, 16.v.1989, 15♀, 20.v.1989, B. Brown, D. Feener, *Eciton burchellii* raid (LACM, MCZC, MUCR, MZSP, USNM), 1♀, 2.iii.1993, ALAS, M/05/20 (INBC), 1♀, 1–15.iii.1993, ALAS, Malaise trap M/07/38, 2♀, 1–15.iv.1993, ALAS, Malaise trap M/05/68, M/11/74 (INBC), 1♀,

1.vi.1993, ALAS, Malaise trap M/12/118 (INBC), 4♀, 15.vi-1.vii.1993, ALAS, Malaise trap M/10/144 (INBC), 2♀, 3.vii.1993, B. Brown, *E. lucanoides* raid (LACM), 1♀, 4.iv.1994, ALAS, Malaise trap M/11/389 (INBC).

### *Apocephalus constrictus* new species

(Figs. 11–12)

**SPECIES RECOGNITION.** The unusually shaped ovipositor, with its extreme narrowing at midlength, is distinctive for this species (Figs. 11–12).

**DESCRIPTION.** Note that this description is somewhat fragmentary because it is based on a single, air-dried specimen. I hope that additional specimens will be found so that the missing character states can be included.

Body length 1.3 mm. Frons dark brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair subequal in size to upper pair. Flagellomere 1 brown, oval. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur of even color anteriorly. Mean costal length 0.54 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Ovipositor (Figs. 11–12) constricted at midlength, slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened, rounded laterally, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 triangular, with narrow anterior projection. Internal sclerite rounded, with a short process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single, mid-elevation site in Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is from a Latin word for constricted, referring to the marked narrowing of the ovipositor at midlength.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: Monteverde, 20–24.vi.1986, W. Hanson, G. Bohart [LACM ENT 012778] (EMUS).

### *Apocephalus crassilatus* new species

(Fig. 13)

**SPECIES RECOGNITION.** This species can be recognized easily by the broad, curved lateral margins of ovipositor and dense ventral setae of the abdomen.

**DESCRIPTION.** Body length 1.6–2.3 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair subequal in size to upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown.

Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.55 wing length; range 0.52–0.58. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites yellow, posteriorly dark brown; tergite 6 completely yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 13) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening broadened, rounded laterally, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens.

**GEOGRAPHICAL DISTRIBUTION.** There are records of this species from Costa Rica, Panama, Colombia, and Brazil.

**WAY OF LIFE.** Females were attracted to injured workers of various species of *Pachycondyla*, including *P. apicalis* (Latreille), *P. impressa* (Roger), *P. unidentata* Mayr, and *P. villosa*.

**DERIVATION OF SPECIFIC EPITHET.** The name is a combination of the Latin words *crassus* and *latus*, referring to the wide lateral darkenings.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 22.vi.1993, B. Brown, injured *Pachycondyla villosa* [LACM ENT 001551] (LACM).

**PARATYPES.** BRAZIL: Minas Gerais: Belo Horizonte, Estação Ecológica, UFMG campus, 1♀, 2–5.vii.1993, S.D. Gaimari, Malaise trap (BHMH). COLOMBIA: Amazonas: Amacayacu National Park, 3.82°S, 70.26°W, 2♀, 2.ix.1997, B. Brown, G. Kung, injured *Pachycondyla apicalis* (LACM, UNBC). COSTA RICA: Alajuela: 20 km S Upala, 1♀, 11–21.vi.1991, F.D. Parker [Malaise trap] (EMUS); Guanacaste: Finca Posmompá, near Pitilla, 11.05°N, 85.43°W, 2♀, 6.vii.1997, B. Brown, J. Paldi, injured *P. villosa* (LACM); Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1♀, 24.vi.1993, 2♀, 6.vii.1993, B. Brown, injured *P. apicalis* (LACM) 1♀, 1.xi.1993, ALAS, Malaise trap M/02/249 (INBC), 2♀, 21.iii.1995, B. Brown, injured *P. villosa* (LACM), Plástico, 10.28°N, 84.02°W, 1♂, 3♀, 11.vii.1993, B. Brown, injured *P. unidentata* (LACM), Rara Avis, 12 km SW Horquetas, 1♀, 18–23.i.1989, D.A. Grimaldi, 550 m (AMNH). PANAMA: Canal Zone: Barro Colorado Island, 9.17°N, 79.83°W, 1♀, 25.viii–1.ix.1993, J. Pickering, Malaise trap #1676 (MIUP), 1♀,

19.viii.1996, S. Morehead, injured *P. impressa* (LACM).

### *Apocephalus dracodermus* new species

(Fig. 14)

**SPECIES RECOGNITION.** This species can be diagnosed by the reticulate surface and the slight narrowing at the midpoint of the ovipositor.

**DESCRIPTION.** Body length 1.1 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.44 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with row of setae on posterior margin. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 14) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening broadened, rounded laterally, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor emarginate on either side, with long medial process. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Abdominal glands in segment 5 white, inconspicuous in cleared specimens.

**GEOGRAPHICAL DISTRIBUTION.** Known only from a single site in Amazonian Peru.

**WAY OF LIFE.** The single specimen was collected over a raid of the army ant *Labidus spininodis* (Emery). Whether it was attracted to the army ants or to some victim of their raid is unknown (see Brown and Feener, 1998).

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin word *draco* for lizard and the Greek *derma* for skin, referring to the reticulate pattern on the ovipositor.

**HOLOTYPE.** ♀, PERU: Madre de Dios: Zona Reserva Manu, Pakitza, 17.ii.1992, B. Brown, D. Feener, raid *Labidus spininodis*, 360 m [LACM ENT 011897] (MUSM).

### *Apocephalus indeptus* new species

(Figs. 15–16)

**SPECIES RECOGNITION.** This species has a slightly rounded look to the apex of the ovipositor. It is separated from the similar *A. inpalpabilis* by having two pairs of supra-antennal setae and by the lateral bars of the venter of the ovipositor, which meet medially (Fig. 16).

**DESCRIPTION.** Body length 1.0–1.1 mm. Frons

dark brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur of even color anteriorly. Mean costal length 0.45 wing length; range 0.45–0.46. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 15–16) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened, rounded laterally, extended anteriorly on ovipositor; margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor with triangular ventral postapical sclerite. Sternite 7 round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from single sites in Costa Rica and Ecuador.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for reached or attained, referring to the lateral darkenings that extend farther anteriorly onto the ovipositor than those of some related species.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 26.vi–1.vii.1993, B. Brown, D. Feener, Malaise trap #3 [LACM ENT 013220] (LACM).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 3♀, 16.ii–2.iii.1993, ALAS, Malaise trap M/07/22, M/05/20, 1♀, 15.iii.1993, ALAS, Malaise trap M/07/38 (INBC). ECUADOR: Pichincha: 17 km E Santo Domingo, Tinalandia, 2♀, 6–13.v.1987, B. Brown, 710 m, windows (LACM).

### *Apocephalus inpalpabilis* new species

(Figs. 17–18)

**SPECIES RECOGNITION.** This species differs from the similar *A. indeptus* by having a single pair of supra-antennal setae and the lateral bars not reaching the center of the ovipositor (Fig. 18).

**DESCRIPTION.** Body length 1.3 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, oval. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal



to posterior setulae of scutum. Legs yellow; apex of hind femur slightly darker on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 17–18) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened, rounded laterally, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from La Selva, Costa Rica.

**WAY OF LIFE.** This fly was collected over a swarm raid of the army ant *Eciton burchellii*. Its host is unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin prefix *in*, meaning not, combined with *palpabilis*, meaning touchable, referring to the ventral, transverse sclerites of the ovipositor, which do not touch.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 13.v.1989, B. Brown, *Eciton burchellii* swarm raid [LACM ENT 011326] (LACM).

### *Apocephalus reticulatus* new species

(Figs. 19–20)

**SPECIES RECOGNITION.** The namesake reticulations of the ovipositor are visible with light microscopy; otherwise, the forked ventral process (Fig. 20) is distinctive.

**DESCRIPTION.** Body length 1.1–1.4 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown to white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face (restricted to apical margin). Mean costal length 0.47 wing length; range 0.44–0.5. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–4 bare, segment 5 with a single row of setae on posterior margin. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row.

Ovipositor (Figs. 19–20) slightly downturned apically, lightly but evenly sclerotized dorsally and with reticulate sculpture. Lateral darkening short, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor emarginate on either side, with long medial process. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, with forked anterior process. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from a mid-elevation site in Costa Rica.

**WAY OF LIFE.** Unknown. One specimen was collected over a raid of the army ant *Labidus praedator* (F. Smith).

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for net-like, referring to the pattern on the dorsal surface of the ovipositor.

**HOLOTYPE.** ♀, COSTA RICA: San José: Zurquí de Moravia, 10.05°N, 84.02°W, 1–15.vi.1993, P. Hanson, Malaise trap, 1600 m [LACM ENT 053562] (LACM).

**PARATYPES.** COSTA RICA: San José: Zurquí de Moravia, 10.05°N, 84.02°W, 1♀, ix–x.1990, 1♀, ii.1991, 1♀, xii.1991–ii.1992, 6♀, v.1992, 5♀, vii.1992, 1♀, iv–v.1993, 5♀, vi.1993, 3♀, ix–x.1993, 1♀, i.1996, P. Hanson, Malaise trap, 1600 m (INBC, LACM, MCZC, MUCR, USNM), 1♀, 8.iii.1995, B. Brown, J. Cantley, over raid of *Labidus praedator* (LACM).

### Other *A. paraponerae*-subgroup Species

*Apocephalus persecutor* Borgmeier  
(Fig. 20)

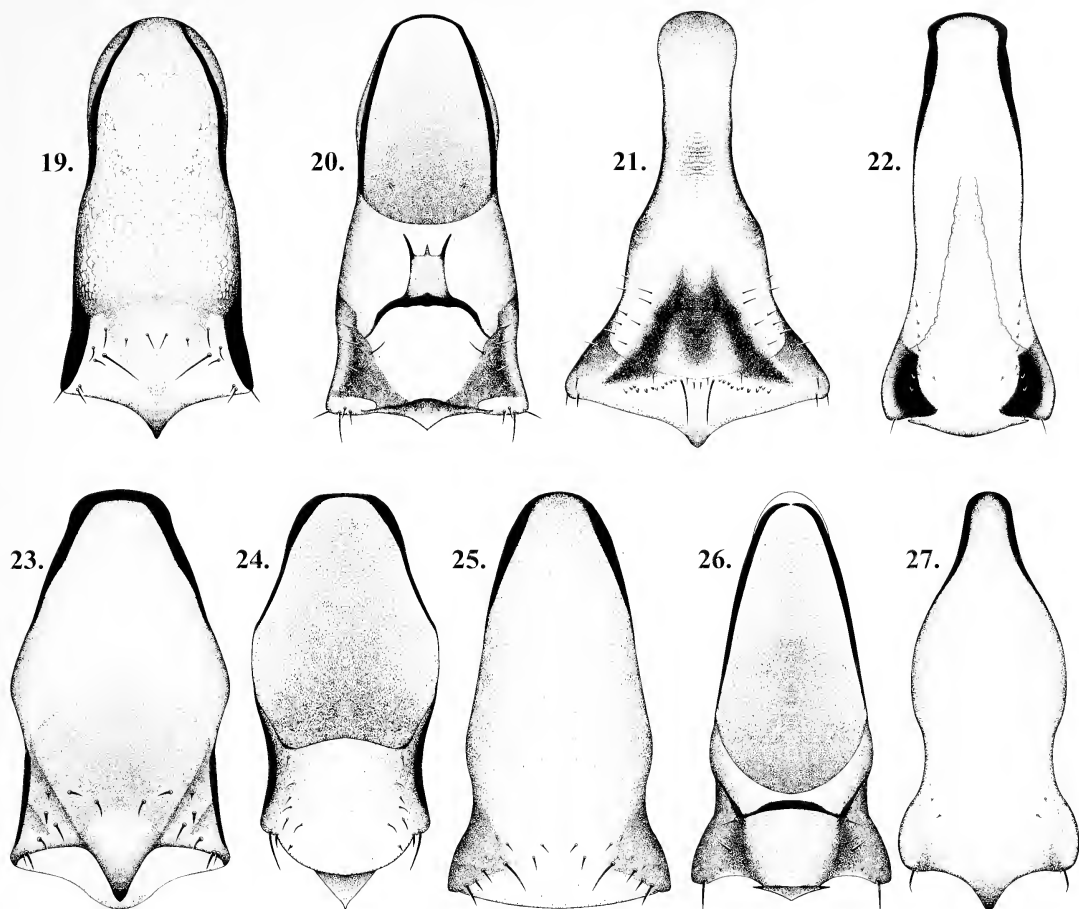
*Apocephalus persecutor* Borgmeier, 1961:44, figs. 54, 80.

**HOLOTYPE.** ♀, BRAZIL: Goiás: Campinas, 26.v.1933, J.S. Schwarzmaier, with *Nomomyrmex ensbecki* (MZSP; examined).

**SPECIES RECOGNITION.** This species is easily recognized by the triangular ovipositor. It is similar to *A. dichocercus* Borgmeier (1958), a species I did not examine. Borgmeier (1971) separated these two species on the basis of the shorter costa in *A. persecutor* (0.38, versus 0.57 for *A. dichocercus*). Further study of *A. dichocercus* is needed.

**DESCRIPTION.** Body length 1.0–1.1 mm. Frons dark brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.39 wing length; range 0.38–0.40. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with setae of





Figures 19–27. Figures 19–20. *Apocephalus reticulatus* new species. 19. Dorsal. 20. Ventral. 21. *Apocephalus persecutor* Borgmeier, dorsal. 22. *Apocephalus curtinotus* new species, dorsal. Figures 23–24. *Apocephalus secus* new species. 23. Dorsal. 24. Ventral. Figures 25–26. *Apocephalus spiculus* new species. 25. Dorsal. 26. Ventral. 27. *Apocephalus torulus*, dorsal.

medium length along posterior margin. Venter of segments 3–5 with row of setae on posterior margin. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Fig. 20) straight in lateral view, lightly sclerotized anteriorly; posteriorly with darkly sclerotized triangle; expanded. Lateral darkening not differentiated. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 not differentiated. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Ecuador and Costa Rica.

**WAY OF LIFE.** The host of this species is unknown, but it has been collected with various species of army ants.

**MATERIAL EXAMINED.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1♀, ix.1992, P. Hanson, Malaise trap (LACM), 2♀, 1–15.iv.1993, ALAS, Malaise trap M/04/67, M/05/68, (INBC), 1♀, 15.v–1.vi.1993, ALAS, Malaise trap M/8/114 (INBC). ECUADOR: Napo: Limoncocha, 0.40°S, 76.58°W, 1♀, 9.xi.1967, C. and M. Rettenmeyer, with *Eciton mexicanum*, E-528, #3673 (UCMS), 1♀, 13.xii.1967, with *E. lucanoides*, E-618, #4108 (UCMS); Pichincha: Rio Palenque Science Center, 3♀, 1–3.v.1987, *E. burchellii* bivouac, B. Brown (LACM).

#### *Apocephalus curtinotus* new species (Fig. 22)

**SPECIES RECOGNITION.** This species has a peculiar, medial darkening of the dorsum, as well as a rounded apical region of the ovipositor.

**DESCRIPTION.** Body length 1.3 mm. Frons

light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 complete, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Fig. 22) slightly downturned apically, with broad median sclerite. Lateral darkening broadened, rounded laterally, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Abdominal glands in segment 5 dark, enlarged, elongate, clearly visible in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Amazonian Brazil.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *curtus* for short and *nota* for mark, referring to the short lateral darkenings.

**HOLOTYPE.** ♀, BRAZIL: Amazonas: Manaus, Reserva Ducke, 3.13°S, 60.02°W, 6–17.vii.1992, J. Vidal, Arm. Cola, 1-B-20 m [LACM ENT 008385] (INPA).

### *Apocephalus secus* new species

(Figs. 23–24)

**SPECIES RECOGNITION.** This species is most similar to *A. conecitonis*, from which it differs by the shape of the ovipositor and the ventral setation, as outlined in the key. It also resembles *A. spiculus* new species, which has a much shorter ventral postapical sclerite.

**DESCRIPTION.** Body length 1.0 mm (both specimens). Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus light brown. Dorsum of thorax light brown; pleuron white to brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.47 wing length; range 0.47–0.48. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emar-

ginate, with long seta at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row; lateral setae shorter. Ovipositor (Figs. 23–24) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening short, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor emarginate on either side, with long medial process. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 not differentiated. Dufour's mechanism not seen. Abdominal glands in segment 5 white, invisible in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from a single, mid-elevation site in Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for different, referring to the fact that although this species is closely similar to *A. conecitonis*, *A. reticulatus*, and *A. torulus* new species, it differs in a few key characters.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: Las Alturas, 8.95°N, 82.38°W, i.1992, P. Hanson, Malaise trap [LACM ENT 016169] (LACM).

**PARATYPE.** 1♀, same data as holotype, except v.1992 (LACM).

### *Apocephalus spiculus* new species

(Figs. 25–26)

**SPECIES RECOGNITION.** This species is recognized by the distinctive short ventral postapical sclerite of the ovipositor (Fig. 26).

**DESCRIPTION.** Body length 1.0 mm. Frons dark brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter light brown. Abdominal tergites dark brown. Venter of abdomen white. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 with row of setae on posterior margin, but rows somewhat irregular. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Figs. 25–26) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening short, apically rounded, divergent, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor emarginate on either side, with long medial process. Apicoventral margin of ovi-

positor straight. Ovipositor with small, triangular ventral postapical sclerite. Sternite 7 broad, without anterior process. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Panama.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a diminutive of the Latin word *spica*, for spike, referring to the small apical triangle of the ovipositor.

**HOLOTYPE.** ♀, PANAMA: San Blas: Nusagandi Reserve, 9.33°N, 79.0°W, 5–12.ii.1994, J. Pickering, Malaise trap #2042 [LACM ENT 101299] (LACM).

### *Apocephalus torulus* new species

(Fig. 27)

**SPECIES RECOGNITION.** This species can be separated from other small species similar to *A. conecitonis* by the rounded, lobe-shaped apices of the lateral darkenings.

**DESCRIPTION.** Body length 0.9–1.0 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length; range 0.44–0.49. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 with row of setae on posterior margin. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row; lateral setae shorter. Ovipositor (Fig. 27) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening short, apically rounded, divergent, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor emarginate on either side, with long medial process. Apicoventral margin of ovipositor straight. Ovipositor with triangular ventral postapical sclerite. Sternite 7 broad, without anterior process. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from two sites in western Colombia and Ecuador.

**WAY OF LIFE.** Unknown. Most specimens were collected with a raid of *Labidus praedator*, but we did not observe any oviposition attempts directed at the ants.

**DERIVATION OF SPECIFIC EPITHET.** The

name is a Latin word for a small, rounded projection, referring to the lateral darkenings of the ovipositor.

**HOLOTYPE.** ♀, ECUADOR: Esmeraldas: Bilsa Biological Station, 0.34°N, 79.71°W, 8.v.1996, B. Brown, P. Hibbs, J. Cantley, raid *Labidus praedator* [LACM ENT 025275] (LACM).

**PARATYPES.** COLOMBIA: Valle: Rio Raposo, 1 ♀, viii.1965, V. Lee, light trap (USNM). ECUADOR: 6 ♀, same data as holotype (LACM, QCAZ).

### *Apocephalus succineus* new species

**SPECIES RECOGNITION.** This is the only species of *Apocephalus* in Dominican Republic amber that has a broad ovipositor, similar in appearance to that of *A. paraponerae*. There are other, undescribed species of *Apocephalus* in this amber, but all have much narrower ovipositors.

Unlike the extant species that it resembles, *A. succineus* apparently lacks dorsal, paired, preapical sclerites. It has a row of long setae on the posterior margins of the venter of abdominal segments 5 and 6 as well as scattered, slightly smaller setae.

**DESCRIPTION.** All specimens of this species are preserved in Dominican Republic amber. All show some evidence of decay and shrivelling, probably because they decomposed to some extent after being caught on the surface of the amber but before being covered with a final coating of resin. Because of this imperfect preservation, a number of character states cannot be seen clearly. When a particularly important character state can be seen best in a single specimen other than the holotype, it is noted in the following description.

Two pairs of supra-antennal setae present. Flagellomere 1 appearing elongate, narrow (possibly an artifact of shrivelling). Palpus normal, small. Anterior scutellar seta enlarged, longer than one-half posterior seta (easily seen in specimen DR-14-105). Mean costal length 0.44 wing length; range 0.44–0.45. Wing vein  $R_{2+3}$  present. Abdominal tergites of normal form. Tergite 6 undivided, tapered posteriorly; without large posterior setae (best seen in JW, March 1996–10). Venter of abdominal segments 5 and 6 with scattered, long setae; longest setae in posterior row of each segment (seen in DR-14-211). Abdomen without dense lateral setae. Ovipositor broad, straight in lateral view, lightly sclerotized, apparently without preapical sclerites (similar to Fig. 1, but lacking paired, preapical sclerites). Lateral darkening thin, subparallel, margin dark, complete. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor not seen but apparently with triangular, postapical sclerite. The actual separation of the ovipositor and the triangular postapical sclerite cannot be seen, so it cannot be ruled out that the postapical sclerite is actually fused to the ovipositor, which would be a relatively primitive character state. Sternite 7 not differentiated. Dufour's mechanism, abdominal glands, and internal sclerite not seen.

**AGE OF FOSSILS.** Dominican amber is assumed to have been deposited in the early to middle Miocene, 15–20 million years ago (Iturralde-Vinent and MacPhee, 1996).

**WAY OF LIFE.** Unknown. Given that this species is similar to *A. paraponerae*, a possible host would be the Dominican amber fossil ant *Paraponera dieteri* Baroni Urbani (1994). The genus *Paraponera*, with its single extant species *P. clavata* (Fabricius), no longer occurs on Hispaniola. Presumably, neither do species of the *A. paraponerae*-series, although collecting has been so limited in this region that such an assumption could not be made with absolute certainty.

Phorids that parasitize injured hosts are expected to be relatively common in amber (Brown, 1997c). Hosts that were caught in amber probably emitted alarm pheromones that attracted the parasitoids, which in turn became trapped.

**DERIVATION OF SPECIFIC EPITHET.** The name is from a Latin word, *succinum*, for amber.

**HOLOTYPE.** ♀, DOMINICAN REPUBLIC AMBER. Santiago/Puerto Plata area (LACM-IP).

**PARATYPES.** DOMINICAN REPUBLIC AMBER. 1♀, north mines, DR-14-211, 4♀, north mines, DR-14-105 (AMNH). 2♀, #3804 (USNM-IP). 1♀, DM, March 1993–5, 1♀, JW, March 1996–10 (Private collection of Mr. Pat Craig).

*A. spatulatus*-subgroup

**DIAGNOSIS.** This group can be diagnosed by the first two synapomorphies listed below (under Phylogenetic relationships). The ovipositors of many of the included species do not resemble other *A. miricauda*-group species, but some still retain the distinctive lateral darkenings (e.g., Figs. 32, 33, 43, 44, 46).

**PHYLOGENETIC RELATIONSHIPS.** A hypothesis of the relationships of some of the species within this group is possible (Table 1, Fig. 121). The following are proposed synapomorphic character states:

- 1. Ovipositor spatulate, dorsally concave (primitive state: ovipositor flat or convex).
- 2. Ovipositor with sclerotization of dorsal, apical region extending ventrally, completely encircling the ovipositor (primitive state: dorsal and ventral sclerotization not so confluent).
- 3. Ovipositor with medial, narrow, elongate, bluntly ending, dorsoapical process (primitive state: dorsal apex of ovipositor without process).
- 4. Ventral apex of ovipositor drawn out into long, extremely thin, filament-like process; substates: (1) long, (2) short (primitive state: apex terminating much more bluntly).

According to the cladogram, the short process in *A. acanthus* new species and *A. spatulatus* Borgmeier is the result of secondary reduction. In *A. striativentris* new species and *A.*

Table 1. Character state matrix for *A. spatulatus*-group.

Outgroup	0000000000
<i>incomptus</i>	1100000000
<i>striativentris</i>	1100000000
<i>brochus</i>	1100000001
<i>fuscipalpis</i>	1100000001
<i>digitalis</i>	1110000000
<i>denotatus</i>	1110000000
<i>pachycondylae</i>	1101000000
<i>atrimarginatus</i>	1101000000
<i>batillus</i>	1101000000
<i>emargilatus</i>	1101100000
<i>magnicauda</i>	1101100000
<i>triangularis</i>	1101011000
<i>quadratus</i>	1101011100
<i>acanthus</i>	1102111211
<i>spatulatus</i>	1102011211

*brochus* new species, there is a pointed ventral apex but no elongate process.

- 5. Apicolateral region of v-shaped darkening thickened (primitive state: apicolateral region thin).

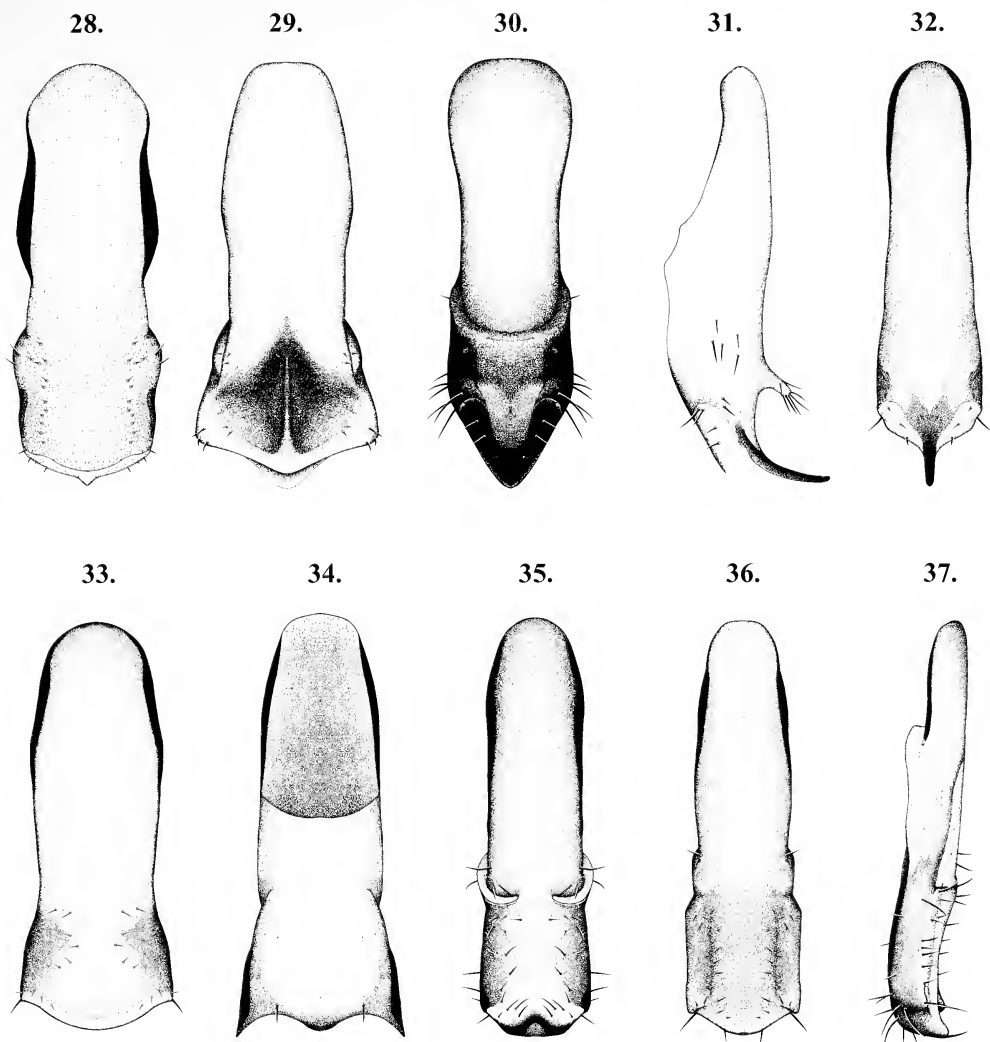
This state appears in *A. emargilatus* new species, *A. magnicauda* new species and, apparently convergently, in *A. acanthus* new species.

- 6. Median carina present on dorsum of ovipositor (primitive state: carina absent).
- 7. Venter of abdomen densely setose (primitive state: abdominal setation sparser or lacking).
- 8. Median carina with (1) bluntly raised area, (2) sharp spine (primitive state: median carina without differentiated raised area).

The polarization of this character state—and thus the sister group relationship between *A. quadratus* Brown and *A. acanthus* + *A. spatulatus*—is speculative. I assume that the high, sharply pointed spine in *A. acanthus* and *A. spatulatus* was preceded by a lower spine, such as that found in *A. quadratus*.

- 9. Anterior portion of ovipositor darkly sclerotized (anterior portion of ovipositor lightly sclerotized, except for lateral, v-shaped darkening).
- 10. Ovipositor greatly expanded at midlength (Figs. 44–46) (primitive state: ovipositor at most slightly expanded at midlength).
- 11. Anterolateral corner of apical region of ovipositor with dorsal, tooth-like swelling (primitive state: without tooth-like swelling).

The outgroup for this analysis was the *A. paraponerae*-subgroup, plus other *Apocephalus* outside of the *A. atrophilus*- and *A. miricauda*-groups. Analysis of these character states with HENNIG-86 resulted in a single tree of length 14, consistency index 92, retention index 95 (Fig. 121).



Figures 28–37. Ovipositors. 28. *Apocephalus incomptus* new species, dorsal. 29. *Apocephalus striativentris* new species, dorsal. 30. *Apocephalus brochus* new species, dorsal. 31. *Apocephalus digitalis* Borgmeier, left lateral. 32. *Apocephalus denotatus* new species, dorsal. Figures 33–34. *Apocephalus pachycondylae* new species. 33. Dorsal. 34. Ventral. 35. *Apocephalus atrimarginatus* new species, dorsal. Figures 36–37. *Apocephalus batillus* new species. 36. Dorsal. 37. Left lateral.

### *Apocephalus incomptus* new species

(Fig. 28)

**SPECIES RECOGNITION.** This relatively plain species can be recognized by the lack of ventral setae and the unmodified ovipositor.

**DESCRIPTION.** Body length 1.5 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow to white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean cos-

tal length 0.5 wing length; range 0.49–0.50. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with seta of medium length at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of small, ventrolateral group and smaller lateral setae. Ovipositor (Fig. 28) straight in lateral view, lightly sclerotized, but with darker apical area. Lateral darkening not differentiated; apical region dark, rectangular. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn

out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Amazonian Brazil and Ecuador.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for unadorned, referring to the relatively simple ovipositor.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°N, 76.5°W, 25.vii–3.viii.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 040968] (LACM).

**PARATYPES.** BRAZIL: Amazonas: Manaus, Reserva Ducke, 3.13°S, 60.02°W, 1♀, 6–17.vii.1992, J. Vidal, Arm. Cola, 1-B 1 m (LACM). ECUADOR: Sucumbios: Sacha Lodge, 0.5°N, 76.5°W, 1♀, 4–14.v.1994, P. Hibbs, Malaise trap, 270 m (LACM).

### *Apocephalus striativentris* new species

(Fig. 29)

**SPECIES RECOGNITION.** This species can be immediately recognized by the darkly sclerotized striations of intersegment 6–7. Other species have these striations (for instance, see Brown, 1992, fig. 35B–D), but they are not black with sclerotization. The dorsum of the ovipositor of this species also has a small, apical ridge (Fig. 29).

**DESCRIPTION.** Body length 1.5–1.8 mm. Frons dark brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus light brown. Dorsum of thorax light brown; pleuron yellow to brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur of even color anteriorly. Mean costal length 0.51 wing length; range 0.49–0.52. Wing vein  $R_{2+3}$  present. Halter light brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 complete, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Intersegment 6–7 ventrally with darkly sclerotized, longitudinal striations. Ovipositor (Fig. 29) slightly upturned apically, dorsally concave, with a median ridge posteriorly; lightly but evenly sclerotized dorsally. Lateral darkening short, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor a rounded point. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 broad, without anterior process. Dufour's mechanism not seen. Abdominal glands in segment 5

white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Brazil, Costa Rica, Ecuador, and Peru.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name refers to the darkened, ventral striations of abdominal intersegment 6–7.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 24.v–3.vi.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 038105] (LACM).

**PARATYPES.** BRAZIL: Amazonas: Reserva Ducke, 3.13°S, 60.02°W, 4♀, 8–15.iv.1992, J. Vidal, Arm-Cola 1-B-1 m, 1♀ Arm. Oleo 1-A-1 m (INPA, LACM). COSTA RICA: Heredia, La Selva Biological Station, 10.43°N, 84.02°W, 1♀, 2.iii.1993, ALAS, Malaise trap, M/05/20 (INBC); Puntarenas: San Vito, Las Cruces, 8.78°N, 83.0°W, 1♀, iii.1988, P. Hanson, Malaise trap, 1300 m (LACM). ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1♀, 23.iv–3.v.1994, 1♀, 4–14.v.1994, 1♀, 14–24.v.1994, 4♀, 24.v–3.vi.1994, 1♀, 3–16.viii.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ). PERU: Madre de Dios: Zona Reserva Manu, Pakitza, 11.95°S, 71.28°W, 2♀, 7–9.iii.1992, R. Cambra, Malaise trap (LACM, MUSM).

### *Apocephalus brochus* new species

(Fig. 30)

**SPECIES RECOGNITION.** This species is distinctive in the broad, dark, pointed, medial process of the dorsum of the ovipositor (Fig. 30). It is most closely related to *A. fuscipalpis* Borgmeier, based on the shared presence of anterior, tooth-like processes on the ovipositor.

**DESCRIPTION.** Body length 1.4–1.6 mm. Frons yellow to light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax yellow; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.5 wing length; range 0.47–0.51. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 short, consisting of a complete ventral and lateral row. Ovipositor (Fig. 30) slightly upturned apically, lightly but evenly sclerotized dorsally, with anterolateral tooth-like swelling. Lateral darkening convergent to apical point, margin dark, complete. Dorsoapical sclerite

of ovipositor not differentiated. Apicodorsal margin of ovipositor pointed, broad, heavily sclerotized. Apicoventral margin of ovipositor drawn out into point, but without long, filament-like process. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Brazil and Colombia.

**WAY OF LIFE.** Females of this species attacked healthy *Camponotus banghaasi* Emery and *C. rapax* (Fabricius) that were attracted to tuna fish baits. Flies hovered over the ants and darted at the posterior part of the heads of their hosts.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for projecting, referring to the extended dorsal apex of the ovipositor.

**HOLOTYPE.** ♀, COLOMBIA: Amazonas: 22 km NW Leticia, 4.04°S, 69.99°W, 6.ix.1997, B. Brown, G. Kung, over baited *Camponotus banghaasi* (UNCB) [LACM ENT 102257].

**PARATYPES.** BRAZIL: Pará: Oriximiná, 1.8°S, 53.83°W, 1♀, 13.x.1992, J. Rafael, Malaise trap (INPA). COLOMBIA: 1♀, same locality and collectors as holotype, 28.viii.1997, over baited *Camponotus rapax* (LACM), 21♀, same data as holotype (LACM, MCZC, MZSP, UNCB, USNM).

*Apocephalus fuscipalpis* Borgmeier  
(Fig. 118)

*Apocephalus fuscipalpis* Borgmeier, 1958:325, figs. 9–10, 13.

**HOLOTYPE.** ♀, BRAZIL: Santa Catarina: Nova Teutônia, iv.1950, F. Plaumann [LACM ENT 033880] (MZSP; examined).

**SPECIES RECOGNITION.** This species differs from its closest relative, *A. brochus*, by the less sclerotized and produced dorsal apex of the ovipositor. Female specimens of *A. fuscipalpis* are also significantly larger in size than those of *A. brochus*.

**DESCRIPTION.** Body length 1.8–1.9 mm. Frons light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair slightly smaller than upper pair. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown. Pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown. Apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.49 wing length (no variation). Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen dark gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a

complete ventral and lateral row. Ovipositor straight in lateral view, lightly but evenly sclerotized dorsally, with anterolateral tooth-like swelling (Fig. 118). Lateral darkening not differentiated. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor pointed. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Ovipositor without separate sclerites laterally. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in southeastern Brazil.

**WAY OF LIFE.** Unknown.

**OTHER MATERIAL EXAMINED.** 1♀ paratype, BRAZIL: Santa Catarina: Nova Teutônia, ix.1958, F. Plaumann (MZSP).

*Apocephalus digitalis* Borgmeier  
(Fig. 31)

*Apocephalus digitalis* Borgmeier, 1971:101, figs. 138–139.

**HOLOTYPE.** ♀, BRAZIL: Santa Catarina: Nova Teutônia, F. Plaumann [LACM ENT 093873] (MZSP; examined).

**SPECIES RECOGNITION.** This species is extremely close to *A. denotatus* new species, but the holotype of *A. digitalis* has a distinctive dorsal process on the ovipositor that is lacking in *A. denotatus*. Both have extremely lightly sclerotized ovipositors, except for the heavily sclerotized, prominent, dorsal process.

**DESCRIPTION.** Body length 1.5 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.54 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites yellow, posteriorly dark brown; tergite 6 completely yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 31) upturned apically, lightly but evenly sclerotized dorsally; with medial, setose process. Lateral darkening short, margin dark, complete. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor pointed, greatly elongate. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 not differen-



tiated. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite small, round.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in southeastern Brazil.

**WAY OF LIFE.** Unknown.

### *Apocephalus denotatus* new species

(Fig. 32)

**SPECIES RECOGNITION.** This species differs from the extremely similar *A. digitalis* by the lack of a dorsomedial process on the ovipositor.

**DESCRIPTION.** Body length 1.3–1.4 mm. Frons light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.59 wing length; range 0.59–0.60. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellowish anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with a pair of large, posterior setae. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 32) slightly upturned apically, lightly but evenly sclerotized dorsally. Lateral darkening not differentiated. Apicodorsal margin of ovipositor pointed, greatly elongate. Apicoventral margin of ovipositor drawn out into pointed process; this process thicker and more rounded than in related species. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, with a short process.

**GEOGRAPHICAL DISTRIBUTION.** Known from lowland Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for conspicuous, referring to the large ventromedial projection of the ovipositor.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: 3 km SW Rincon, 8.68°N, 83.48°W, iii–v.1989, P. Hanson, Malaise trap, 10 m [LACM ENT 050925] (LACM).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 2 ♀, 1–15.iv.1993, ALAS, Malaise trap M/04/67, M/15/78 (INBC); Puntarenas: 23 km NW Puerto Jimenez, 8.67°N, 83.45°W, 1 ♀, i–iv.1991, P. Hanson, Malaise trap, 10 m (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 4 ♀, iii.1989, P. Hanson, Malaise trap, 10 m (LACM, MUCR).

### *Apocephalus pachycondylae* new species

(Figs. 33–34)

**SPECIES RECOGNITION.** This species is somewhat nondescript. It differs from other species with a long, filamentlike, ventral process by the lack of ornamentation of the ovipositor and the distinct lateral darkenings.

**DESCRIPTION.** Body length 1.1–1.5 mm. Frons light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron light brown to white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.55 wing length; range 0.54–0.56. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with a pair of large, posterior setae. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 33–34) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening short, ill-defined, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from one site each in Panama and Costa Rica.

**WAY OF LIFE.** Most specimens were collected over a raid of army ants, *Eciton lucanoides*. The army ants were raiding *Pachycondyla obscuricornis* (Emery), among others; at one point I observed the flies circling around army ants that were trying to pry open a hole on a tree trunk. One specimen was attracted to an injured worker of *P. apicalis*.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on that of the presumed hosts, species of the ant genus *Pachycondyla* (F. Smith).

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 3.vii.1993, B. Brown, over raid *Eciton lucanoides* [LACM ENT 012797] (LACM).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1 ♀, 24.vi.1993, B. Brown, injured *Pachycondyla apicalis* (LACM), 1 ♂, 7 ♀, same data as holotype (male collected *in copula* with one of the females) (INBC, LACM, MUCR). PANAMA: San Blas: Nusagandi Reserve, 9.33°N, 79°W, 1 ♀, 16–



23.iv.1994, J. Pickering, Malaise trap #2862 (LACM).

*Apocephalus atrimarginatus* new species  
(Fig. 35)

**SPECIES RECOGNITION.** This species is similar to *A. batillus* new species but has an ovipositor with a much darker posterior margin.

**DESCRIPTION.** Body length 1.4–1.8 mm. Frons light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.52 wing length; range 0.50–0.55. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 35) slightly upturned apically, lightly sclerotized, but with darker apical area. Lateral darkening not differentiated; apical region dark, especially posterior margin. Apicodorsal margin of ovipositor sinuous. Apicoventral margin of ovipositor drawn out into extremely long, pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite small, oval.

**GEOGRAPHICAL DISTRIBUTION.** Known from a few sites on the Osa Peninsula in Costa Rica.

**WAY OF LIFE.** Females were attracted to injured workers of *Pachycondyla unidentata*. One was attracted to an injured *Odontomachus laticeps* Roger, but it was collected at the same time as another anomalous species for this host, *A. comosus* new species. It is possible that there was some contamination from fluids of other ants that I was crushing on this day. One was also attracted to an injured *Odontomachus bauri* Emery.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on Latin words for black and margin, referring to the darkened posterodorsal margin of the ovipositor.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: 5 km SW Rincon, 8.7°N, 83.51°W, 6.vi.1998, B. Brown, injured *Pachycondyla unidentata* [LACM ENT 116694] (LACM).

**PARATYPES.** COSTA RICA: Puntarenas: Coopemarti, 8.63°N, 83.47°W, 1♀, ii.1991, P. Hanson,

Malaise trap (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 1♀, vi–viii.1989, 1♀, x–xii.1990, 2♀, x.1991, P. Hanson, Malaise trap (LACM, MUCR), 5 km SW Rincon, 8.7°N, 83.51°W, 1♀, 3.vi.1998, B. Brown, injured *Odontomachus laticeps* (LACM), 1♀, 4.vi.1998, *O. bauri* (LACM), 3♀, 5.vi.1998, 2♀, 6.vi.1998, B. Brown, injured *Pachycondyla unidentata* (INBC, LACM).

*Apocephalus batillus* new species  
(Figs. 36–37)

**SPECIES RECOGNITION.** This species most closely resembles *A. atrimarginatus* but has a less darkened posterior margin of the ovipositor. Females of *A. incomptus* (Fig. 28) are somewhat similar but lack the long, filament-like process on the ventral apex of the ovipositor.

**DESCRIPTION.** Body length 1.0–1.8 mm. Frons light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.51 wing length; range 0.49–0.53. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 36–37) slightly upturned apically, lightly sclerotized, but with darker apical area. Lateral darkening not differentiated; apical region dark, with small, lateral incision. Apicodorsal margin of ovipositor pointed. Apicoventral margin of ovipositor drawn out into extremely long, thin, pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

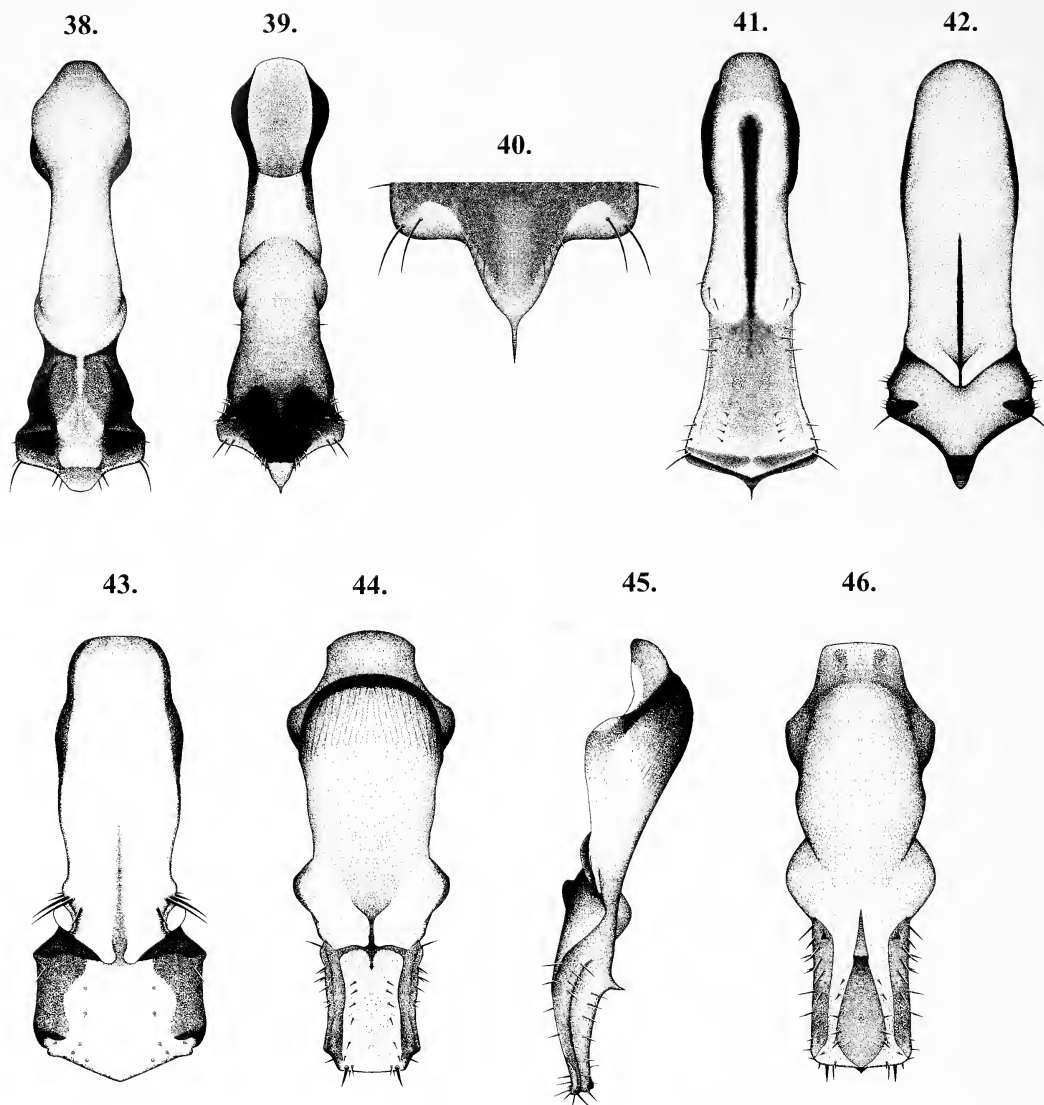
**GEOGRAPHICAL DISTRIBUTION.** Known only from Barro Colorado Island, Panama.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for shovel, referring to the shape of the ovipositor.

**HOLOTYPE.** ♀, PANAMA: Canal Zone: Barro Colorado Island, 9.15°N, 79.85°W, 10–17.iii.1993, J. Pickering, Malaise trap #957 [LACM ENT 094017] (LACM).

**PARATYPES.** PANAMA: Canal Zone: Barro Colorado Island, 9.15°N, 79.85°W, 1♀, 13–20.i.1993, Malaise trap, 3♀, 20–27.i.1993, Mal-



Figures 38–46. Ovipositors. Figures 38–40. *Apocephalus emargilatus* new species. 38. Dorsal. 39. Ventral. 40. Tip of ovipositor, ventral. 41. *Apocephalus magnicauda* new species, dorsal. 42. *Apocephalus triangularis* new species, dorsal. 43. *Apocephalus quadratus* Brown, dorsal. Figures 44–45. *Apocephalus acanthus* new species. 44. Dorsal. 45. Left lateral. 46. *Apocephalus spatulatus* Borgmeier, dorsal.

aise trap #736, 2♀, 24–31.iii.1993, Malaise trap, #959, 1♀, 4–11.viii.1993, Malaise trap #1670, 1♀, 6–13.iv.1994, Malaise trap #2419, 4♀, 20–27.iv.1994, Malaise trap #2421, J. Pickering (LACM, MCZC, MIUP, MZSP, USNM).

*Apocephalus emargilatus* new species  
(Figs. 38–40)

**SPECIES RECOGNITION.** This species can be recognized by the expanded proximal portion of the ovipositor and lateral emargination of the apical portion of the ovipositor.

**DESCRIPTION.** Body length 1.3–1.8 mm. Frons

yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair slightly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron white to light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur of even color anteriorly. Mean costal length 0.5 wing length; range 0.49–0.51. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite

3 evenly colored. Tergite 6 anteriorly and posteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row; lateral setae much shorter. Ovipositor (Figs. 38–39) slightly upturned apically, lightly sclerotized, but with darker apical area. Lateral darkening not differentiated; apical region dark, with transverse ridges and laterally emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process (Fig. 40). Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from two sites on the Osa Peninsula in Costa Rica.

**WAY OF LIFE.** One specimen was attracted to an injured worker of *Camponotus sericeiventris* (Guérin-Ménéville).

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the lateral emargination of ovipositor.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: Sirena, 8.48°N, 83.6°W, 1♀, 11.vii.1993, D. Feener, injured *Camponotus sericeiventris* [LACM ENT 024158] (LACM).

**PARATYPES.** COSTA RICA: Puntarenas, 3♀, Coopemarti, 8.63°N, 83.47°W, ii.1991, P. Hanson, Malaise trap (LACM).

### *Apocephalus magnicauda* new species

(Fig. 41)

**SPECIES RECOGNITION.** The ovipositor of this species is apically expanded, without lateral emarginations; otherwise it is similar to *A. emargilatus*.

**DESCRIPTION.** Body length 1.7–2.1 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron yellow to white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.52 wing length; range 0.51–0.53. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly and posteriorly emarginate, with setae of medium length along posterior margin. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row; lateral setae slender. Ovipositor

(Fig. 41) slightly upturned apically, lightly sclerotized, but with darker apical area. Lateral darkening not differentiated; apical region dark, posteriorly expanded. Apicodorsal margin of ovipositor pointed. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Amazonian Ecuador and Peru.

**WAY OF LIFE.** I collected two females that were flying above *Camponotus sericeiventris* attracted to a tuna fish bait. The ants were agitated, running around in a seeming panic response.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word *magnus*, for large, referring to the apically enlarged ovipositor.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°N, 76.5°W, 3–13.vi.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 027779] (LACM).

**PARATYPES.** ECUADOR: Sucumbios: Sacha Lodge, 0.5°N, 76.5°W, 2♀, 22.ii–4.iii.1994, 1♀, 13–23.iv.1994, 1♀, 13–25.vii.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ). PERU: Madre de Dios: Zona Reserva Manu, Pakitza, 11.95°S, 71.28°W, 2♀, 25.ii.1992, B. Brown, D. Feener, over baited *Camponotus sericeiventris* (LACM, MUSM).

### *Apocephalus triangularis* new species

(Fig. 42)

*Apocephalus fuscipalpis* Borgmeier, 1958:325, figs. 9–10, 13 (in part).

**SPECIES RECOGNITION.** This species is easily recognized by the triangular apex of the ovipositor and its distinctive dark markings and by the prominent, medial ridge.

Specimens of this species were among Borgmeier's paratypes of *A. fuscipalpis*.

**DESCRIPTION.** Body length 1.8 mm. Frons light brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.46 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with three long setae on posterior margin of each sclerite. Venter of segments 3–5 with small, dense setae medially. Abdomen without dense lateral setae.

Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 42) slightly upturned apically, lightly sclerotized, but with darker apical area and prominent, medial ridge. Lateral darkening not differentiated; much of apical region dark, triangular with lateral, darker patches. Apicodorsal margin of ovipositor pointed. Apicoventral margin of ovipositor drawn out into pointed process; process extremely long and heavily sclerotized. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from Brazil and Mexico.

**WAY OF LIFE.** Unknown.

**HOLOTYPE.** ♀, MEXICO: Chiapas: Montebello, vii.1969, W. Mason, Malaise trap (LACM).

**PARATYPE.** BRAZIL: Nova Teutônia, 1 ♀, xi.1958, F. Plaumann (MCZC).

*Apocephalus quadratus* Brown  
(Fig. 43)

*Apocephalus quadratus* Brown, 1997b:47–48, fig. 67.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 12–22.ii.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 006850] (LACM; examined).

**SPECIES RECOGNITION.** This species has an extremely distinctive ovipositor, with a broad apical region and with large, dark, heavily sculpted lateral darkenings. There is a medial ridge with a low prominence or spine at midlength.

I considered this a species of the *A. attophilus*-group (Brown, 1997b) before my more precise definition of the *A. miricauda*-group was formulated.

**DESCRIPTION.** See Brown, 1997b.

**GEOGRAPHICAL DISTRIBUTION.** Ecuador, Brazil.

**WAY OF LIFE.** Unknown.

**NEW MATERIAL EXAMINED.** BRAZIL: Minas Gerais: Belo Horizonte, Estação Ecológica, UFMG campus, 1 ♀, 12–15.vii.1993, S. Gaimari, Malaise trap, 800 m (BHMH).

*Apocephalus acanthus* new species  
(Figs. 44–45)

**SPECIES RECOGNITION.** This species, like *A. spatulatus*, has an ovipositor with a dorsal spine and distinctive lateral darkenings. The ovipositor of *A. acanthus* differs in many small ways, however, the most easily qualified being in the apex of the ovipositor, which is obliquely truncate.

**DESCRIPTION.** Body length 1.4 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow to

light brown. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.5 wing length; range 0.49–0.50. Wing vein  $R_{2+3}$  present. Halter mostly yellow, but with dark brown spot on knob. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with a pair of large, posterior setae. Venter of segments 3–5 with small, dense setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row, but lateral setae shorter. Ovipositor (Figs. 44–45) slightly upturned apically, lightly sclerotized, but with darker apical area; dorsally with medial spine. Lateral darkening thin, subparallel, margin dark, complete. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight, laterally with oblique truncation. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from two lowland sites in Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is from a Greek word for spine, referring to the mid-dorsal spine of the ovipositor.

**HOLOTYPE.** COSTA RICA: Puntarenas: 3 km SW Rincon, 8.68°N, 83.48°W, viii.1991, P. Hanson, Malaise trap, 10 m [LACM ENT 048759] (LACM).

**PARATYPE.** COSTA RICA: Guanacaste: Al Taboga Forest Reserve, 9 km SW Cañas, 1 ♀, 17–27.ii.1987, W.L. Rubink, Malaise trap (EMUS).

*Apocephalus spatulatus* Borgmeier  
(Fig. 46)

*Apocephalus spatulatus* Borgmeier, 1958:322, figs. 7, 12.

**HOLOTYPE.** ♀, BRAZIL: Santa Catarina: Nova Teutônia, F. Plaumann [LACM ENT 061158] (MZSP; examined).

**SPECIES RECOGNITION.** This species, like the preceding one, has a distinctive dorsal spine on the ovipositor. Unlike *A. acanthus*, however, *A. spatulatus* has the posterior corners of the apex of the ovipositor squared, not obliquely truncate (Fig. 46).

**DESCRIPTION.** The single specimen of this species apparently was air-dried and has not retained its natural color. Some references to color were therefore made by referring to the original description.

Body length 1.8 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal

setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax yellow; pleuron yellow. Anterior scutellar seta small, fine, slightly larger than posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.45 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, yellow medially and anteriorly, tergite 6 yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with several long setae on posterior margin. Venter of segments 3–5 with small, dense setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 46) slightly upturned apically, with dark anterior and lighter posterior sclerotization; dorsally with medial spine. Lateral darkening thin, subparallel, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 not differentiated but anteriorly encircling segment. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Brazil.

**WAY OF LIFE.** Unknown.

### *Apocephalus miricauda*-subgroup

**DIAGNOSIS.** Ovipositor strongly bent dorsally at midlength.

**PHYLOGENETIC RELATIONSHIPS.** Unknown.

**WAY OF LIFE.** Two species are known to attack injured ants of the genus *Dinoponera* Roger. The other two species, *A. flexus* and *A. orbiculus*, occur outside the published distribution of *Dinoponera* species (Kempf, 1971) and must use different hosts.

### *Apocephalus miricauda* Borgmeier

(Figs. 47–49)

*Apocephalus miricauda* Borgmeier 1971:111; figs. 150–152.

**HOLOTYPE.** ♀, BRAZIL: Pará: Utinga, xii.1966, S.J. de Oliveira (MZSP; examined).

**SPECIES RECOGNITION.** This species can be recognized by the curved ovipositor in lateral view (Fig. 49) and the extremely expanded sternite 7, which is visible projecting laterally from above (Fig. 47).

**DESCRIPTION.** Body length 2.4–2.9 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow.

Dorsum of thorax yellow; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellow; apex of hind femur of even color anteriorly. Mean costal length 0.54 wing length; range 0.53–0.55. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, lighter medially. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly and posteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 short, consisting of single median pair. Ovipositor (Figs. 47–49) deflected dorsally posterior to midpoint, with triangular median sclerite. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor triangular. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular, apically flared with small lateral projections. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

**GEOGRAPHICAL DISTRIBUTION.** Known only from Brazil. The host ant is known from Brazil and Peru (Kempf, 1971).

**WAY OF LIFE.** The life history of this species was described by Silveira-Costa and Moutinho (1996), who found that it was attracted to injured workers of *Dinoponera gigantea* (Perty).

**PHYLOGENETIC RELATIONSHIPS.** This species and *A. kungae* new species are hypothesized to be sister-species, based on the enlarged, broadened sternite 7 with particularly distinct fringes of lateral processes.

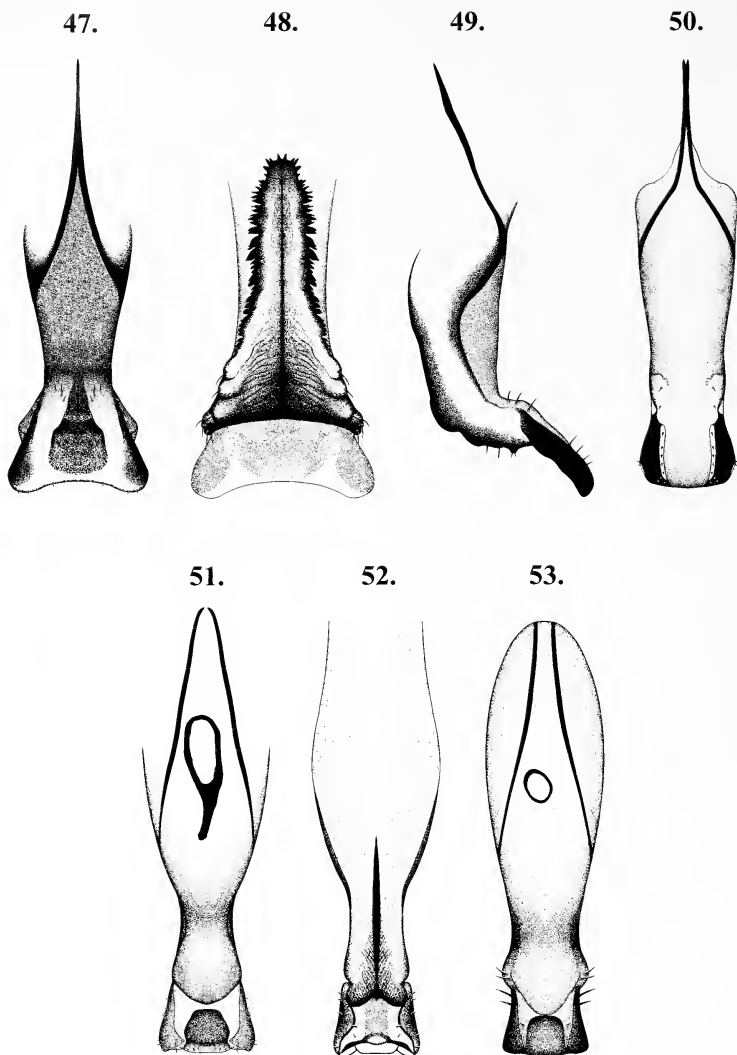
**MATERIAL EXAMINED.** BRAZIL: Pará: Paragominas, 2.92°S, 47.58°W, 1♀, v.1994, 3♀, 10.v.1995, A. Silveira-Costa, injured *Dinoponera gigantea* (LACM).

### *Apocephalus kungae* new species

(Figs. 50, 108)

**SPECIES RECOGNITION.** This species differs from the others in this group by the extremely broad area of medium sclerotization between the lateral darkenings of the ovipositor (Fig. 50). It is similar in many respects to *A. dinoponerae* new species, with which it was collected, but *A. dinoponerae* does not have a dorsally flexed ovipositor and its sternite 7 is of a different form.

**DESCRIPTION.** Body length 1.9 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white to light brown. Anterior scutellar seta large, bristle-like. Legs yellowish-brown; apex of hind femur with abrupt, but small, darkening on anterior face. Mean costal length 0.56 wing length. Wing vein



Figures 47-53. Ovipositors. Figures 47-49. *Apocephalus miricauda* Borgmeier. 47. Dorsal. 48. Ventral. 49. Left lateral. 50. *Apocephalus kungae* new species, dorsal. Figures 51-52. *Apocephalus flexus* new species. 51. Dorsal (showing internal, sclerotized loop). 52. Ventral. 53. *Apocephalus orbiculus* new species, dorsal (showing internal, sclerotized loop).

$R_{2+3}$  present. Halter brown. Abdominal tergites yellowish-brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3-5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 50) deflected dorsally at midpoint, lightly but evenly sclerotized dorsally. Lateral darkening apically convergent and lighter in color, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor rounded. Ovipositor without ventral postapical sclerite. Sternite 7 triangular, apically flared with small lateral projec-

tions. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop (Fig. 108).

**GEOGRAPHICAL DISTRIBUTION.** Known only from southeastern Colombia. The host ant is known from Brazil and Peru (Kempf, 1971).

**WAY OF LIFE.** An injured worker of *Dinoponera longipes* Emery attracted this fly.

**PHYLOGENETIC RELATIONSHIPS.** See *A. miricauda*.

**DERIVATION OF SPECIFIC EPITHET.** This species is named after Ms. Giar-Ann Kung, who helped me study its way of life and collect the holotype.

**HOLOTYPE.** ♀, COLOMBIA: Amazonas: Amacayacu National Park, 3.82°S, 70.26°W,

5.ix.1997, B. Brown, G. Kung, injured *Dinoponera longipes* [LACM ENT 102143] (UNCB).

### *Apocephalus flexus* new species

(Figs. 51–52, 107)

**SPECIES RECOGNITION.** This species is extremely similar to *A. orbiculus* but differs in having a much larger sclerotized loop (compare Figs. 51 and 53).

**DESCRIPTION.** Body length 1.5 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with a pair of large, posterior setae. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Figs. 51–52) deflected dorsally posterior to midpoint, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor rounded anteriorly. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, with long process (Fig. 107).

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in western Ecuador.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for bend, referring to the ovipositor, which is curved dorsally in lateral view.

**HOLOTYPE.** ♀, ECUADOR: Pichincha: 17 km E Santo Domingo, Tinalandia, 6–13.v.1987, B. Brown, windows, 710 m [LACM ENT 012773] (LACM).

### *Apocephalus orbiculus* new species

(Fig. 53)

**SPECIES RECOGNITION.** This species is extremely similar to *A. flexus* but has a slightly different preapical sclerite and a much smaller sclerotized loop (compare Figs. 51 and 53).

**DESCRIPTION.** Body length 1.3 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, oval. Proboscis normal, small. Palpus light brown. Dorsum of thorax light brown; pleuron yellowish brown. Anterior scutellar seta large, bristle-like. Legs yellowish-brown; apex

of hind femur with abrupt darkening on anterior face. Mean costal length 0.44 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, divided, with short setae at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 53) deflected dorsally at midpoint, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor rectangular. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite small, round.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single lowland site in Costa Rica.

**WAY OF LIFE.** Unknown. Almost all of the Malaise trap captures were from a single site (trap 12).

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for small circle, referring to the sclerotized loop, which is much smaller than that of the similar *A. flexus*.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 3.v.1993, ALAS, Malaise trap M/12/91 [INBI-OCRI002273758] (INBC).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1♀, 16.iii.1993, ALAS, Malaise trap M/12/43, 1♀, 2.iv.1993, ALAS, Malaise trap M/12/59, 1♀, 3.v.1993, ALAS, Malaise trap M/12/91, 3♀, 19.v.1993, ALAS, Malaise trap M/12/006, 1♀, 4.iv.1994, ALAS, Malaise trap M/09/387, 1♀, 17.xi.1998, ALAS, light L/08/513 (INBC, LACM).

### *A. meniscus*-subgroup

**DIAGNOSIS.** Dorsomedial preapical sclerite of ovipositor attached to lateral darkenings by distinctive bar of sclerotization; in most species, lateral postapical sclerites present.

**PHYLOGENETIC RELATIONSHIPS.** The relationships within this group are not resolved.

Although it is divergent in structure from all other *A. miricauda*-group species, *A. lopesi* (Borgmeier) clearly belongs in this group. It has the postapical sclerites present but has apparently lost the dorsal preapical sclerite.

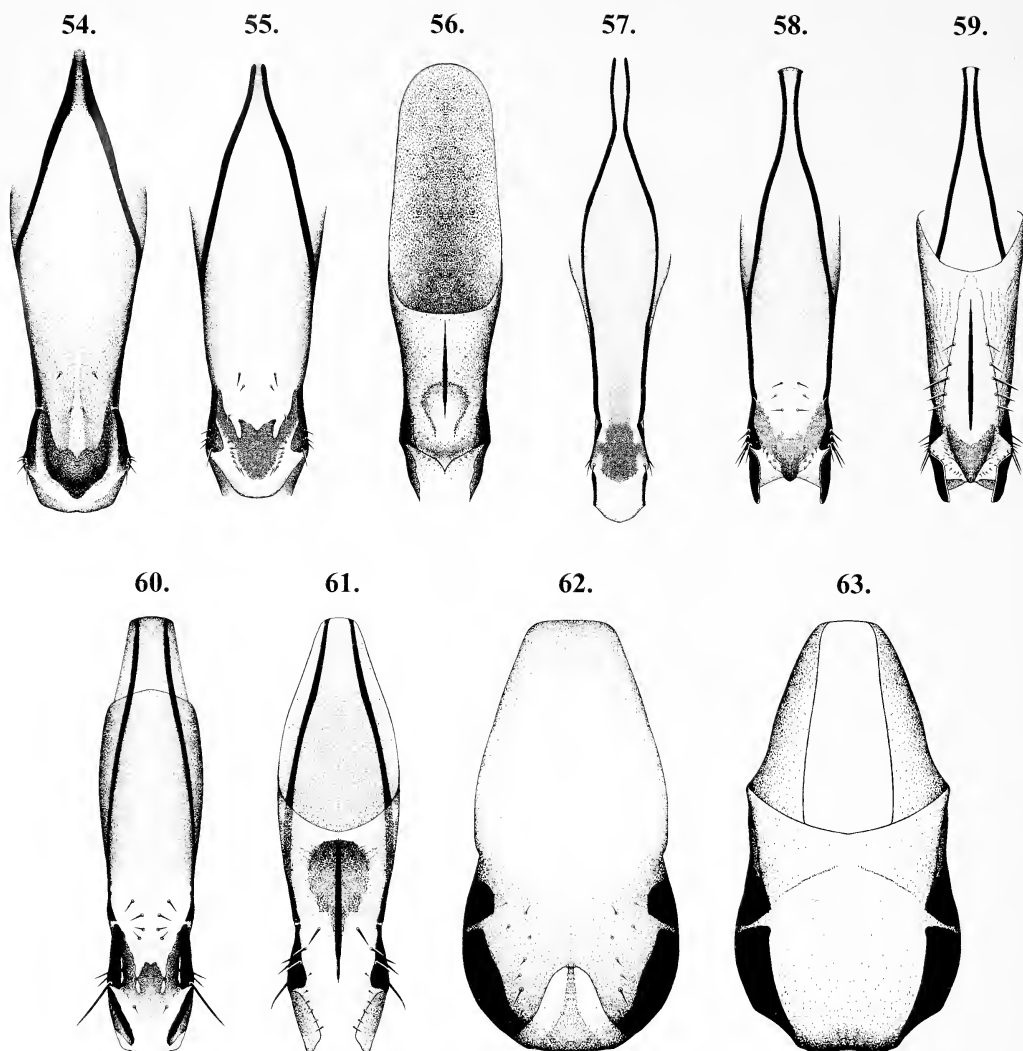
**WAY OF LIFE.** The two species with known hosts are parasitoids of injured ants of the genus *Odontomachus* Latreille.

### *Apocephalus meniscus* new species

(Fig. 54)

**SPECIES RECOGNITION.** This species can be recognized by the long, dense ventral setae and the





Figures 54–63. Ovipositors. 54. *Apocephalus meniscus* new species, dorsal. Figures 55–56. *Apocephalus barbiventris* new species. 55. Dorsal. 56. Ventral. 57. *Apocephalus amplidiscus* new species, dorsal. Figures 58–59. *Apocephalus paldiae* new species. 58. Dorsal. 59. Ventral. Figures 60–61. *Apocephalus cycloclidiscus* new species. 60. Dorsal. 61. Ventral. Figures 62–63. *Apocephalus lopesi* (Borgmeier). 62. Dorsal. 63. Ventral.

preapical sclerite that does not markedly extend anterior to the lateral bars of sclerotization.

**DESCRIPTION.** Body length 1.1–1.3 mm. Frons yellow to light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.49 wing length; range no range. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at

posterolateral corner. Venter of segments 3–5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 54) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening thin, subparallel, margin dark, complete. Dorsoapical sclerite of ovipositor trapezoidal. Apicodorsal margin of ovipositor straight. Apicoven-tral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from Pakitz, Peru.



**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Greek word *meniskos* for crescent, referring to the shape formed by the preapical sclerite and the lateral bars of the ovipositor.

**HOLOTYPE.** ♀, PERU: Madre de Dios, Zona Reserva Manu, Pakitza, 11.95°S, 71.28°W, 13–18.ii.1992, B. Brown, D. Feener, Malaise trap #1 [LACM ENT 012211] (MUSM).

**PARATYPE.** 1♀, same data as holotype (LACM).

### *Apocephalus barbiventris* new species

(Figs. 55–56)

**SPECIES RECOGNITION.** This species is also densely setose ventrally, similar to *A. meniscus*, but has a preapical sclerite that is shaped differently, projecting farther anteriorly on the ovipositor. It also has lateral postapical sclerites, which are lacking in *A. meniscus*.

**DESCRIPTION.** Body length 1.2–1.4 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax yellow; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum (slightly larger). Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.48 wing length; range 0.47–0.5. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 with long, dense setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 55–56) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsal apical sclerite of ovipositor rectangular, anteriorly emarginate; with lateral bars extended to anterior apex of lateral darkenings. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 thin, with lighter, expanded area at midlength. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a few sites on the Osa Peninsula in Costa Rica.

**WAY OF LIFE.** One female was attracted to injured *Odontomachus bauri*.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *barba* and *ven-*

*tris*, for beard and belly, referring to the setose venter of the abdomen.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: 24 km W Piedras Blancas, 8.77°N, 83.4°W, ii.1992, P. Hanson, Malaise trap, 200 m [LACM ENT 012698] (LACM).

**PARATYPES.** COSTA RICA: Puntarenas: 10 km W Piedras Blancas, 8.75°N, 83.3°W, 2♀, iii–v.1989, P. Hanson, Malaise trap (INBC, LACM), 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♀, ii.1992, P. Hanson, Malaise trap, 200 m (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 1♀, ii–iii.1989, 1♀, iii.1989, 1♀, iii–iv.1991, P. Hanson, Malaise trap, 10 m (LACM, MUCR), 5 km SW Rincon, 8.7°N, 83.51°W, 1♀, 4.vi.1998, B. Brown, injured *Odontomachus bauri* (LACM).

### *Apocephalus amplidiscus* new species

(Fig. 57)

**SPECIES RECOGNITION.** This species has a distinctive large preapical sclerite that fills most of the space between the lateral darkenings.

**DESCRIPTION.** Body length 1.4 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.48 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 57) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening thin, subparallel, margin dark, with separate apical sclerite. Dorsal apical sclerite of ovipositor large, round, dark, shiny. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, small, with a short process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single lowland site in Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *amplus* and *discus*, for large and plate, referring to the large preapical sclerite of this species.

**HOLOTYPE.** ♀, COSTA RICA: Limon: 7 km SW Bribri, 9.58°N, 82.88°W, xii.1989–ii.1990, P.

Hanson, Malaise trap, 50 m [LACM ENT 047431] (LACM).

*Apocephalus paldiae* new species

(Figs. 58–59)

**SPECIES RECOGNITION.** This species is similar to *A. barbiiventris*, but the ventral setae of the abdomen are much shorter and fewer.

**DESCRIPTION.** Body length 1.3–1.9 mm. Frons yellow to light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 basally yellow, apically brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax yellow; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length; range 0.45–0.51. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 58–59) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, with separate apical sclerite. Dorsoapical sclerite of ovipositor heart-shaped; with lateral bars extended to anterior apex of lateral darkenings. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in northern Costa Rica.

**WAY OF LIFE.** These flies are attracted to, and oviposit in, injured workers of *Odontomachus chelifer* (Latreille). Pairs of flies arrive in copula, but the male immediately departs when they land near an injured ant. Both egg-layers and feeders were observed in this species. A single egg ( $n = 6$ ), or in one instance two eggs, are laid in the abdomen, and newly hatched larvae apparently migrate internally through the ant's body to the head, where feeding takes place. Larval feeding ended after  $\bar{x} = 4.75$  days ( $n = 4; 4, 3, 6, 6$  days).

**DERIVATION OF SPECIFIC EPITHET.** This species is named after Ms. Jill Paldi, who helped me study its way of life and collect the type series.

**HOLOTYPE.** ♀, COSTA RICA: Guanacaste: Estación Pitilla, 11.0°N, 85.43°W, 5.vii.1997, J. Paldi, injured *Odontomachus chelifer* [LACM ENT 101744] (LACM).

**PARATYPES.** COSTA RICA: Guanacaste: Estación Biología Pitilla, 11.0°N, 85.43°W, 2♀,

3.vii.1997, 1♂, 13♀, 4.vii.1997, 9♀, 5.vii.1997, B. Brown, J. Paldi, injured *Odontomachus chelifer* (INBC, LACM, MCZC, MUCR, USNM).

*Apocephalus cyclodiscus* new species

(Figs. 60–61)

**SPECIES RECOGNITION.** This species has a distinctive ventral sclerite on segment 7, being expanded and rounded anteriorly, then narrowed posteriorly (Fig. 61).

**DESCRIPTION.** Body length 1.2–1.4 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow to white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.46 wing length; range 0.45–0.47. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with long seta at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Figs. 60–61) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening thin, subparallel, apically divergent, margin dark, with separate apical sclerite. Dorsoapical sclerite of ovipositor rectangular, anteriorly emarginate; with lateral bars extended to anterior apex of lateral darkenings. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 anteriorly rounded, dark; posteriorly narrow. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from two sites in Panama.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on two Latin words, *cyclos* for round and *discus* for plate, referring to the shape of sternite 7.

**HOLOTYPE.** ♀, PANAMA: San Blas: Nusagandi Reserve, 9.33°N, 79.0°W, 16–23.iv.1994, J. Pickering, Malaise trap #2862 [LACM ENT 101530] (LACM).

**PARATYPES.** PANAMA: Canal Zone: Barro Colorado Island, 9.17°N, 79.83°W, 1♀, 17–24.ii.1993, 1♀, 24–31.iii.1993, J. Pickering, Malaise trap #740, #959 (LACM); San Blas: Nusagandi Reserve, 9.33°N, 79.0°W, 1♀, 5–12.ii.1994, J. Pickering, Malaise trap #2042 (MIUP).

*Apocephalus lopesi* (Borgmeier)

(Figs. 62–63, 104)

*Anaclinus lopesi* Borgmeier, 1969:64–65, figs. 35–37; 1971:5–6, fig. 6, new combination.

**HOLOTYPE.** ♀, BRAZIL: Pará: Belém, vii.1965, H.S. Lopes (MZSP; examined).

**SPECIES RECOGNITION.** This species is extremely distinctive, with the reclinate supra-antennal setae on the unusually modified frons (in both sexes) and the characteristic broad ovipositor. It was previously considered to belong in a separate genus.

**DESCRIPTION.** Body length 1.5 mm. Frons yellow, anterior margin produced between antennae (Fig. 104). One pair of divergent, reclinate supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 62–63) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly narrowed, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor wedge-shaped, posteriorly widened. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 round. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from lowland sites in Brazil, Colombia, Costa Rica, and Guyana.

**WAY OF LIFE.** Females were attracted to crushed workers of *Odontomachus haematodus* (Linnaeus), the presumed host, in Colombia and Guyana. This ant, whose taxonomic history is particularly convoluted (Brown, 1976), apparently occurs only in Amazonian South America. Therefore, *A. lopesi* must attack another host in Costa Rica.

**MATERIAL EXAMINED.** BRAZIL: Pará: Uttinga, near Belém, 1♂, 1♀, xii.1966, Malaise trap, S.J. de Oliveira (MZSP). COLOMBIA: Amazonas: Amacayacu National Park, 3.82°S, 70.26°W, 1♀, 4.ix.1997, B. Brown, G. Kung, injured *Odontomachus haematodus* (LACM). COSTA RICA: Limon: 16 km W Guapiles, 10.15°N, 83.92°W, 1♀, ii.1989, P. Hanson, Malaise trap, 400 m (LACM); Puntarenas: Cerro Rincon, 8.52°N, 83.47°W, 1♀,

iii.1991, P. Hanson, Malaise trap, 745 m [LACM ENT 017042] (LACM). GUYANA: Berbice: Dubulay Ranch, 5.68°N, 57.86°W, 3♂, 17–22.i.1999, B. Brown, M. Sharkey, Malaise trap #10, #12, #14 (LACM), 4♀, 18.i.1999, B. Brown, injured *O. haematodus* (LACM, UGGG).

*Apocephalus funditus*-subgroup

**DIAGNOSIS.** Setation of dorsum of abdomen short, bristle-like. Ovipositor unusually darkly sclerotized throughout; strongly downturned at midlength.

**PHYLOGENETIC RELATIONSHIPS.** All three of the diagnostic characters are potential synapomorphies of a clade including these two species.

*Apocephalus funditus* new species

(Fig. 64–65)

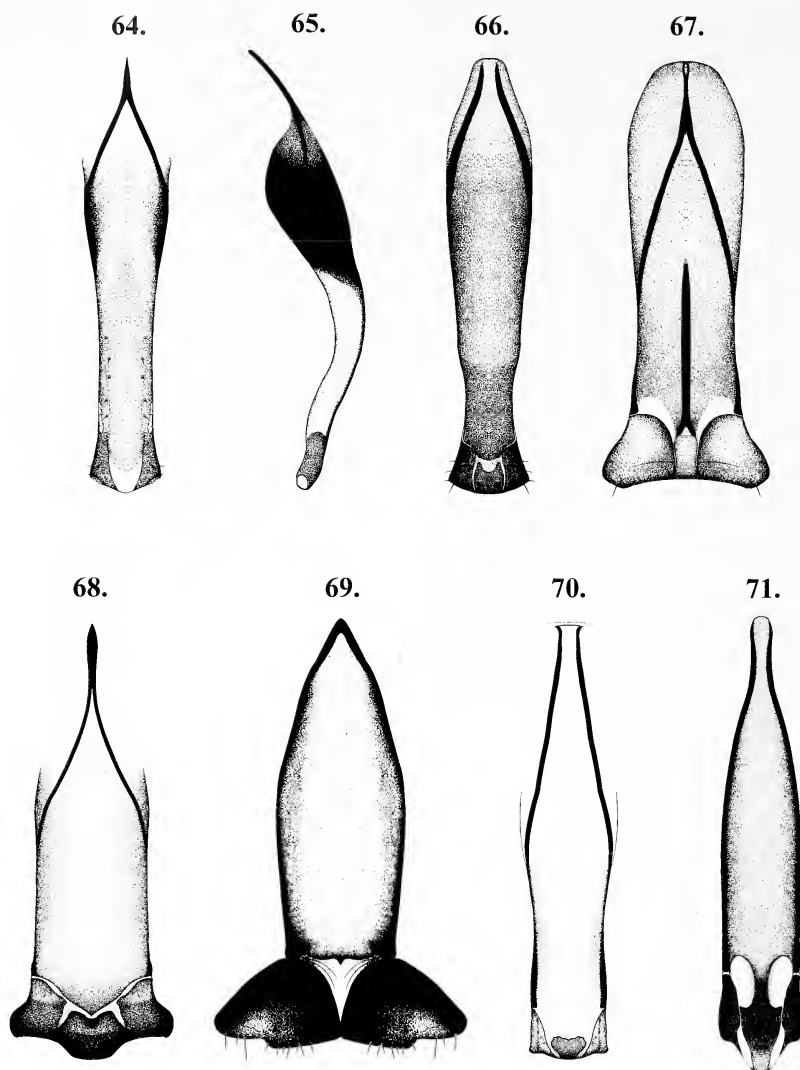
**SPECIES RECOGNITION.** This species has extensive sclerotization, with all sclerotized portions of the ovipositor appearing shiny, dark brown. Unlike *A. intonsus* new species, it lacks a separate preapical sclerite.

**DESCRIPTION.** Body length 1.4–1.6 mm. Frons yellow to light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow to light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.44 wing length; range 0.4–0.46. Wing vein  $R_{2+3}$  present. Halter light brown to brown. Abdominal tergites dark brown (yellowish brown in one Costa Rican specimen). Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 65) deflected ventrally at midpoint, darkly sclerotized, with sclerotization extended completely to posterior apex. Lateral darkening posteriorly enlarged, inner margin extended medially, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor rounded. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 broad, narrowed apically but widened abruptly at apex. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from Brazil, Costa Rica, Ecuador, and Peru.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for complete or wholly, re-



Figures 64–71. Ovipositors. Figures 64–65. *Apocephalus funditus* new species. 64. Dorsal. 65. Left lateral. 66. *Apocephalus intonsus* new species, dorsal. 67. *Apocephalus spatulicauda* Borgmeier, dorsal. 68. *Apocephalus inimicus* Borgmeier, dorsal. 69. *Apocephalus brevifrons* new species, dorsal. 70. *Apocephalus densepilosus* Borgmeier, dorsal. 71. *Apocephalus comosus* new species, dorsal.

ferring to the extensive, dark sclerotization of the ovipositor.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: 24 km W Piedras Blancas, 8.77°N, 83.4°W, ii.1992, P. Hanson, Malaise trap, 200 m [LACM ENT 012697] (LACM).

**PARATYPES.** BRAZIL: Roraima: Ilha de Maracá, 3.37°N, 61.43°W, 5 ♀, 2–13.v.1987, J. Rafael, Malaise trap (INPA, LACM). COSTA RICA: 1 ♀, same data as holotype. ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1 ♀, 12–22.ii.1994, 1 ♀, 24.iii–3.iv.1994, 2 ♀, 21–31.x.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ). PERU: Madre de Dios, Zona Reserva Manu, Pakitza, 11.95°S, 71.28°W, 1 ♀, 7–9.iii.1992, R. Cambra, Malaise trap (LACM).

### *Apocephalus intonsus* new species (Figs. 66)

**SPECIES RECOGNITION.** The similarities of this species to *A. funditus* are discussed above. It is also similar to *A. indistinctus* new species, except that the ovipositor is downturned sharply at mid-length.

**DESCRIPTION.** Body length 1.1–1.3 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with

abrupt darkening on anterior face. Mean costal length 0.44 wing length; range 0.42–0.45. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, with short, bristly setae. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 with few, medial setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 66) deflected ventrally at midpoint, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, inner margin extended medially (slightly), margin dark, complete. Dorsal apical sclerite of ovipositor rectangular, anteriorly emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 broadly, evenly developed across entire venter of ovipositor. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Panama.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for unshaven referring to the short, bristly setae of the tergites.

**HOLOTYPE.** ♀, PANAMA: Canal Zone: Barro Colorado Island, 9.17°N, 79.83°W, 11–18.v.1994, J. Pickering, Malaise trap #2424 [LACM ENT 093710] (LACM).

**PARATYPES.** PANAMA: Canal Zone: Barro Colorado Island, 9.17°N, 79.83°W, 1♀, 10–17.iii.1993, 1♀, 6–13.iv.1994, 1♀, 15–22.vi.1994, J. Pickering, Malaise trap #957, #2419, #2384 (LACM, MIUP).

#### *A. spatulicauda*-subgroup

**DIAGNOSIS.** Frons short. Ovipositor with distinctive line across lateral darkenings, indicating abrupt downturn of direction. Lateral darkenings broad. Ventral apex of ovipositor with dark, heavily sclerotized, transverse sclerite.

**PHYLOGENETIC RELATIONSHIPS.** The characters in the diagnosis are all potential synapomorphies of the group. The relationships among the three species are not resolved.

**WAY OF LIFE.** Unknown.

#### *Apocephalus spatulicauda* Borgmeier (Fig. 67)

*Apocephalus spatulicauda* Borgmeier, 1961:45, figs. 64, 73, 85.

**HOLOTYPE.** ♀, BRAZIL: Rio de Janeiro: Petropolis, 15.vi.1923, T. Borgmeier [LACM ENT 122183] (MZSP; examined).

**SPECIES RECOGNITION.** This species has a distinct ovipositor, with broad lateral darkenings and a narrow preapical sclerite.

**DESCRIPTION.** Unfortunately, the unique female holotype was heavily damaged in the mail. Little remains except the abdomen, so the following description is fragmentary and based in part on the original description of the species.

Body length 1.5 mm. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Mean costal length 0.44 wing length. Halter yellow. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ovipositor (Fig. 67) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened, with apical concavity, margin dark, complete. Dorsal apical sclerite of ovipositor elongate, anteriorly emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded and with short, broad, black, apical darkening. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in southeastern Brazil.

**WAY OF LIFE.** Unknown.

#### *Apocephalus inimicus* Borgmeier (Fig. 68)

*Apocephalus inimicus* Borgmeier, 1961:42, fig. 63.

**HOLOTYPE.** ♀, BRAZIL: Santa Catarina: Nova Teutônia, vii.1952, F. Plaumann, with *Labidus coecus* [LACM ENT 122468] (MZSP; examined).

**SPECIES RECOGNITION.** This species has broad lateral darkenings and an extremely broad, heavily sclerotized preapical sclerite.

**DESCRIPTION.** Body length 1.3–1.4 mm. Frons light brown (bleached from alcohol), anterior margin relatively straight, frons short. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair, greatly reduced. Flagellomere 1 brown, oval. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.42 wing length; range 0.42–0.43. Wing vein  $R_{2+3}$  present. Halter light brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with a few, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 68) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened,

with apical concavity, margin dark, complete. Dorsal apical sclerite of ovipositor rectangular, anteriorly emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded and with short, broad, black apical darkening. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in southeastern Brazil.

**WAY OF LIFE.** Although the type specimens were collected with army ants, the host of this species is unknown.

**OTHER MATERIAL EXAMINED.** Paratype ♂, ♀, same data as holotype (MZSP).

### *Apocephalus brevifrons* new species

(Figs. 69, 105)

**SPECIES RECOGNITION.** This species is easily recognized by the extremely enlarged lateral darkenings of the ovipositor, the lack of wing vein  $R_{2+3}$ , and the lack of lower fronto-orbital setae.

**DESCRIPTION.** Body length 1.3–1.4 mm. Frons (Fig. 105) light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, oval (slightly pointed in the male, shown in Fig. 105). Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.46 wing length; range 0.43–0.49, slightly thickened. Wing vein  $R_{2+3}$  absent. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with setae of medium length along posterior margin. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 69) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened, with apical concavity, margin dark, complete. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor pointed. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded and with short, broad, black apical darkening. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

**GEOGRAPHICAL DISTRIBUTION.** Known from mid-elevation sites in Mexico and Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** This species is named for the short frons.

**HOLOTYPE.** ♀, COSTA RICA: San José: Zurquí de Moravia, 10.05°N, 84.02°W, ix–x.1993, P. Hanson, Malaise trap, 1600 m [LACM ENT 014242] (LACM).

**PARATYPES.** MEXICO: Chiapas: Montebello, 1♀, 16.12°N, 91.67°W, 19.vi.1969 (LACM). COSTA RICA: Puntarenas: Monteverde Biological Station, 10.32°N, 84.8°W, 1♂, 25–28.v.1998, B. Brown, V. Berezovskiy, Malaise trap #4, 1500 m (LACM); San José: Zurquí de Moravia, 10.05°N, 84.02°W, 1♂, ii.1989, 1♀, iii.1989, 1♂, 1♀, x–xii.1990, 1♂, 1♀, i.1991, 2♂, iii.1992, 1♀, v.1992, 5♂, vi.1992, 10♂, 3♀, vii.1992, 3♂, iv–v.1993, 12♂, 1♀, 1–15.vi.1993, 9♂, 5♀, ix–x.1993, 5♂, 1♀, ii.1994, 6♂, 3♀, iii.1994, 3♂, 1♀, iv.1994, 4♂, v.1994, 3♂, i.1996, P. Hanson, Malaise trap (INBC, LACM, MCZC, MUCR, MZSP, USNM).

### Other Taxa (subgroup unknown)

#### *Apocephalus densepilosus* Borgmeier

(Figs. 70, 112)

*Apocephalus densepilosus* Borgmeier, 1971:110, figs. 147–148.

**HOLOTYPE.** ♀, BRAZIL: Pará: Utinga, xii.1966, S.J. de Oliveira [LACM ENT 049341] (MZSP; examined).

**SPECIES RECOGNITION.** This species has distinctive extremely dense setation laterally on abdominal segments 4 and 5, unlike other species that have none at all on segment 4 and usually segment 5.

**DESCRIPTION.** Body length 1.5–2.1 mm. Frons yellow, anterior margin relatively straight. One or two pairs of supra-antennal setae present; lower pair smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.55 wing length; range 0.53–0.56. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly and posteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 with few, medial setae. Abdomen with dense lateral setae on segments 4 and 5 (Fig. 112). Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 70) slightly downturned apically, with broad median sclerite. Lateral darkening thin, subparallel, margin dark, complete. Dorsal apical sclerite of ovipositor heart-shaped. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white,

inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from Brazil, Colombia, Ecuador, and Peru. The host ant has also been recorded from French Guiana, Trinidad, and Venezuela.

**WAY OF LIFE.** Females are attracted to injured workers of the presumed host species, *Pachycondyla crassinoda* (Latreille).

**MATERIAL EXAMINED.** BRAZIL: Roraima: Ilha de Maracá, 3.37°N, 61.43°W, 2♀, 2-13.v.1987, J. Rafael, Malaise trap (INPA, LACM). COLOMBIA: Amazonas: 7 km W Leticia, 4.13°S, 69.9°W, 1♀, 26.viii.1997, B. Brown, G. Kung, injured *Pachycondyla crassinoda* (LACM). ECUADOR: Napo: Yasuni Biological Research Station, 0.67°S, 76.36°W, 1♀, 24.v.1996, B. Brown, injured *P. crassinoda* (LACM); Sucumbios: Añagu, 0.48°S, 76.38°W, 1♀, 9.ix.1997, P. DeVries, injured *P. crassinoda* (LACM), Sacha Lodge, 0.5°S, 76.5°W, 1♀, 14-24.iii.1994, 1♀, 14-24.v.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ). PERU: Madre de Dios, Zona Reserva Pakitzta, 11.94°S, 71.28°W, 1♀, 14.ii.1992, 1♀, 27.ii.1992, B. Brown, D. Feener, injured *P. crassinoda* (MUSM, USNM).

### *Apocephalus comosus* new species

(Figs. 71, 113)

**SPECIES RECOGNITION.** This species is easily recognized by the lateral group of setae on abdominal segment 5 and the distinctive shape of the preapical sclerite.

**DESCRIPTION.** Body length 1.8-2.5 mm. Frons yellow to dark brown, anterior margin produced between antennae. One pair of supra-antennal setae present. Flagellomere 1 yellow to light brown, round. Proboscis elongate; anterior margin of frons produced anteriorly. Palpus brown. Dorsum of thorax light brown; pleuron white, strongly and sharply contrasting with scutum. Anterior scutellar seta slightly enlarged, bristle-like. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.58 wing length; range 0.55-0.61. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites 2 extremely short; 3-5 elongate in compensation. Tergite 3 dark, with round, yellow spot laterally. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3-5 bare. Abdomen with patch of long, dense lateral setae on a small evagination on segment 6 (Fig. 113). Ventral setae of segment 6 long, consisting of single median pair. Ovipositor (Fig. 71) slightly upturned apically, evenly sclerotized, with long, thin, posteromedial process dorsally. Lateral darkening thin, subparallel, margin dark, complete. Dorsal apical sclerite of ovipositor spade-shaped. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor rounded. Ovipositor without ventral

postapical sclerite. Sternite 7 broad, with pointed, mediolateral projection. Dufour's mechanism round. Abdominal glands in segment 5 dark, enlarged, elongate, clearly visible in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** This species is widely distributed in the lowlands throughout the Neotropical Region, from southern Mexico to Ecuador.

**WAY OF LIFE.** One female of this species was attracted to injured *Ectatomma tuberculatum* workers; one was attracted to an injured *Odontomachus laticeps*. The actual host ant of this relatively commonly collected species is still unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for hairy, referring to the highly setose abdomen.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: 3 km SW Rincon, 8.68°N, 83.48°W, iii-v.1991, P. Hanson, Malaise trap, 10 m [LACM ENT 012879] (LACM).

**PARATYPES.** COSTA RICA: Alajuela: San Pedro de la Tigua, 10.37°N, 84.57°W, 1♀, ii.1990, P. Hanson, Malaise trap, 200 m (LACM); Guanacaste: Volcan Cacao, Cerro Pedregal, 10.93°N, 85.48°W, 1♀, ii-iv.1989, I. Gauld, D. Janzen, Malaise trap, 1000 m (LACM); Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 2♀, 1-8.v.1989, 1♀, 8-15.v.1989, 1♀, 15-21.v.1989, B. Brown, D. Feener, Malaise trap, SHO@SOR (LACM), 2♀, iii.1991, P. Hanson, Malaise trap (LACM, MUCR), 1♀, 15.ii-1.iii.1993, ALAS, Malaise trap M/10/25 (INBC), 1♀, 1-15.iii.1993, ALAS, Malaise trap M/10/41 (INBC), 3♀, 1-15.iv.1993, ALAS, Malaise trap M/08/71, M/12/75, M/15/78 (INBC), 2♀, 1-15.v.1993, ALAS, Malaise trap M/10/104 (INBC), 1♀, 15.vi-1.vii.1993, ALAS, Malaise trap M/06/151 (INBC), 1♀, 15.vi-1.vii.1993, ALAS, Malaise trap M/12/118 (INBC), 1♀, 22-24.vi.1993, B. Brown, D. Feener, Malaise trap #1 (LACM), 1♀, 24.vi.1993, B. Brown, injured *Ectatomma tuberculatum* (LACM), 2♀, 1.vii.1993, ALAS, Malaise trap M/12/146 (INBC), 2♀, 15.vii.1993, ALAS, Malaise trap M/12/162 (INBC), 2♀, 3.viii.1993, ALAS, Malaise trap, M/12/174 (INBC), 1♀, 15.xi.1993, ALAS, Malaise trap M/04/267 (INBC), 4♀, 15.xi.1993, ALAS, Malaise trap M/12/274 (INBC), 2♀, 3.i.1994, ALAS, Malaise trap, M/01/304, M/09/311 (INBC), 1♀, 15.i.1994, ALAS, Malaise trap M/08/326 (INBC), 1♀, 15.ii.1994, ALAS, Malaise trap, M/05/352 (INBC), 1♀, 1.iii.1994, ALAS, Malaise trap, M/04/363 (INBC), 1♀, 30.vi.1995, ALAS, Malaise trap M/01/388 (INBC), 1♀, 1.xii.1995, ALAS, Malaise trap M/01/507 (INBC), 1♀, 15.x.1997, ALAS, Malaise trap M/18/686 (INBC); Limón: 4 km NE Bribri, 9.63°N, 82.82°W, 2♀, xii.1989-iii.1990, P. Hanson, Malaise trap, 50 m (LACM), 7 km SW Bribri, 9.58°N, 82.88°W, 2♀, ix-x.1989, P. Hanson, Malaise trap (LACM), 16 km W Guapiles, 10.15°N, 83.92°W, 1♀, i-iv.1991, P. Hanson, Malaise trap, 400 m (LACM); Puntar-



enas: Coopemarti, 8.63°N, 83.47°W, 6♀, ii.1991, P. Hanson, Malaise trap, 30 m (LACM), 5 km W Piedras Blancas, 8.77°N, 83.28°W, 1♀, vi–viii.1989, 2♀, vi.1991, 1♀, vii.1991, 1♀, viii.1991, P. Hanson, Malaise trap, 100 m (LACM), 10 km W Piedras Blancas, 8.75°N, 83.3°W, 2♀, iii–v.1989, P. Hanson, Malaise trap, 100 m (LACM), 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♀, iii–v.1989, 1♀, xii.1991, P. Hanson, Malaise trap (LACM), 5 km NW Puerto Jimenez, 8.55°N, 83.35°W, 1♀, v.1991, P. Hanson, Malaise trap, 10 m (LACM), 23 km N Puerto Jimenez, 8.67°N, 83.45°W, 1♀, i–iv.1991, 2♀, viii.1991, P. Hanson, Malaise trap, 10 m (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 1♀, iii.1989, 1♀, xii.1989, 1♀, iii–vi.1990, 1♀, vii–ix.1990, 6♀, iii–v.1991, 2♀, viii.1991, 1♀, x.1991, 1♀, ii.1992, P. Hanson, Malaise trap, 10 m (LACM, MUCR), 5 km SW Rincon, 8.7°N, 83.51°W, 4♀, 31.v–7.vi.1998, B. Brown, V. Berezovskiy, Malaise trap #3, Malaise trap #5 (LACM), 1♀, 3.vi.1998, B. Brown, injured *Odontomachus laticeps* (LACM), Rio Piro, 8.28°N, 83.32°W, 1♀, ii.1991, P. Hanson, Malaise trap, 75 m (LACM); San José: Zurquí de Moravia, 10.05°N, 84.02°W, 1♀, vii.1990, P. Hanson, Malaise trap, 1600 m (LACM). ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1♀, 3–13.vi.1994, P. Hibbs, Malaise trap, 270 m (QCAZ), Tiputini Station, 0.67°S, 76.25°W, 1♀, 28–30.vi.1998, E. Holscher, C. Carter, Malaise trap (LACM). MEXICO: Veracruz: 33 km NE Catemaco, Los Tuxtlas Biological Station, 1♀, 1.vii–1.viii.1983, S. and J. Peck, FIT, rain forest, 160 m (LACM). PANAMA: Canal Zone: Barro Colorado Island, 9.15°N, 79.85°W, 1♀, 20–27.i.1993, J. Pickering, Malaise trap #736 (LACM), 1♀, 10–17.iii.1993, J. Pickering, Malaise trap #957, 9♀, 24–31.iii.1993, J. Pickering, Malaise trap #935, #959 (LACM, MIUP), 1♀, 28.iv–5.v.1993, J. Pickering, Malaise trap #940 (LACM), 3♀, 5–12.v.1993, J. Pickering, Malaise trap #941 (LACM), 1♀, 9–23.vi.1993, J. Pickering, Malaise trap #946 (LACM), 1♀, 25.viii–1.ix.1993, J. Pickering, Malaise trap #1676 (LACM), 1♀, 8–15.ix.1993, J. Pickering, Malaise trap #1672 (LACM), 23♀, 6–13.x.1993, J. Pickering, Malaise trap #1693 (LACM, MCZC, MIUP, MUSP, USNM), 1♀, 2–9.ii.1994, J. Pickering, Malaise trap #2366 (LACM), 1♀, 11–18.v.1994, J. Pickering, Malaise trap #2424 (LACM), 1♀, 22–29.vi.1994, J. Pickering, Malaise trap #2385 (LACM), 2♀, 24–31.viii.1994, J. Pickering, Malaise trap #2394 (LACM), 4♀, 6–13.xi.1996, J. Pickering, Malaise trap #7046 (LACM); San Blas: Nusagandi Reserve, 9.33°N, 79°W, 1♀, 14–21.v.1994, J. Pickering, Malaise trap #2871 (LACM).

### *Apocephalus lobicauda* new species

(Fig. 72)

**SPECIES RECOGNITION.** This species is recognized by its short, broad, rounded lateral darkenings.

**DESCRIPTION.** Body length 1.1–1.4 mm. Frons yellow to light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.43 wing length; range 0.40–0.45. Wing vein  $R_{2+3}$  present. Halter light brown. Abdominal tergites dark brown. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 72) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening broadened, enlarging posteriorly, apically rounded, margin dark, complete. Dorsal apical sclerite of ovipositor trapezoidal, but anteriorly emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a number of lowland sites in Costa Rica.

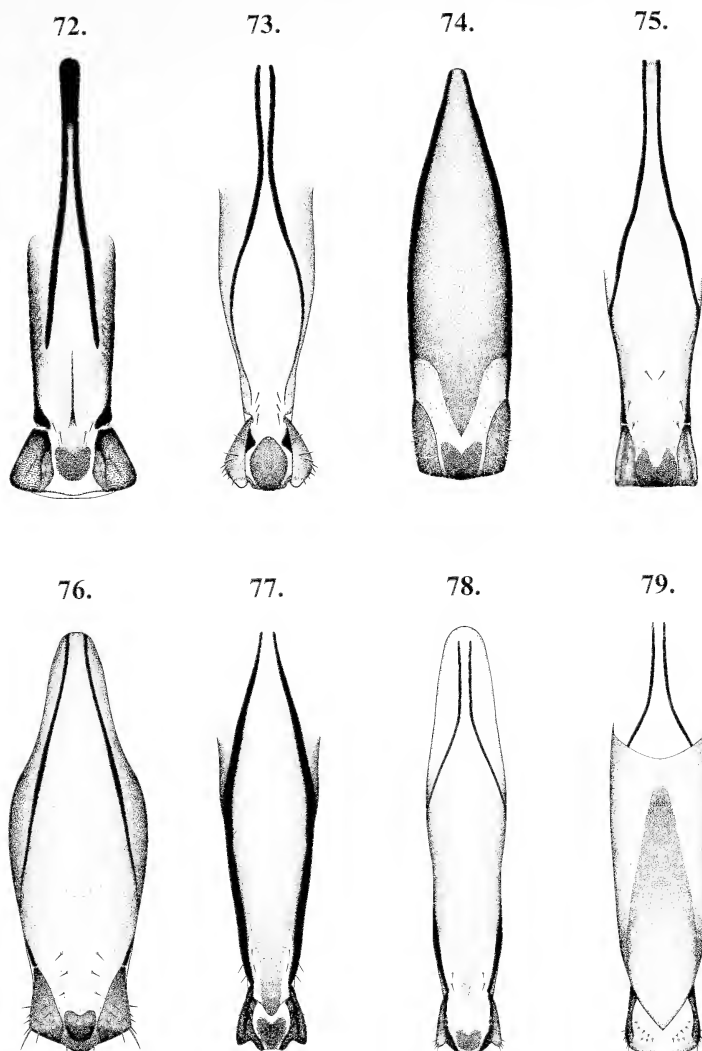
**WAY OF LIFE.** Females are attracted to injured *Ectatomma tuberculatum* workers.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *lobus* and *cauda*, for lobe and tail, referring to the shape of the lateral darkenings.

**HOLOTYPE.** ♀, COSTA RICA: Limón: 7 km SW Bribri, 9.58°N, 82.88°W, ix–xi.1989, P. Hanson, Malaise trap [LACM ENT 005279] (LACM).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 2♀, 1–15.iv.1993, ALAS, Malaise trap M/15/78, M/01/64 (INBC), 1♀, 1.vi.1993, ALAS, Malaise trap M/7/113 (INBC), 1♀, 1.vii.1993, ALAS, Malaise trap M/06/151 (INBC), 1♀, 1–15.vii.1993, ALAS, Malaise trap M/10/160 (INBC), 1♀, 1.xi.1993, ALAS, Malaise trap M/01/248 (INBC), 10♀, 1.xii.1993, ALAS, Malaise trap M/01/276 (INBC, LACM), 8♀, 3.i.1994, ALAS, Malaise trap M/01/304 (INBC, MCZ, USNM) 1♀, 1.iii.1994, ALAS, Malaise trap M/01/360 (INBC), 2♀, 4.iv.1994, ALAS, Malaise trap M/01/384 (INBC), 2♀, 15.vii.1995, 2♀, 19.vii.1995, D. Feener, injured *Ectatomma tuberculatum* (LACM); Limón: 4 km NE Bribri, 9.63°N, 82.82°W, 1♀, xii.1989–iii.1990, P. Hanson, Malaise trap, 50 m (LACM), 7 km SW Bribri, 9.58°N, 82.88°W, 4♀, ix–xi.1989, P. Hanson, Malaise trap (LACM, MUCR); Puntarenas: 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♀, iv–v.1991, P. Hanson, Malaise trap (LACM), 3 km SW Rincon,





Figures 72-79. Ovipositors. 72. *Apocephalus lobicauda* new species, dorsal. 73. *Apocephalus globosus* new species, dorsal. 74. *Apocephalus maculosus* new species, dorsal. 75. *Apocephalus glabriventris* new species, dorsal. 76. *Apocephalus minutus* Borgmeier, dorsal. 77. *Apocephalus cardiacus* new species, dorsal. Figures 78-79. *Apocephalus petiolus* new species. 78. Dorsal. 79. Ventral.

8.68°N, 83.48°W, 2 ♀, x-xii.1990, P. Hanson, Malaise trap (LACM), Sirena, 8.48°N, 83.6°W, 1 ♀, 9.vii.1993, D. Feener, injured *E. tuberculatum* (LACM).

### *Apocephalus globosus* new species (Fig. 73)

**SPECIES RECOGNITION.** This species is recognized by the distinctive large rounded preapical sclerite.

**DESCRIPTION.** Body length 1.4 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light

brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3-5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 73) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening broadened, en-

larging posteriorly, apically rounded, margin dark, complete. Dorsoapical sclerite of ovipositor large, round, dark, shiny. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular, apically tridentate and with apical, triangular sclerite. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in northern Costa Rica.

**WAY OF LIFE.** The single specimen was attracted to injured *Pachycondyla villosa* workers.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for round, referring to the shape of the preapical sclerite.

**HOLOTYPE.** ♀, COSTA RICA: Guanacaste: Estación Biología Pitilla, 11.0°N, 85.43°W, 5.vii.1997, B. Brown, injured *Pachycondyla villosa* [LACM ENT 099871] (LACM).

### *Apocephalus maculosus* new species

(Figs. 74, 110)

**SPECIES RECOGNITION.** This species is distinguished by light-colored spots on tergite 3 and the unusual structure of the ovipositor.

**DESCRIPTION.** Body length 1.5 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellow; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.55 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 dark, with round, yellow spot laterally (Fig. 110). Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 bare, except for small patch of setae mediolaterally on segment 5. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 74) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening broad, margin dark, complete. Dorsoapical sclerite of ovipositor trapezoidal, but anteriorly emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, with a short process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Amazonian Ecuador.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin word *maculosus* for

spotted, referring to the light-colored, round spots on tergite 3.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1–31.xii.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 050741] (LACM).

### *Apocephalus glabriventris* new species

(Fig. 75)

**SPECIES RECOGNITION.** This species belongs to a group of similar species with small preapical sclerites on the ovipositor. It is recognized by the large notch in the anterior margin of the sclerite, as well as the bare venter of the abdomen.

**DESCRIPTION.** Body length 1.0 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 75) straight in lateral view, lightly but evenly sclerotized dorsally, darker than in similar species. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor heart-shaped. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in western Mexico.

**WAY OF LIFE.** The single known specimen of this species was attracted to a pair of fighting *Ectatomma ruidum* (Roger).

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *glaber* and *ventris*, for bare and belly, referring to the bare venter of the abdomen.

**HOLOTYPE.** ♀, MEXICO: Jalisco: Chamela, 19.52°N, 105.08°W, 1.x.1990, W. Eberhard, over fighting *Ectatomma ruidum* [LACM ENT 012756] (LACM).

### *Apocephalus minutus* Borgmeier

(Fig. 76)

*Apocephalus minutus* Borgmeier, 1958:329, figs. 20, 20a, 39.

*Apocephalus angularis* Borgmeier, 1971:106–107, fig. 149, new synonymy.

**HOLOTYPE.** ♀, BRAZIL: Rio de Janeiro: Jacarepaguá, 1957, T. Borgmeier (MZSP; not examined).

**SPECIES RECOGNITION.** This species is distinguished by the small heart-shaped preapical sclerite and the downturned apex of the ovipositor.

In his last key to *Apocephalus* species, Borgmeier (1971) stated that *A. angularis* Borgmeier had an apically pointed ovipositor, unlike *A. minutus*, which was stated to have a small, triangular excision. This apparent excision, however, was an artifact of the drying of the intersegmental membrane posterior to the ovipositor. Examination of specimens of *A. angularis* showed that they are identical to *A. minutus*.

**DESCRIPTION.** Body length 1.0 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur slightly darker on anterior face. Mean costal length 0.46 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 76) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor elongate, anteriorly emarginate. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 thin, with lighter, expanded area at midlength. Dufour's mechanism not seen. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in southeastern Brazil.

**WAY OF LIFE.** Unknown.

**MATERIAL EXAMINED.** BRAZIL: Rio de Janeiro: Jacarepaguá, 1 ♀ [paratype], 18.xi.1957, T. Borgmeier (MCZC); São Paulo: Nova Teutonia, 2 ♀ [holotype and paratype of *A. angularis*], F. Plaumann (MZSP).

### *Apocephalus cardiacus* new species

(Fig. 77)

**SPECIES RECOGNITION.** This species can be recognized by the heart-shaped preapical sclerite and the small, internally directed arms of the apex of the lateral darkenings. It differs from the most

similar species, *A. petiolus* new species, by the relatively short, sparse setae on the venter of the abdomen.

**DESCRIPTION.** Body length 1.4–1.8 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta large, bristle-like. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.52 wing length; range 0.50–0.56. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown (some specimens with tergite 3 light brown). Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 relatively short, consisting of a complete ventral and lateral row. Ovipositor (Fig. 77) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor heart-shaped. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 broad, narrowed apically, but widened abruptly at apex. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, with long process.

**GEOGRAPHICAL DISTRIBUTION.** Known from several lowland sites in Costa Rica.

**WAY OF LIFE.** Host unknown. This species was collected almost exclusively by Malaise trap #10 in the 16-trap ALAS survey. In Brown and Feener (1995, as "species 143"), the increase in abundance of this species in trap #10 was hypothesized to be correlated with the onset of the rainy season.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Greek word *kardia* for heart, referring to the shape of the preapical sclerite.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1–15.v.1993, ALAS, Malaise trap M/10/104 [INBI-OCRI001264537] (INBC).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 3 ♀, ix.1992, P. Hanson, Malaise trap (LACM, MUCR), 2 ♀, 15.ii–1.iii.1993, ALAS, Malaise trap M/10/25 (INBC), 2 ♀, 15.iv–1.v.1993, ALAS, Malaise trap M/10/89 (INBC), 12 ♀, 1–15.v.1993, ALAS, Malaise trap M/10/104 (INBC), 17 ♀, 15.v–1.vi.1993, ALAS, Malaise trap M/10/116 (INBC, LACM), 11 ♀, 1–15.vi.1993, ALAS, Malaise trap M/10/132 (INBC, LACM), 1 ♀, 15.vi–1.vii.1993, ALAS, Malaise trap M/04/139 (INBC), 25 ♀, 15.vi–1.vii.1993, ALAS, Malaise trap M/10/144 (INBC, LACM), 12 ♀, 1–15.vii.1993, ALAS, Malaise trap M/10/160 (INBC, LACM), 17 ♀, 15.vii–3.viii.1993, ALAS,

Malaise trap M/10/172 (INBC, MCZC, USNM), 3♀, 3.viii.1993, ALAS, Malaise trap M/12/174 (INBC), 14♀, 3–14.viii.1993, ALAS, Malaise trap M/10/188 (INBC), 11♀, 15.viii–1.ix.1993, ALAS, Malaise trap M/10/200 (INBC), 1♀, 1.xi.1993, ALAS, Malaise trap M/02/249 (INBC), 1♀, 2.i.1996, ALAS, Malaise trap M/01/531 (INBC), Rara Avis, 12 km SW Horquetas, 1♀, 18–23.i.1989, D.A. Grimaldi, 550 m (AMNH); Puntarenas: 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♀, i.1992, P. Hanson, Malaise trap, 200 m (LACM), 23 km N Puerto Jimenez, 8.67°N, 83.45°W, 1♀, viii.1991, P. Hanson, Malaise trap (LACM).

### *Apocephalus petiolus* new species

(Fig. 78–79, 109)

**SPECIES RECOGNITION.** This species is recognized by the shape of the preapical sclerite and by the densely setose, “hairy” appearance of the venter of the abdomen.

**DESCRIPTION.** Body length 1.4 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellow; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.55 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 complete, with short setae at posterolateral corner. Venter of segments 3–5 with long, dense setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 78–79) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, inner margin extended medially, margin dark, complete. Dorsoapical sclerite of ovipositor small, triangular. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 broad, narrowed apically. Dufour’s mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, with long process (Fig. 109).

**GEOGRAPHICAL DISTRIBUTION.** Known from a few lowland sites in Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for small stem, referring to the sclerotized loop.

**HOLOTYPE.** ♀, COSTA RICA: Puntarenas: Rio Piro, 8.28°N, 83.32°W, ii.1991, P. Hanson, Malaise trap, 75 m [LACM ENT 004854] (LACM).

**PARATYPES.** COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1♀,

2.iii.1993, ALAS, Malaise trap, M/05/20, 1♀, 4.iv.1994, ALAS, Malaise trap, M/11/389 (INBC); Puntarenas: 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♀, xi.1990, P. Hanson, Malaise trap, 200 m (LACM).

### *Apocephalus gigantivorus* new species

(Figs. 80–81)

**SPECIES RECOGNITION.** This species has a distinctive preapical sclerite that is much longer than broad.

**DESCRIPTION.** Body length 1.9–2.3 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 basally yellow, apically brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax yellow; pleuron white. Anterior scutellar seta large, bristle-like. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.52 wing length; range 0.51–0.54. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, lighter medially. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 80–81) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, inner margin extended posteriorly, margin dark, complete. Dorsoapical sclerite of ovipositor elongate, rounded anteriorly. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular. Dufour’s mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known only from Brazil, but the host ant is also known from Peru (Kempf, 1971).

**WAY OF LIFE.** Females were attracted to injured *Dinoponera gigantea*. They were mentioned by Silveira-Costa and Moutinho (1996, p. 94) in their paper about phorid parasitoids of *Dinoponera*.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the species name of the host and the Latin word *voro*, for eat.

**HOLOTYPE.** ♀, BRAZIL: Paragominas: 3°S, 47.5°W, 10.v.1995, A. Silveira-Costa, over *Dinoponera gigantea* [LACM ENT 006557] (MZSP).

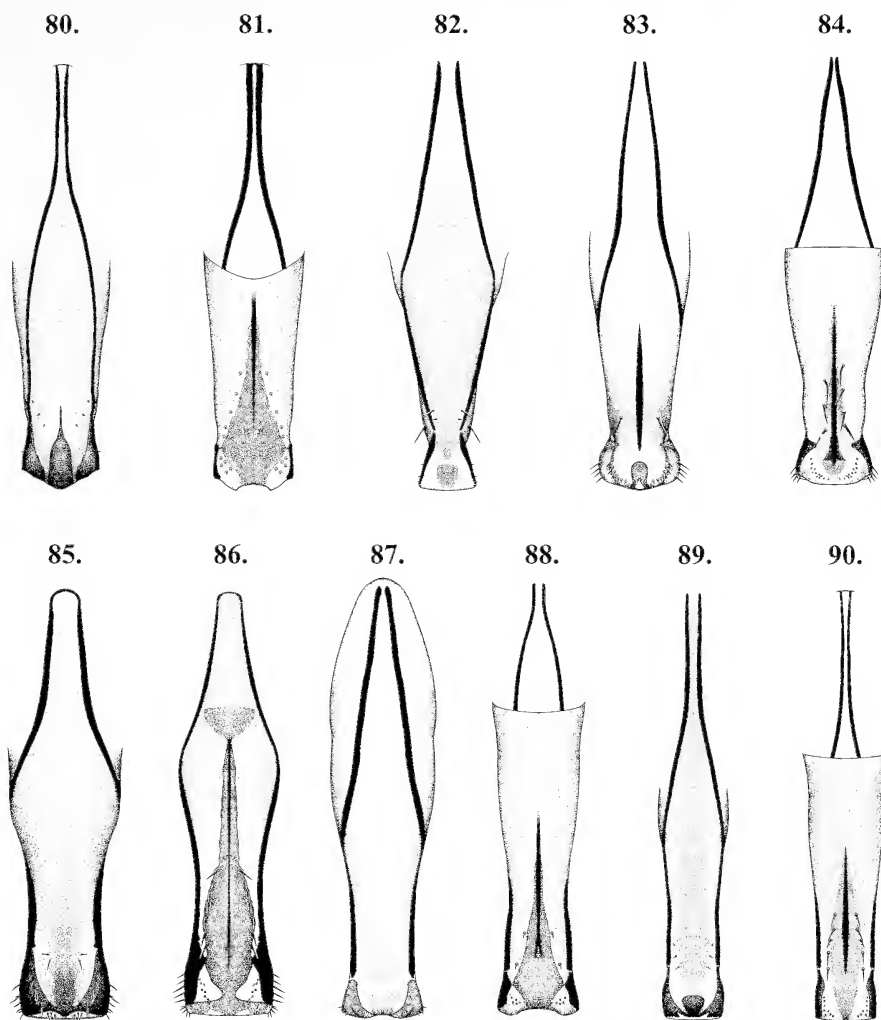
**PARATYPES.** BRAZIL: Paragominas: 3°S, 47.5°W, 1♀, v.1994, 5♀, 10.v.1995, A. Silveira-Costa, over *Dinoponera gigantea* (LACM, MZSP).

### *Apocephalus piliiventris* Borgmeier

(Fig. 82)

*Apocephalus piliiventris* Borgmeier, 1925:186, figs. 18, 19, Plate VIII, fig. 39.

*Lectotype* (here designated). ♀, BRAZIL: Rio de



Figures 80-90. Ovipositors. Figures 80-81. *Apocephalus gigantivorus* new species. 80. Dorsal. 81. Ventral. 82. *Apocephalus piliventris* Borgmeier, dorsal. Figures 83-84. *Apocephalus annulatus* new species. 83. Dorsal. 84. Ventral. Figures 85-86. *Apocephalus contortiventris* new species. 85. Dorsal. 86. Ventral. Figures 87-88. *Apocephalus eurydomus* new species. 87. Dorsal. 88. Ventral. Figures 89-90. *Apocephalus conformalis* new species. 89. Dorsal. 90. Ventral.

Janeiro, Petrópolis, 22.52°S, 43.17°W [LACMENT 121126] (MZSP).

**SPECIES RECOGNITION.** This species is most easily recognized by the thin, divergent lateral darkenings of the ovipositor.

**DESCRIPTION.** Body length 1.4-1.6 mm. Frons yellow, anterior margin relatively straight. One to two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellow; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.51 wing length; range 0.50-0.52. Wing vein  $R_{2+3}$  present. Halter brown.

Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3-5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 82) straight in lateral view, lightly and evenly sclerotized dorsally with thin, dark, median line. Lateral darkening thin, apically divergent, margin dark, complete. Dorsoapical sclerite of ovipositor heart-shaped. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular. Abdominal glands in segment 5 white,

inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a few sites in southeastern Brazil.

**WAY OF LIFE.** Females were attracted to injured workers of *Pachycondyla striata* Smith in the urban park next to the Museu de Zoologia, São Paulo, Brazil.

**MATERIAL EXAMINED.** BRAZIL: Minas Gerais: Congonhas, 1♀, 22–24.ii.1990, S.A. Marshall, pan trap (DEBU); Rio de Janeiro: Petropolis, 1♀, 2.iii.1923, 1♀, 7.iv.1923, 1♂, 24.iv.1923, 1♀, 2.v.1923, Ronchi (MCZC, USNM), 1♂, 3♀, no other data (LACM, MZSP); Santa Catarina: Nova Teutonia, 1♀ [no date], F. Plaumann (MZSP); São Paulo: Parque do Ipiranga, 23.59°S, 46.61°W, 2♀, 29.iv.1999, 6♀, 1.v.1999, B. Brown, injured *Pachycondyla striata* (LACM, MZSP).

### *Apocephalus annulatus* new species

(Figs. 83–84)

**SPECIES RECOGNITION.** This species is recognized by the posterior cleft in the dorsal preapical sclerite and by the rounded lateral darkenings.

**DESCRIPTION.** Body length 1.5–1.8 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length; range 0. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites yellow, posteriorly dark brown; tergite 6 completely yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 moderately long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 83–84) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, inner margin extended medially, margin dark, complete. Dorsoapical sclerite of ovipositor rectangular, posteriorly cleft. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 triangular, apically tridentate and with apical, triangular sclerite. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite rounded, with a short process.

**GEOGRAPHICAL DISTRIBUTION.** Known from two sites in eastern Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The

name is a Latin word for circular, referring to the rounded lateral darkenings of this species.

**HOLOTYPE.** ♀, COSTA RICA: Limon: 16 km W Guapiles, 10.15°N, 83.92°W, i–iv.1991, P. Hanson, Malaise trap, 400 m [LACM ENT 013196] (LACM).

**PARATYPES.** COSTA RICA: Limon: 4 km NE Bribri, 9.63°N, 82.82°W, 1♀, vii–ix.1990, P. Hanson, Malaise trap, 50 m (LACM).

### *Apocephalus contortiventris* new species

(Figs. 85–86)

**SPECIES RECOGNITION.** This species can be recognized by the extremely complex shape of sternite 7.

**DESCRIPTION.** Body length 1.5 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus brown. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.5 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with several long setae on posterior margin. Venter of segments 3–5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 85–86) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, inner margin extended medially, margin dark, complete. Dorsoapical sclerite of ovipositor rectangular. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 anteriorly triangular, posteriorly narrowed, then broadly expanded to an oval with numerous lateral setae, then narrowed and expanded to broad posterior apex. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in western Ecuador.

**WAY OF LIFE.** The single specimen was attracted to an injured worker of *Pachycondyla impressa*.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *contortus* and *venter*, for complex and belly, referring to the complicated structure of sternite 7.

**HOLOTYPE.** ♀, ECUADOR: Esmeraldas: Bilsa Biological Station, 0.34°N, 79.71°W, 10.v.1996, B. Brown, injured *Pachycondyla impressa*, 500 m [LACM ENT 053897] (LACM).

### *Apocephalus eurydomus* new species

(Figs. 87–88, 106, 111)

*Apocephalus* sp., Brown 1992, fig. 35B–D.

**SPECIES RECOGNITION.** This species is best recognized by the medial ventral setae of the abdomen, the apically expanded sternite 7 and the small preapical sclerite. The most similar species is *A. conformalis* new species, which differs in the form of sternite 7.

**DESCRIPTION.** Body length 1.3–1.6 mm. Frons yellow to light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow to light brown. Anterior scutellar seta slightly enlarged, bristle-like. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.49 wing length; range 0.47–0.5. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially (Fig. 111). Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 87–88) slightly downturned apically, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor trapezoidal. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process (Fig. 106).

**GEOGRAPHICAL DISTRIBUTION.** Known from the southern USA to Panama.

**WAY OF LIFE.** Presumably, this species is a parasitoid of *Pachycondyla harpax* (Fabricius). Females were attracted to a chemical extract of workers of this ant in Texas.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Greek words *eury*s, for wide-spread, and *doma* for home. It refers to the large geographic range of this species, the only member of the *A. miricauda*-group to occur in the Nearctic Region.

**HOLOTYPE.** ♀, USA: Texas: Travis County, Austin 30.3°N, 97.78°W, 9.vii.1994, D. Feener, attracted to *Pachycondyla harpax* extract [LACM ENT 031026] (LACM).

**PARATYPES.** COSTA RICA: Cartago: Dulce Nombre, 9.83°N, 83.92°W, 2♀, vi–viii.1993, P. Hanson, Malaise trap, 1400 m (LACM); San José: Ciudad Colon, 9.92°N, 84.25°W, 3♀, ii.1990, 7♀, iii–iv.1990, 2♀, iv–v.1990, P. Hanson, Malaise trap, 800 m (INBC, LACM, MUCR). PANAMA:

Canal Zone: Balboa, Ancon Hill, 2♀, 26–29.iv.1983, G. Otis, pan trap (LACM). USA: Texas: Bastrop County, Bastrop State Park, 30.12°N, 97.35°W, 1♀, 1–12.iii.1991, R. Wharton, Malaise trap (TAMU), Travis County, Austin, 30.3°N, 97.78°W, 1♀, 9.vii.1994, D. Feener, attracted to *Pachycondyla harpax* extract (LACM).

### *Apocephalus conformalis* new species

(Figs. 89–90)

**SPECIES RECOGNITION.** This species is similar to *A. eurydomus* but has a different form of sternite 7.

**DESCRIPTION.** Body length 1.4–1.6 mm. Frons light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white to light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length; range 0.45–0.48. Wing vein  $R_{2+3}$  present. Halter light brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 89–90) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor trapezoidal. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 broad, narrowed apically but widened abruptly at apex. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Amazonian Brazil.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for similar, referring to the close similarity of this species to *A. eurydomus*.

**HOLOTYPE.** ♀, BRAZIL: Roraima: Ilha de Maracá, 3.37°N, 61.43°W, 2–13.v.1987, J. Rafael, Malaise trap [LACM ENT 012754] (INPA).

**PARATYPES.** 30♀, same data as holotype (INPA, LACM, MCZC, MZSP, USNM).

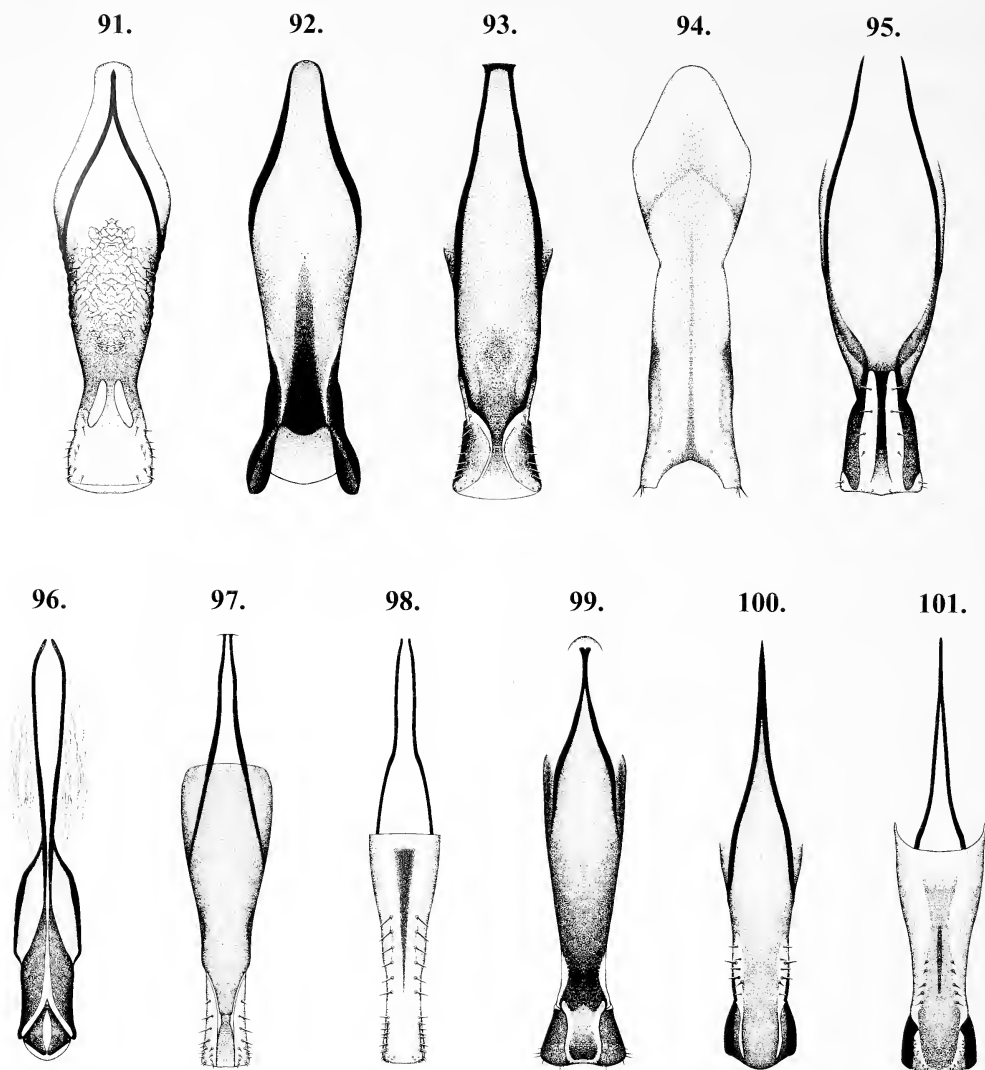
### *Apocephalus fenestratus* new species

(Fig. 91)

**SPECIES RECOGNITION.** This species is instantly recognizable by the peculiar clear sections in the ovipositor.

**DESCRIPTION.** Body length 1.3 mm. Frons





Figures 91-101. Ovipositors. 91. *Apocephalus fenestratus* new species, dorsal. 92. *Apocephalus asyndetus* new species, dorsal. 93. *Apocephalus catholicus* new species, dorsal. 94. *Apocephalus lyratus* Borgmeier, dorsal. 95. *Apocephalus trifidus* new species, dorsal. 96. *Apocephalus tanyurus* new species, dorsal. Figures 97-98. *Apocephalus contracticauda* new species. 97. Dorsal. 98. Ventral. 99. *Apocephalus indistinctus* new species, dorsal. Figures 100-101. *Apocephalus dinoponerae* new species. 100. Dorsal. 101. Ventral.

light brown, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, oval. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron light brown. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.48 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen white. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with several long setae on posterior margin. Venter of segments 3-5 with a few,

scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 91) slightly upturned apically, evenly sclerotized, but with a pair of clear areas. Lateral darkening not differentiated. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single mid-elevation site in Costa Rica.



**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is from a Latin word, *fenestra*, for window.

**HOLOTYPE.** ♀, COSTA RICA: Cartago: La Cangreja, 9.8°N, 83.97°W, iii–v.1992, P. Hanson, Malaise trap, 1950 m [LACM ENT 013053] (LACM).

**PARATYPE.** COSTA RICA: Cartago: La Cangreja, 9.8°N, 83.97°W, 1 ♀, vi–vii.1992, P. Hanson, Malaise trap, 1950 m (LACM).

### *Apocephalus asyndetus* new species

(Fig. 92)

**SPECIES RECOGNITION.** This widespread species is easily recognized by the distinctive ovipositor. Specimens from South America are consistently lighter in color, especially in flagellomere 1, but do not differ from Central American specimens in any other substantial way.

**DESCRIPTION.** Body length 1.4–1.9 mm. Frons yellow to dark brown, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair extremely small. Flagellomere 1 light brown to brown, oval, enlarged. Proboscis normal, small. Palpus brown. Dorsum of thorax yellow to light brown; pleuron yellow to white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.49 wing length; range 0.45–0.52. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown to yellow, posteriorly dark brown; tergite 6 completely yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete lateral row and a medial group centered on a small sclerite. Ovipositor (Fig. 92) straight in lateral view, with broad median sclerite. Lateral darkening thin, extended posteriorly from apex of ovipositor, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 broad, lightly sclerotized. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Lowland Brazil, Costa Rica, Ecuador, Panama, and Peru. The host ant, *Gnamptogenys bispinosa* (Emery), is known from Costa Rica and Colombia (Lattke, 1995).

**WAY OF LIFE.** One specimen was collected attacking workers of *Gnamptogenys bispinosa* as they were being raided by the army ant *Eciton vagans* (Olivier) (Brown and Feener, 1998).

**DERIVATION OF SPECIFIC EPITHET.** The

name is derived from the Greek *asyndetos* for unconnected, referring to the freely ending lateral darkenings.

**HOLOTYPE.** ♀, COSTA RICA: Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 6–11.vii.1993, B. Brown, D. Feener, Malaise trap #1 [LACM ENT 003497] (LACM).

**PARATYPES.** BRAZIL: Pará: Tucuruí, 3.83°S, 49.67°W, 1 ♀, 20.vii–8.viii.1982, J. Vidal, CDC trap (INPA); Roraima: Ilha de Maracá, 3.37°N, 61.43°W, 3 ♀, 2–13.v.1987, J. Rafael, Malaise trap (INPA, LACM). COSTA RICA: Guanacaste: 14 km S Cañas, 1 ♀, 24–31.v.1990, F.D. Parker (EMUS), Estación Pitilla, 11.0°N, 85.43°W, 1 ♀, iv.1989, P. Hanson, Malaise trap, 200 m (LACM), Santa Rosa National Park, 10.95°N, 85.62°W, 1 ♀, 21.ii–14.iii.1987, 3 ♀, 14.iii–4.iv.1987, I. Gauld and D. Janzen, Malaise trap, 300 m (LACM); Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1 ♀, 17.v.1988, B. Brown, over *Gnamptogenys bispinosa* raided by *Eciton vagans* (LACM) 2 ♀, 21.i–3.ii.1991, J. Noyes, Malaise trap (LACM), 3 ♀, 15.iv.1993, ALAS, Malaise trap, M/01/64 (INBC), 1 ♀, 1–15.iv.1993, ALAS, Malaise trap, M/11/74 (INBC), 2 ♀, 15.iv–1.v.1993, ALAS, Malaise trap, M/8/87 (INBC), 16 ♀, 1–15.v.1993, ALAS, Malaise trap, M/04/83, M/8/102 (INBC), 2 ♀, 1–15.vi.1993, ALAS, Malaise trap, M/8/130 (INBC), 1 ♀, 6–11.vii.1993, B. Brown, D. Feener, Malaise trap #1 (LACM), 8 ♀, 15.x.1993, ALAS, Malaise trap M/09/243 (INBC), 1 ♀, 3.i.1994, ALAS, Malaise trap M/03/306 (INBC), 2 ♀, 4.iv.1994, ALAS, Malaise trap M/01/384, M/09/387 (INBC), 1 ♀, 2.i.1996, ALAS, Malaise trap M/01/531 (INBC), 1 ♀, 4.ix.1997, ALAS, Malaise trap M/17/679 (INBC), 1 ♀, 30.x.1997, ALAS, M/17/698 (INBC); Limón: 4 km NE Bribri, 9.63°N, 82.82°W, 1 ♀, vii–ix.1990, P. Hanson, Malaise trap, 50 m (LACM), Pandora, Estrella Valley, 1 ♀, 28.iii.1984, G.V. Manley, Malaise trap (LACM); Puntarenas: Cerro Rincon, 8.52°N, 83.47°W, 3 ♀, i.1991, 1 ♀, ii.1991, 1 ♀, iii.1991, P. Hanson, Malaise trap, 745 m (LACM), 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1 ♀, x.1990, P. Hanson, Malaise trap, 200 m (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 2 ♀, ix–xi.1989, 1 ♀, x.1991, 8 ♀, xi. 1991, P. Hanson, Malaise trap, 10 m (LACM, MUCR). ECUADOR: Pichincha, E. Santo Domingo [Tinalandia], 1 ♀, 8–14.v.1988, Bohart and Hanson (EMUS); Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1 ♀, 4–14.iii.1994, 2 ♀, 24.v–3.vi.1994, 1 ♀, 27.viii–10.ix.1994, 2 ♀, 10–21.x.1994, 1 ♀, 21.xi–1.xii.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ). PANAMA: Darien: Cruce de Mono, 7.92°N, 77.62°W, 1 ♀, 6.ii–4.iii.1993, R. Cambra, J. Coronado, Malaise trap (LACM). PERU: Madre de Dios: Manu National Park, Cocha Cashu Station, 1 ♀, 23–30.viii.1986, D.C. Darling, Malaise trap, 380 m (ROME), Zona Reserva Pakitza, 11.94°S, 71.28°W, 1 ♀, 18.ii.1992, B. Brown, D. Feener, Malaise trap #4 (LACM) 4 ♀, 13–18.ii.1992, D. Quintero, Malaise trap (MIUP,

USNM), 1♀, 8.iii.1992, B. Brown, D. Feener, blacklight trap (LACM). TRINIDAD: Asa Wright Nature Center, 1♀, 15.i.1981, G.E. Bohart (EMUS).

### *Apocephalus catholicus* new species

(Fig. 93)

**SPECIES RECOGNITION.** This species is easily recognized by the apicodorsal region of the ovipositor, which has relatively broad lateral darkenings and medial sclerotization that expands posteriorly.

**DESCRIPTION.** Body length 1.1–1.6 mm. Frons yellow to dark brown, anterior margin relatively straight. One to two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 light brown to brown, round. Proboscis normal, small. Palpus yellow to brown. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta slightly enlarged, bristle-like. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.57 wing length; range 0.55–0.6. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow to gray. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with a few scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 93) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening broad, margin dark, complete. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor wedge-shaped, posteriorly widened. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 wedge-shaped, narrowed toward apex but abruptly widened at apex. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

**GEOGRAPHICAL DISTRIBUTION.** This species is known from lowland Brazil, Colombia, Costa Rica, Ecuador, and Panama.

**WAY OF LIFE.** Females of this species have been attracted to injured ants of a number of species, including *Ectatomma goninion* Kugler and Brown, *Odontomachus bauri*, *O. chelifer* (Latreille), *O. hastatus* (Fabricius), *O. laticeps*, *Pachycondyla crassinoda*, *P. harpax*, and *P. impressa*. All of the specimens collected at Bilsa Biological Station in Ecuador were feeders (see Behavioral Aspects).

At Bilsa, we conducted preference trials using *Pachycondyla impressa* and *Odontomachus bauri*. One bait with three injured *P. impressa* and one with three injured *O. bauri* was offered simultaneously. The number of flies landing on each bait was recorded for twelve 15-minute periods. According to these trials, the flies were much more attracted to injured *P. impressa* ( $\bar{x} = 2.25$  flies/trial)

than to injured *O. bauri* ( $\bar{x} = 0.33$  flies/trial); the difference was highly significant (99%;  $T = -4.60$ ,  $p = 0.0003$ ,  $df = 16$ ).

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for universal or general, referring to the wide variety of ants that attracted females of this species.

**HOLOTYPE.** ♀, COSTA RICA: Limón: 7 km SW Bribri, 9.58°N, 82.88°W, ix–xi.1989, P. Hanson, Malaise trap [LACM ENT 005282] (LACM).

**PARATYPES.** BRAZIL: Amazonas: Manaus, Reserva Ducke, 3.13°S, 60.02°W, 1♀, 8–15.iv.1992, Arm-Cola, 1-B-1 m, J. Vidal (INPA). COLOMBIA: Amazonas: 22 km NW Leticia, 0.4°S, 69.99°W, 1♀, 28.viii.1997, B. Brown, G. Kung, injured *Pachycondyla crassinoda* (LACM); Valle: Rio Raposo, 1♀, v.1965, V.H. Lee, light trap (USNM). COSTA RICA: Alajuela: La Virgen del Socorro, near Carriablanca, 1♀, 16.ii.1989, D. Grimaldi, P. DeVries, 700 m (AMNH); Guanacaste: Estación Pitilla, 11°N, 85.43°W, 2♀, 4.vii.1997, B. Brown, J. Paldi, injured *Odontomachus chelifer* (LACM); Heredia: La Selva Biological Station, 10.43°N, 84.02°W, 1♀, 15.iii–1.iv.1993, ALAS, Malaise trap M/10/57 (INBC), 1♀, 4.vii.1993, B. Brown, injured *Pachycondyla harpax* (LACM), 1♀, 15.i.1994, ALAS, Malaise trap M/08/326 (INBC), 1♀, 2.i.1996, ALAS, Malaise trap M/01/531 (INBC), Rara Avis, 12 km SW Horquetas, 1♀, 18–23.i.1989, D.A. Grimaldi, 550 m (AMNH); Limón: 4 km NE Bribri, 9.63°N, 82.82°W, 7♀, xii.1989–iii.1990, 1♀, vii–ix.1990, P. Hanson, Malaise trap, 50 m (LACM), 7 km SW Bribri, 9.58°N, 82.88°W, 2♀, ix–xi.1989, P. Hanson, Malaise trap (LACM), 16 km W Guapiles, 10.15°N, 83.92°W, 1♀, viii–ix.1989, 3♀, iii–v.1990, 2♀, i–iv.1991, P. Hanson, Malaise trap, 400 m (LACM); Puntarenas: Cerro Rincon, 8.52°N, 83.47°W, 1♀, ii.1991, P. Hanson, Malaise trap, 745 m (LACM), 3 km SW Rincon, 8.68°N, 83.48°W, 2♀, iii.1989, 1♀, ix–xi.1989, 1♀, xii.1991, P. Hanson, Malaise trap, 10 m (LACM, MUCR), 5 km SW Rincon, 8.7°N, 83.51°W, 8♀, 3.vi.1998, 16♀, 6.vi.1998, B. Brown, injured *Pachycondyla impressa* (LACM), 4♀, 3.vi.1998, B. Brown, injured *Odontomachus laticeps* (LACM), 2♀, 4.vi.1998, 2♀, 5.vi.1998, 4♀, 6.vi.1998, B. Brown, injured *Odontomachus bauri* (LACM). ECUADOR: Esmeraldas: Bilsa Biological Station, 0.34°N, 79.71°W, 1♀, 8.v.1996, B. Brown, injured *Ectatomma goninion* (LACM), 3♂, 20♀, 8.v.1996, B. Brown, injured *Pachycondyla impressa* (LACM, QCAZ, UNCB), 20♀, 8.v.1996, B. Brown, injured *Odontomachus bauri* (LACM, QCAZ), 1♀, 8.v.1996, B. Brown, injured *Odontomachus hastatus* (LACM), 1♀, 9.v.1996, B. Brown, injured *Odontomachus bauri* (LACM), 1♂, 19♀, 10.v.1996, B. Brown, injured *Pachycondyla impressa*, 500 m (LACM, MCZC, QCAZ), 2♀, 10.v.1996, B. Brown, injured *Odontomachus bauri* (LACM); Napo: Yasuni Biological Research Station, 0.67°S, 76.36°W, 1♀, 24.v.1996, B. Brown, injured *Pachycondyla crassinoda* (LACM); Pichin-

cha: Maquipucuna Biological Reserve, 0.12°N, 78.63°W, 1♀, 3.v.1996, B. Brown, injured *Pachycondyla impressa* (LACM), 47 km S Santo Domingo, Rio Palenque Science Center, 1♀, 2-4.v.1987, B. Brown, L.Coote, FIT, 180 m, primary rain forest (LACM), 17 km E Santo Domingo, Tinalandia, 3♀, 11.v.1987, B. Brown, injured *Pachycondyla impressa* (LACM). PANAMA: Darien: Cruce de Mono, 7.92°N, 77.62°W, 1♀, 6.ii-4.iii.1993, R. Cambra, J. Coronado, Malaise trap (MIUP).

*Apocephalus lyratus* Borgmeier

(Fig. 94)

*Apocephalus lyratus* Borgmeier, 1971:100; fig. 137.

**HOLOTYPE.** ♀, BRAZIL: Santa Catarina: Nova Teutonia, F. Plaumann [LACM ENT 122350] (MZSP; examined).

**SPECIES RECOGNITION.** This species is recognized by the broad, flat ovipositor with thin, light-colored lateral darkenings and a narrow sclerite between them.

**DESCRIPTION.** Borgmeier (1971) lists four male paratypes, but the manner in which they were associated with the females is unknown. Therefore, I am skeptical that they belong in the same species.

Body length 1.2-1.4 mm. Frons yellow, anterior margin relatively straight. Two pairs of supra-antennal setae present; lower pair markedly smaller than upper pair. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax yellow; pleuron yellow. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.47 wing length; range 0.46-0.5. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites yellow, posteriorly dark brown; tergite 6 completely yellow. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with several long setae on posterior margin. Venter of segments 3-5 with long, dense setae concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Fig. 94) straight in lateral view, evenly sclerotized, with long, thin, posteromedial process dorsally. Lateral darkening thin, subparallel, apically divergent, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor concave. Apicoventral margin of ovipositor concave. Ovipositor without ventral postapical sclerite. Sternite 7 anteriorly rounded, dark, posteriorly narrow. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Brazil and Ecuador.

**WAY OF LIFE.** Unknown.

**MATERIAL EXAMINED.** BRAZIL: Amazonas: Manaus, Reserva Ducke, 3.13°S, 60.02°W, 3♀, 8-15.iv.1992, Arm-Cola, 1-B-1 m, 2♀, 6-17.vii.1992,

10 m, J. Vidal (INPA, LACM); Santa Catarina: Nova Teutonia, 1♀, F. Plaumann (MZSP). ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1♀, 12-22.ii.1994, 1♀, 4-14.iii.1994, 1♀, 23.vi-3.vii.1994, 2♀, 16-27.viii.1994, 1♀, 27.viii-10.ix.1994, 2♀, 31.x-10.xi.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ).

*Apocephalus trifidus* new species

(Fig. 95)

**SPECIES RECOGNITION.** The distinctive ovipositor makes this species instantly recognizable: the median projection of the ovipositor is subequal in length and breadth to the lateral, sclerotized margins, making the apex of the ovipositor appear three-pronged.

**DESCRIPTION.** Body length 1.3-2.5 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, slightly pyriform (pointed). Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.56 wing length; range 0.53-0.59. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen gray to white. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3-5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 95) straight in lateral view, evenly sclerotized, with long, thin posteromedial process dorsally. Lateral darkening thin, subparallel, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 thin. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite with small opening and broad, moderately sclerotized process.

**GEOGRAPHICAL DISTRIBUTION.** This species is known from Brazil, Colombia, Ecuador, Guyana, and Peru. The host ant also has been recorded from French Guiana, Trinidad, and Venezuela.

**WAY OF LIFE.** Females of this species are attracted to, and oviposit in, injured *Pachycondyla crassinoda* workers. An average of 3.67 eggs were laid per host ( $n = 3$  oviposition events,  $sd = 1.16$  eggs), and larval feeding averaged 4.21 days ( $n = 14$  larvae,  $sd = 1.05$  days).

**DERIVATION OF SPECIFIC EPITHET.** The name is a Latin word for trifurcated, referring to the structure of the ovipositor.

**HOLOTYPE.** ♀, PERU: Madre de Dios: Zona Reserva Manu, Pakitza, 27.ii.1992, B. Brown, D.

Feener, injured *Pachycondyla crassinoda* [LACM ENT 012199] (MUSM).

**PARATYPES.** BRAZIL: Pará: Belem, 1 ♀, ix.1970, T.H.G. Aitken, sticky trap (USNM); Roraima: Ilha de Maracá, 3.37°N, 61.43°W, 2 ♀, 2-13.v.1987, J. Rafael, Malaise trap (INPA, LACM). COLOMBIA: Amazonas: 22 km NW Leticia, 4.04°S, 69.99°W, 1 ♀, 26.viii.1997, 11 ♀, 27.viii.1997, 27 ♀, 28.viii.1997, 1 ♀, 6.ix.1997, B. Brown, G. Kung, injured *Pachycondyla crassinoda* (LACM, MCZC, MZSP, UNCB, USNM). ECUADOR: Napo: Yasuni Biological Research Station, 0.67°S, 76.36°W, 3 ♀, 21.v.1996, B. Brown, injured *Pachycondyla crassinoda* (LACM, QCAZ); Sucumbios: Añagu, 0.48°S, 76.38°W, 3 ♀, 9.ix.1997, P.J. DeVries, injured *Pachycondyla crassinoda* (LACM, QCAZ). GUYANA: Berbice: Dubulay Ranch, 5.68°N, 57.86°W, 3 ♀, 23.i.1999, B. Brown, injured *Pachycondyla crassinoda* (LACM), Warniabo Creek, Dubulay Ranch, 5.66°N, 57.88°W, 10 ♀, 16.i.1999, B. Brown, injured *Pachycondyla crassinoda* (LACM, UGGG). PERU: Madre de Dios, Zona Reserva Manu, Pakitza, 11.95°S, 71.28°W, 1 ♀, 13-18.ii.1992, D. Quintero, Malaise trap (MIUP), 2 ♀, 14.ii.1992, 4 ♀, 17.ii.1992, 5 ♀, 27.ii.1992, B. Brown, D. Feener, injured *Pachycondyla crassinoda* (LACM, MUSM), 1 ♀, 7.iii.1992, B. Brown, D. Feener, blacklight trap (LACM).

### *Apocephalus tanyurus* new species

(Fig. 96)

**SPECIES RECOGNITION.** This species has an extremely aberrant ovipositor. It can be recognized by the pair of large preapical sclerites and the unusual elongate shape of the other sclerotized portions of the ovipositor.

**DESCRIPTION.** Body length 1.6–1.8 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.49 wing length; range 0.47–0.5. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown, except tergite 6, which is partly to completely yellowish. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with long seta at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 short, consisting of a patch of setae, progressively increasing in size posteriorly. Ovipositor (Fig. 96) straight in lateral view, slightly sclerotized, but with small pair of darker preapical sclerites. Lateral darkening greatly elongate, posteriorly diverging, margin dark, complete. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor

drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 broad, lightly sclerotized, with large lateral spine. Dufour's mechanism round. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from Ecuador and Colombia.

**WAY OF LIFE.** One female was attracted to an injured worker of *Paraponera clavata*.

**PHYLOGENETIC RELATIONSHIPS.** Based on the pair of preapical sclerites and the round Dufour's mechanism, this species might be an extremely aberrant member of the *A. paraponerae*-series.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Greek words *tany* and *oura*, for elongate and tail, referring to the elongate ovipositor.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 1–31.xii.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 050785] (LACM).

**PARATYPES.** COLOMBIA: Valle: Rio Raposo, 1 ♀, x.1964, V. Lee, light trap (USNM). ECUADOR: Sucumbios: Añagu, 0.48°S, 76.38°W, 1 ♀, 10.ix.1997, P. DeVries, injured *Paraponera clavata* (LACM), Sacha Lodge, 0.5°S, 76.5°W, 2 ♀, 10–21.x.1994, P. Hibbs, Malaise trap, 270 m (LACM, QCAZ).

### *Apocephalus contracticauda* new species

(Figs. 97–98)

**SPECIES RECOGNITION.** The narrow, elongate apex of the ovipositor is diagnostic for this species.

**DESCRIPTION.** Body length 1.3 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.43 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 bare. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of several setae in a straight row. Ovipositor (Figs. 97–98) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening thin, elongate, margin dark, complete. Dorsal apical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared speci-

mens. Internal sclerite rounded, with a short process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in eastern Costa Rica.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *contractus* and *cauda*, for narrow and tail, referring to the narrow apex of the ovipositor.

**HOLOTYPE.** COSTA RICA: Limon: 7 km SW Bribri, 9.58°N, 82.88°W, ix–xi.1989, P. Hanson, Malaise trap, 50 m [LACM ENT 005293] (LACM).

### *Apocephalus indistinctus* new species

(Fig. 99)

**SPECIES RECOGNITION.** This species has a heavily sclerotized ovipositor, similar to those of the *A. funditus*-subgroup species. It differs from them by the relatively straight line of the ovipositor in lateral view.

**DESCRIPTION.** Body length 1.1 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron yellow. Anterior scutellar seta large, bristle-like. Legs yellow; apex of hind femur slightly darker on anterior face. Mean costal length 0.48 wing length. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with long, scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Fig. 99) slightly sinuous in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening broadened, enlarging posteriorly, apically rounded, margin dark, complete. Dorsoapical sclerite of ovipositor rounded anteriorly. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Sternite 7 narrow but apically expanded. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite somewhat rectangular, with long, broad process.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Amazonian Ecuador.

**WAY OF LIFE.** Unknown.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *in* and *distinctus*, for not and different, referring to the lack of a distinct sternite 7.

**HOLOTYPE.** ♀, ECUADOR: Sucumbios: Sacha Lodge, 0.5°S, 76.5°W, 14–24.iii.1994, P. Hibbs, Malaise trap, 270 m [LACM ENT 036449] (LACM).

### *Apocephalus dinoponeræ* new species

(Figs. 100–101)

**SPECIES RECOGNITION.** With its broad medial sclerite and black lateral darkenings, this species is similar to *A. kungæ*, with which it occurs. In *A. dinoponeræ*, however, the ovipositor is straight in lateral view, rather than curved upward as in *A. kungæ*.

**DESCRIPTION.** Body length 2–2.4 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present. Flagellomere 1 yellow, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta slightly enlarged. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.53 wing length; range 0.51–0.55. Wing vein  $R_{2+3}$  present. Halter brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 anteriorly emarginate, with short setae at posterolateral corner. Venter of segments 3–5 with short setae, concentrated medially. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 100–101) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, inner margin extended medially, margin dark, complete. Dorsoapical sclerite of ovipositor not differentiated. Apicodorsal margin of ovipositor rounded. Apicoventral margin of ovipositor drawn out into pointed process. Ovipositor without ventral postapical sclerite. Sternite 7 triangular. Dufour's mechanism elongate. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite a simple, round loop.

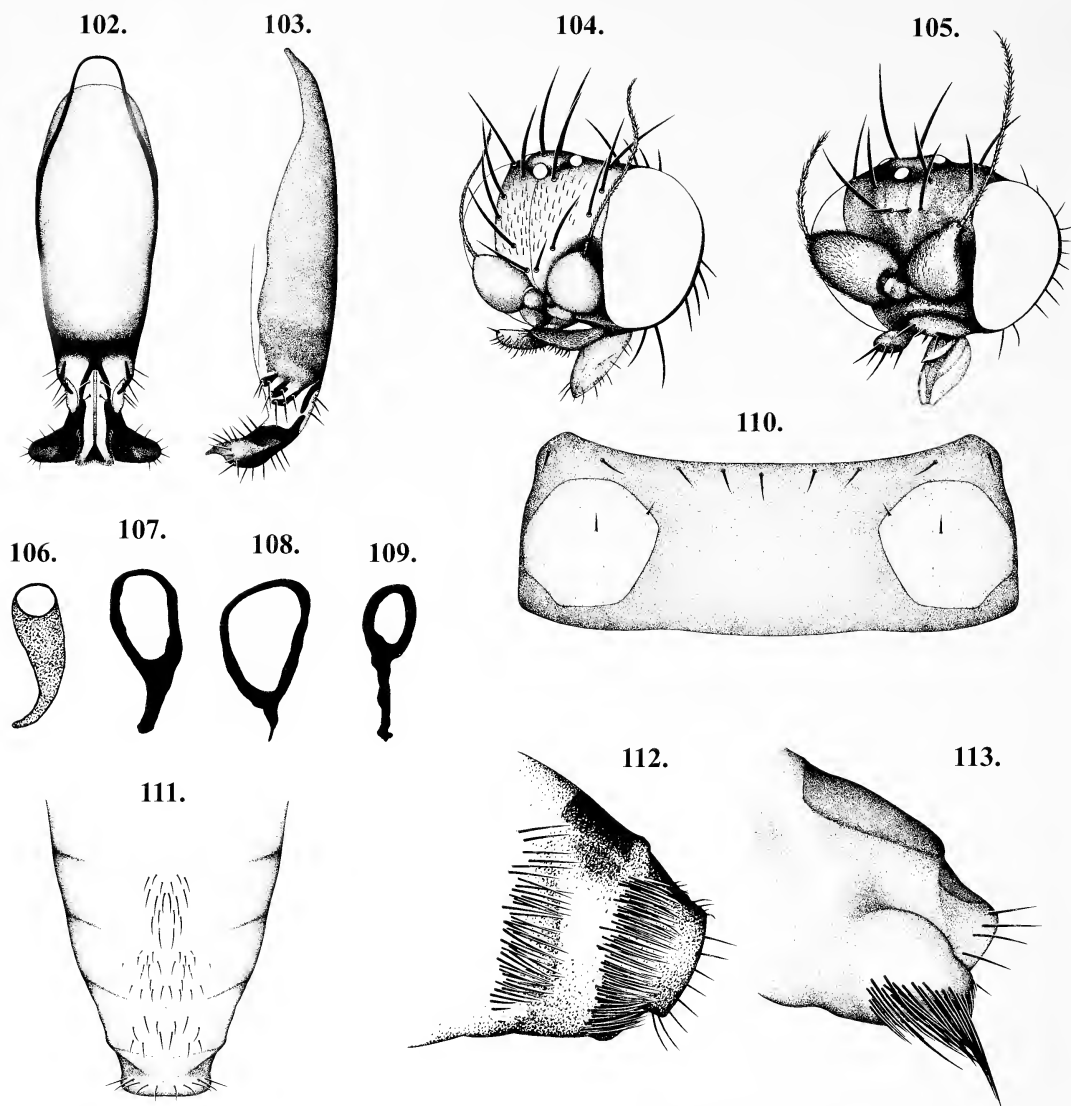
**GEOGRAPHICAL DISTRIBUTION.** Known only from southeastern Colombia. The host ant, *Dinoponera longipes*, is known from Brazil and Peru (Kempf, 1971).

**WAY OF LIFE.** Females, both egg-layers and feeders (see Behavioral Aspects), were attracted to injured workers of *Dinoponera longipes*. Four to nine eggs ( $n = 3$  oviposition events,  $\bar{x} = 6.00$  eggs,  $sd = 2.65$ ) were laid, usually through the suture between the propodeum and the petiole but on at least one occasion through the antennal suture in the head. Larvae finished feeding and emerged from the host after 1–7 days ( $n = 22$  larvae,  $\bar{x} = 4.00$  days,  $sd = 1.95$ ).

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the genus name of its host, *Dinoponera longipes*.

**HOLOTYPE.** ♀, COLOMBIA: Amazonas: 22 km NW Leticia, 4.04°S, 69.99°W, 28.viii.1997, B. Brown, G. Kung, injured *Dinoponera longipes* [LACM ENT 093676] (UNCB).

**PARATYPES.** COLOMBIA: Amazonas: Amacayacu National Park, 3.82°S, 70.26°W, 1♀, 4.ix.1997, 5♀, 5.ix.1997, B. Brown, G. Kung, in-



Figures 102–113. *Apocephalus* species. Figures 102–103. *Apocephalus latinsulosus* new species. 100. Dorsal. 101. Left lateral. Figures 104–105. Heads, anterolateral view. 104. *Apocephalus lopesi* (Borgmeier). 105. *Apocephalus brevifrons* new species. Figures 106–109. Internal, sclerotized loop. 106. *Apocephalus eurydomus* new species. 107. *Apocephalus flexus* new species. 108. *Apocephalus kungae* new species. 109. *Apocephalus petiolus* new species. Figure 110. Tergite 3, *Apocephalus maculosus* new species. Figure 111. Venter of abdomen, *Apocephalus eurydomus* new species. Figures 112–113. Segments 5 and 6 of abdomen, lateral. 112. *Apocephalus densepilosus* Borgmeier. 113. *Apocephalus comosus* new species.

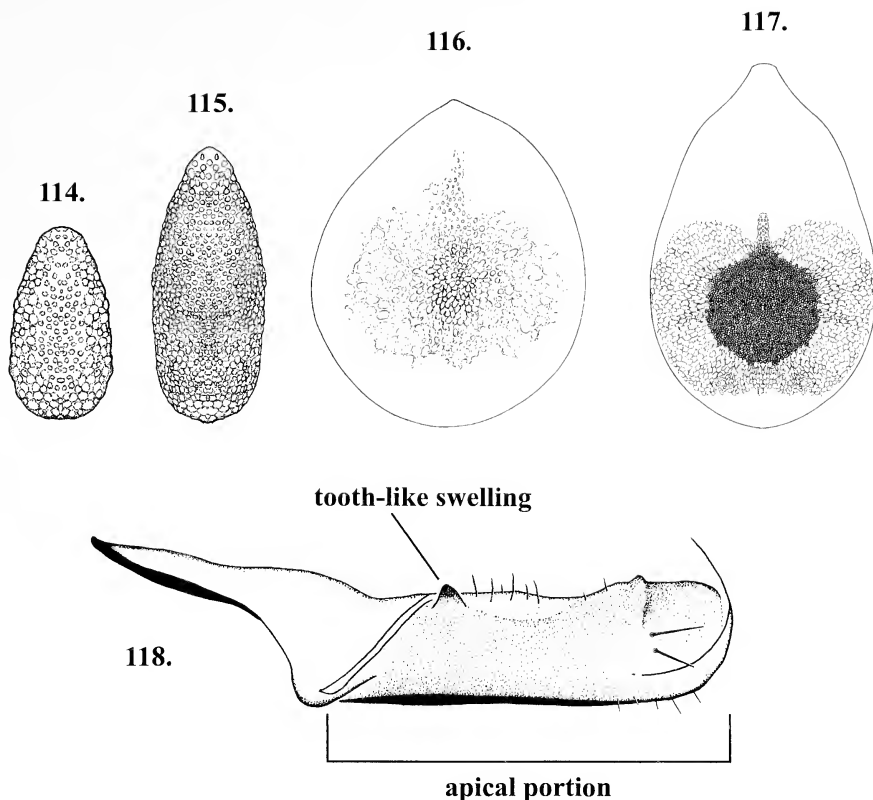
jured *Dinoponera longipes* (LACM), 22 km NW Leticia, 4.04°S, 69.99°W, 22 ♀, 27.viii.1997, 3 ♀, 28.viii.1997, 1 ♀, 7.ix.1997, B. Brown, G. Kung, injured *Dinoponera longipes* (LACM, MCZC, MZSP, UNCB, USNM).

#### *Apocephalus latinsulosus* new species

(Figs. 102–103)

**SPECIES RECOGNITION.** The small, separate lateral sclerites of the ovipositor are diagnostic for this species.

**DESCRIPTION.** Body length 1.9–2.5 mm. Frons yellow, anterior margin relatively straight. One pair of supra-antennal setae present (but one specimen has a second small pair). Flagellomere 1 light brown, round. Proboscis normal, small. Palpus yellow. Dorsum of thorax light brown; pleuron white. Anterior scutellar seta small, fine, subequal to posterior setulae of scutum. Legs yellowish-brown; apex of hind femur with abrupt darkening on anterior face. Mean costal length 0.63 wing length; range 0.61–0.67. Wing vein  $R_{2+3}$  present. Halter



Figures 114–118. *Apocephalus* species. Figures 114–117. Dufour's mechanisms. 114. *Apocephalus dichromatus* Brown. 115. *Apocephalus pseudocercus* Brown. 116. *Apocephalus* sp. 116 (unnamed *A. grandipalpis*-group species). 117. *Apocephalus paraponerae* Borgmeier. Figure 118. *Apocephalus fuscipalpis* Borgmeier. Ovipositor, lateral.

brown. Abdominal tergites dark brown. Venter of abdomen yellow. Abdominal tergites of normal form. Tergite 3 evenly colored. Tergite 6 completely divided, with short setae at posterolateral corner. Venter of segments 3–5 with a few scattered setae. Abdomen without dense lateral setae. Ventral setae of segment 6 long, consisting of a complete ventral and lateral row. Ovipositor (Figs. 102–103) straight in lateral view, lightly but evenly sclerotized dorsally. Lateral darkening posteriorly enlarged, truncate, margin dark, complete. Dorsoapical sclerite of ovipositor thin, triangular. Apicodorsal margin of ovipositor straight. Apicoventral margin of ovipositor straight. Ovipositor without ventral postapical sclerite. Ovipositor with small, separate sclerites posterolaterally. Sternite 7 narrow but apically expanded. Abdominal glands in segment 5 white, inconspicuous in cleared specimens. Internal sclerite not seen.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single mid-elevation site in Costa Rica.

**WAY OF LIFE.** Females of this species were attracted to injured workers of the presumed host, *Pachycondyla impressa* (Roger). However, we observed no ovipositions; indeed, most of the females were without mature eggs and could not possibly

have parasitized hosts. They apparently were only interested in feeding (see Behavioral Aspects).

**PHYLOGENETIC RELATIONSHIPS.** This species is nearly a perfect intermediate between the *A. attophilus* and *A. miricauda*-groups. It has a highly differentiated apical sclerite that is nevertheless still articulated with the anterior portion of the ovipositor by a forked process in addition to the thin median strip. This multiple articulation is all that excludes it from the *A. attophilus*-group.

**DERIVATION OF SPECIFIC EPITHET.** The name is based on the Latin words *latus*, for side, and *insulosus*, for islands, referring to the many separate lateral sclerites on the ovipositor.

**HOLOTYPE.** ♀, COSTA RICA: Guanacaste: Estación Cacao, 10.93°N, 85.47°W, 30.vi.1997, B. Brown, injured *Pachycondyla impressa* [LACM ENT 093422] (LACM).

**PARATYPES.** COSTA RICA: Guanacaste: Estación Cacao, 10.93°N, 85.47°W, 2♀, ii.1989, P. Hanson, Malaise trap (LACM), 1♀, vii.1993, R.M. Guzman, 1♀, 12–17.vii.1993, F.A. Quesada (INBC), 2♀, 29.vi.1997, 7♀, 30.vi.1997, B. Brown, J. Paldi, E. Holscher, injured *Pachycondyla impressa* (LACM, MUCR).



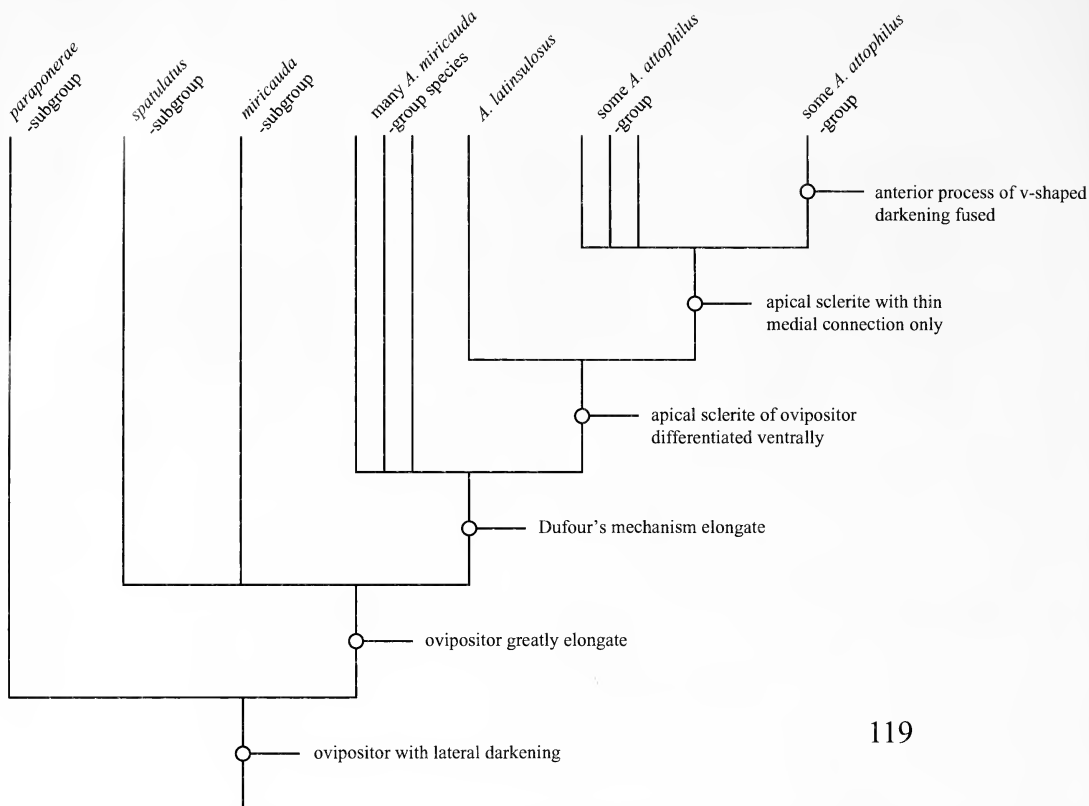


Figure 119. Hypothesis of relationships among *A. miricauda*-group and *A. atrophilus*-group taxa.

## KEY TO FEMALES

Many species treated in this work are externally similar, with few characters to separate them besides those found in the female ovipositor. Therefore, dissection of the female abdomen will possibly be necessary to obtain an accurate identification.

I did not examine specimens of *A. maculicauda* Borgmeier, a species that might belong in the *A. miricauda*-group.

The fossil species, *A. succineus*, is not included in this key.

- 1 Abdominal segments 4 and 5 with long lateral setae (Fig. 112); ovipositor as in Fig. 70, with small, medial preapical sclerite ..... *A. densepilosus* Borgmeier [*Pachycondyla crassinoda*; Amazon]
- Abdominal segments 4, and usually 5, bare laterally ..... 2
- 2 Abdominal segment 5 with dense patch of long setae on ventrolateral lobe (Fig. 113) ..... *A. comosus* new species [*Ectatomma tuberculatum*; Central America]
- Abdominal segment 5 without ventrolateral, lobe-like process bearing dense, long setae ... 3
- 3 Frons with narrow anterior process bearing reclinate supra-antennal seta directly below lower

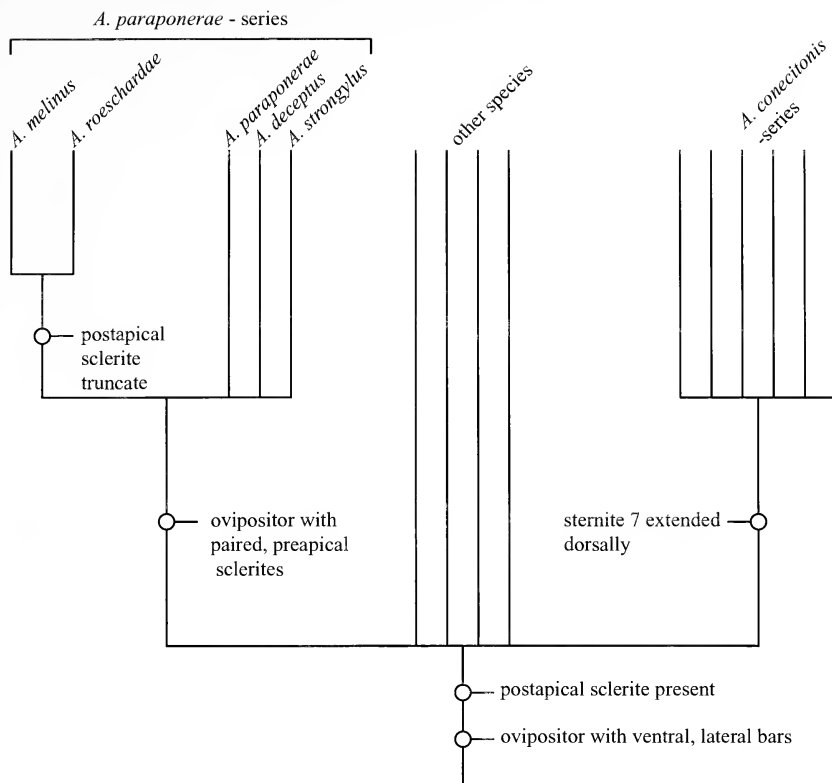
interfrontal seta (Fig. 104) .....

..... *A. lopesi* (Borgmeier)

[*Odontomachus haematodus*;  
Brazil, Colombia,  
Costa Rica, Guyana]

- Frons with straight anterior margin with normal, proclinate supra-antennal setae; if supra-antennal setae somewhat porrect or reclinate, then not located directly below lower interfrontal setae (Fig. 105) ..... 4
- 4 Ovipositor broad, with lateral darkenings well-defined, long (usually comprising about one-half of ovipositor length), subparallel, relatively narrow (Figs. 1–9); most species with a pair of preapical sclerites dorsally (Figs. 1, 3, 6), one with none (Fig. 8); ventrally ovipositor with separate, triangular, postapical sclerite with pointed (Figs. 2, 4) or truncate (Figs. 7, 9) apex ..... 5
- Ovipositor of most species thinner and more elongate, with lateral darkenings less defined, shorter, not parallel, or broader; 1–2 dorsal preapical sclerites present in some species, others with none; ventrally with or without separate postapical sclerite, which—if present—is always pointed ..... 8
- 5 Lateral darkenings of ovipositor yellowish-





120

Figure 120. Hypothesis of relationships within *A. paraponerae*-subgroup.

brown in color; ovipositor posteriorly with pair of dark, round, preapical sclerites (Fig. 6); apex of ventral postapical sclerite truncate (Fig. 7)

..... *A. melinus* new species  
[*Dolichoderus attelaboides*; Amazon]

- Lateral darkenings of ovipositor black; ovipositor with or without dorsal preapical sclerites; apex of ventral postapical sclerite pointed or truncate ..... 6

- 6 Dorsally with area of moderate sclerotization reaching to apex and without preapical sclerites (Fig. 8); apex of ventral postapical sclerite truncate (Fig. 9); one pair of supra-antennal setae present ..... *A. roescharidae* new species

[*Cephalotes atratus*; Amazon]

- Dorsally with posterior portion of ovipositor relatively unsclerotized except for pair of small preapical sclerites; apex of ventral postapical sclerite pointed; two pairs of supra-antennal setae present ..... 7

- 7 Lateral darkenings relatively thin (Fig. 1); preapical pair of sclerites larger, darker; venter of abdominal segment 6 usually with only 2 setae (sometimes with up to four) ..... *A. paraponerae* Borgmeier

[*Paraponera clavata*, *Ectatomma tuberculatum*,

*Pachycondyla* spp.; widespread in lowlands of Neotropical Region]

- Lateral darkenings relatively thicker (Fig. 3); preapical pair of sclerites relatively thin, light-colored; venter of abdominal segment 6 with row of several setae ... *A. deceptus* new species

[*Pachycondyla commutata*; Ecuador]

- 8 Ovipositor spatulate (dorsally concave), apically upturned, often with lateral, upturned apices (Fig. 37); ovipositor usually without differentiated medial preapical sclerite, sometimes with lateral darkenings indistinct or not differentiated; ovipositor of most species with long posteroventral filament-like process (Fig. 40); in most species, apical region of darker sclerotization encircles entire ovipositor (Fig. 39) ... 9

- Ovipositor apically flat or convex, often with preapical sclerites; lateral darkenings usually distinctive; ovipositor without narrow, thread-like extension; ventral sclerotization not encircling entire sclerite ..... 23

- 9 Abdominal segments 3-5 bare ventrally ... 10

- Abdominal segments 3-5 with black setae ... 11

- 10 Intersegment 6-7 with sclerotized, black, clearly visible striations ..... 11

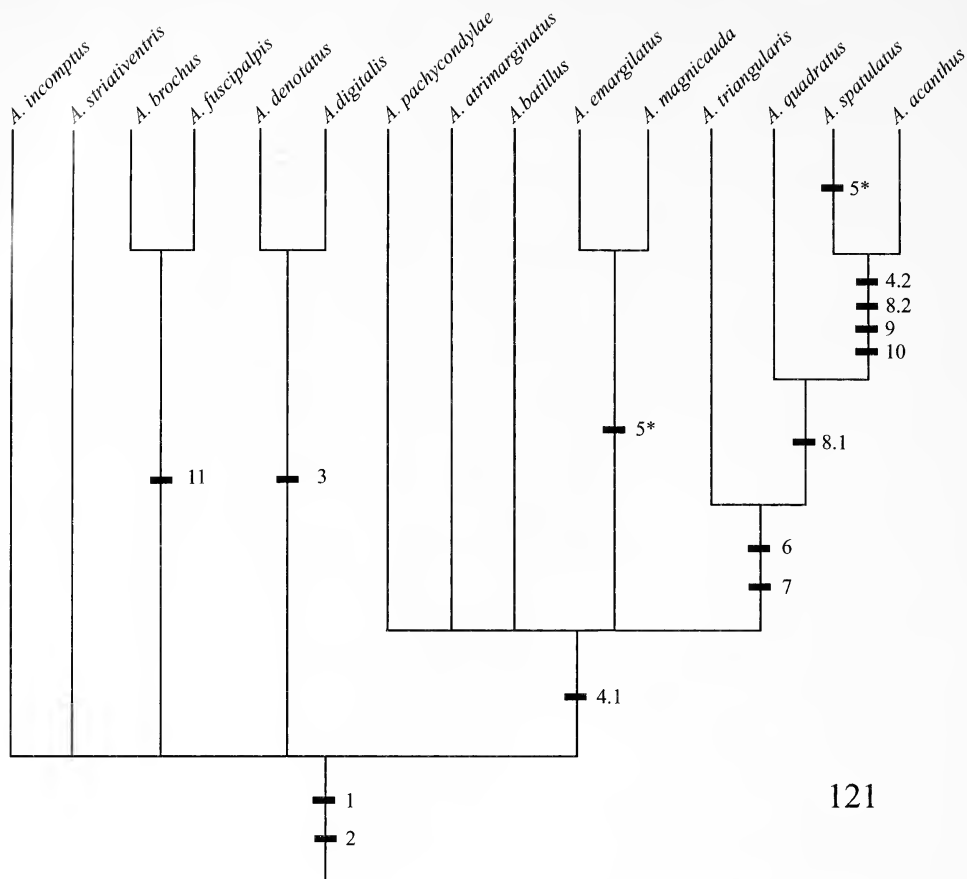


Figure 121. Hypothesis of relationships within *A. spatulatus*-subgroup.

- ..... *A. striativentris* new species  
[host unknown; Brazil, Costa Rica, Ecuador, Peru]
- Intersegment 6-7 without darkened striations  
..... *A. incomptus* new species  
[host unknown; Ecuador]
- 11 Abdominal setae dense, numerous, sometimes short ..... 12
- Abdominal setae scattered, relatively few, relatively long ..... 15
- 12 Ovipositor with dorsal spine (Fig. 45) ... 13
- Ovipositor without dorsal spine ..... 14
- 13 Posterolateral apex of ovipositor truncate (Fig. 44) ..... *A. acanthus* new species  
[host unknown; Costa Rica]
- Posterolateral apex of ovipositor right-angled (Fig. 46) ..... *A. spatulatus* Borgmeier  
[host unknown; Brazil]
- 14 Apical region of ovipositor triangular (Fig. 42) ..... *A. triangularis* new species  
[host unknown; Brazil, Mexico]
- Apical region of ovipositor quadrate (Fig. 43) ..... *A. quadratus* Brown  
[host unknown; Brazil, Ecuador]
- 15 Tergite 6 entire, not divided into two separate sclerites ..... 16
- Tergite 6 divided into two separate sclerites ... 17
- 16 Lateral margin of ovipositor smooth, not interrupted by emarginations (Fig. 41) ..... *A. magnicauda* new species  
[*Camponotus sericeiventris*; Ecuador, Peru]
- Lateral margin of ovipositor with emargination and tooth-like process in lateral view (Fig. 38) ..... *A. emargilatus* new species  
[*Camponotus sericeiventris*; Costa Rica]
- 17 Dorsal apex of ovipositor drawn out in long, narrow, parallel-sided process (Figs. 31-32) ... 18
- Dorsal apex of ovipositor without process of this type ..... 19
- 18 Dorsum of ovipositor with prominent, finger-like process (Fig. 31) ... *A. digitalis* Borgmeier  
[host unknown; Brazil]
- Dorsum of ovipositor without process (Fig. 32) ..... *A. denotatus* new species  
[host unknown; Costa Rica, Panama]
- 19 Apex of ovipositor narrowed, pointed (Fig. 30);

- laterodorsal tooth-like swelling present (Fig. 118) . . . . . 20
- Apex of ovipositor truncate (Figs. 33, 35, 36); ovipositor without tooth-like swelling . . . 21
- 20 Apex of ovipositor darkly sclerotized (Fig. 30) . . . . . *A. brochus* new species  
[*Camponotus banghaasi*, *C. rapax*; Brazil, Colombia]
- Apex of ovipositor not darkly sclerotized . . . . . *A. fuscipalpis* Borgmeier  
[host unknown; Brazil]
- 21 Posterolateral notch of ovipositor not prominent; lateral darkening of ovipositor short but distinct (Fig. 33) . . . . . *A. pachycondylae* new species  
[*Pachycondyla apicalis*, *P. obscuricornis*; Costa Rica]
- Ovipositor with well-differentiated posterolateral, raised notch (Fig. 37); lateral darkenings not distinct . . . . . 22
- 22 Posterodorsal apex of ovipositor with thick, black sclerotized margin (Fig. 35) . . . . . *A. atrimarginatus* new species  
[*Pachycondyla unidentata*; Costa Rica]
- Posterodorsal apex of ovipositor with at most thin dark margin (Fig. 36) . . . . . *A. batillus* new species  
[host unknown; Panama]
- 23 Ventral apex of ovipositor with well-developed, pointed, triangular postapical sclerite (Figs. 16, 18, 20, 24, 26) and lateral bars of sclerotization that extend medially (Fig. 18); dorsally without central preapical sclerite (but with small pair of sclerites in one species; Fig. 5); lateral darkenings of some species thickened, rounded, and projecting laterally (Figs. 6, 11, 13) . . . . . 24
- Ventral apex of ovipositor usually truncate; lacking postapical sclerite and lateral bars; dorsally, in some species with differentiated central preapical sclerite (one species with aberrant paired sclerites) (Fig. 96); lateral darkenings otherwise . . . . . 36
- 24 Posterodorsal apex of ovipositor concave, with thin, medial process (Fig. 14); ovipositor distinctly constricted in middle; ventrally with well-developed, prominent triangular pointed apex . . . . . *A. dracodermus* new species  
[host unknown; Peru]
- Ovipositor not as above . . . . . 25
- 25 Ovipositor broad and triangular in appearance, broadest at apex (Fig. 21) . . . . . *A. persecutor* Borgmeier  
[host unknown; Brazil, Costa Rica, Ecuador]
- Ovipositor more parallel-sided, usually broadest at midlength of lateral darkenings . . . 26
- 26 Lateral darkenings relatively straight, not giving ovipositor a rounded appearance (Figs. 10, 19, 23, 25, 27), although one species with small, rounded apical lobes . . . . . 27
- Lateral darkenings curved, giving posterior one-third of ovipositor a rounded appearance (Figs. 5, 11, 13, 15, 17, 22) . . . . . 31
- 27 Venter of segments 4–5 bare; postapical sclerite extremely short, triangular-shaped (Fig. 26) . . . . . *A. spiculus* new species  
[host unknown; Panama]
- Venter of segments 4–5 with black setae; postapical sclerite of various forms . . . . . 28
- 28 Lateral darkenings rounded, thickened, lobe-like (Fig. 27); venter of abdomen with row of setae present on segments 4–6 . . . . . *A. torulus* new species  
[host unknown; Colombia, Ecuador]
- Lateral darkenings thin; ventral setation of abdomen various . . . . . 29
- 29 Dorsum of ovipositor with reticulate sculpture, medially light-colored (Fig. 19); venter of ovipositor with forked, anteriorly projecting process (Fig. 20) . . . . . *A. reticulatus* new species  
[host unknown; Costa Rica]
- Dorsum of ovipositor smooth, without reticulate sculpture; ventrally without forked process . . . . . 30
- 30 Ovipositor medially darkened; laterally parallel-sided, with apical darkenings not divergent (Fig. 10); venter of abdominal segment 6 with row of long setae, segments 4–5 with relatively small, black setae . . . . . *A. conecitonis* new species  
[host unknown, but usually found with army ants; Costa Rica]
- Ovipositor not medially darkened; laterally with small expansion, apical darkenings slightly divergent (Fig. 23); venter of abdominal segment 6 with row of long setae, segments 4–5 with few, short, almost invisible setae . . . . . *A. secus* new species  
[host unknown; Costa Rica]
- 31 Venter of ovipositor with dark-colored, posteriorly expanded, triangular sclerite (Fig. 12); dorsum of ovipositor as in Fig. 11 . . . . . *A. constrictus* new species  
[host unknown; Costa Rica]
- Venter of ovipositor without a well-defined sternite . . . . . 32
- 32 Venter of abdominal segments 3–5 with dense long setae, especially medially; lateral darkenings extremely broad, black (Fig. 13) . . . . . *A. crassilatus* new species  
[*Pachycondyla* spp.; widespread in Neotropical lowlands]
- Venter of abdominal segments 3–5 with at most thin, short, scattered setae; lateral darkenings various . . . . . 33
- 33 Ovipositor dorsally with small preapical sclerites (Fig. 5); expanded portion of ovipositor more than twice as broad as rest of ovipositor; frons with two pairs of subequal supra-antennal setae . . . . . *A. strongylus* new species  
[host unknown; Brazil]
- Ovipositor without preapical sclerites; expanded portion less than twice as broad as rest of ovipositor; frons at most with a smaller, lower pair of supra-antennal setae (most species with only one pair) . . . . . 34

- 34 Ovipositor with medial, moderately sclerotized triangular area dorsally (Fig. 22) .....  
*A. curtinotus* new species  
[host unknown; Brazil]
- Ovipositor without medial sclerotization ... 35
- 35 One pair of supra-antennal setae present. Ventrally, ovipositor with transverse, posterior sclerites not touching (Fig. 18); postapical sclerite elongate; tergite 6 only slightly emarginate anteriorly; posteriorly with large pair of setae .....  
*A. inpalpabilis* new species  
[host unknown; Costa Rica]
- A second, extremely small pair of supra-antennal setae present. Ventrally, ovipositor with transverse sclerites joined to form a single structure (Fig. 16); postapical sclerite short, broad; tergite 6 deeply emarginate anteriorly; posteriorly with less differentiated pair of setae .....  
*A. indeptus* new species  
[host unknown; Costa Rica]
- 36 Ovipositor curved dorsally at midlength (Fig. 49); sternite 7 with lateral fringe of small processes (Fig. 48) ..... 37
- Ovipositor relatively straight or curved ventrally at midpoint in lateral view; sternite 7 without lateral processes ..... 40
- 37 Sternite 7 extremely broad, posteriorly exceeding width of dorsum of ovipositor (Fig. 47); two pairs of supra-antennal setae .....  
*A. miricauda* Borgmeier  
[*Dinoponera gigantea*; Brazil]
- Sternite 7 narrower, not exceeding width of dorsum of ovipositor; one pair of supra-antennal setae ..... 38
- 38 Without separate dorsal preapical sclerite; instead, broad, sclerotized lobe extending to apex (Fig. 50); sternite 7 with posterior rounded expansion extending across most of segment; sclerotized loop relatively small .....  
*A. kungae* new species  
[*Dinoponera longipes*; Colombia]
- Ovipositor with distinct preapical sclerite (Figs. 51, 53); sternite 7 much narrower, only slightly expanded posteriorly; sclerotized loop extremely large or small ..... 39
- 39 Sclerotized loop extremely large, over one-half width of ovipositor (Fig. 51) .....  
*A. flexus* new species  
[host unknown; Ecuador]
- Sclerotized loop much smaller than one-half width of ovipositor (Fig. 53) .....  
*A. orbiculus* new species  
[host unknown; Costa Rica]
- 40 Dorsum of ovipositor with separate (i.e., not anteriorly attached to other sclerites), single distinct preapical sclerite (e.g., Fig. 78) ..... 41
- Sclerites of ovipositor various (Figs. 54, 55, 57, 58, 60, 62, 64, 71), but not as above ..... 56
- 41 Lateral darkenings extremely broad, thickened (Figs. 67, 68, 72) ..... 42
- Lateral darkenings narrower ..... 44
- 42 Lateral darkenings rounded, lobe-like (Fig. 72); ventral apex of ovipositor without dark, heavily sclerotized plate; frons subequal in length and width .....  
*A. lobicauda* new species  
[*Ectatomma tuberculatum*; Costa Rica]
- Lateral darkenings shaped differently; ventral apex of ovipositor with dark-colored, heavily sclerotized median sclerite; frons short ... 43
- 43 Dorsal preapical sclerite narrow, much longer than broad (Fig. 67) .....  
*A. spatulicauda* Borgmeier  
[host unknown; Brazil]
- Dorsal preapical sclerite broader than long (Fig. 68) .....  
*A. inimicus* Borgmeier  
[host unknown; Brazil]
- 44 Preapical sclerite large, oval, shiny (Fig. 73) .....  
*A. globosus* new species  
[*Pachycondyla villosa*; Costa Rica]
- Preapical sclerite not oval, trapezoidal in most species (Figs. 74–78) ..... 45
- 45 Ovipositor, in lateral view, strongly downturned at midlength (as in Fig. 65); ovipositor dorsally as in Fig. 66 .....  
*A. intonsus* new species  
[host unknown; Panama]
- Ovipositor, in lateral view, straight or only slightly deflected at apex ..... 46
- 46 Abdominal tergite 3 with lateral, round light patch (Fig. 110); venter of abdomen with small patch of short setae mediolaterally on segment 5, otherwise 3–5 bare .....  
*A. maculosus* new species  
[host unknown; Ecuador]
- Abdominal tergite 3 uniformly dark-colored; abdominal setation various but not as above ... 47
- 47 Anterior margin of preapical sclerite deeply cleft (Figs. 74–78) ..... 48
- Anterior margin of preapical sclerite entire (Figs. 80, 82, 83) ..... 51
- 48 Venter of abdomen bare; apices of lateral darkening not markedly convergent posteriorly (Figs. 75–76); sclerotized loop with broad process (Fig. 106) ..... 49
- Venter of abdomen setose; apices of lateral darkening markedly convergent posteriorly (Figs. 77–78); sclerotized loop with long, narrow process (Fig. 109) ..... 50
- 49 Dorsal preapical sclerite broadly and deeply cleft (Fig. 75); apex of ovipositor flat .....  
*A. glabriventris* new species  
[*Ectatomma tuberculatum*; Mexico]
- Dorsal preapical sclerite with narrow cleft (Fig. 76); apex of ovipositor downturned .....  
*A. minutus* Borgmeier  
[host unknown; Brazil]
- 50 Ventral setae of abdominal segments 3–5 short, about one-half length of long ventral setae on posterior margin of segment 6; tergite 6 divided .....  
*A. cardiacus* new species  
[host unknown; Costa Rica]
- Ventral setae of abdomen long, dense, giving it a markedly “hairy” appearance; ventral setae subequal in length to ventral setae on posterior

- margin of segment 6; tergite 6 entire ..... *A. petiolus* new species  
[host unknown; Costa Rica]
- 51 Preapical sclerite much longer than wide, anteriorly rounded (Fig. 80); sternite 7 broad, triangular (Fig. 81) ..... *A. gigantivorus* new species  
[*Dinoponera gigantea*; Brazil]
- Preapical sclerite about as long as wide, anterior margin not rounded (Figs. 82–83); sternite 7 various ..... 52
- 52 Apices of lateral darkening markedly convergent posteriorly (Figs. 83, 85, 87, 89) ... 53
- Apices of lateral darkening not convergent posteriorly (Fig. 82) .... *A. piliventris* Borgmeier  
[*Pachycondyla striata*; Brazil]
- 53 Preapical sclerite posteriorly cleft (Fig. 83); sternite 7 thin triangular, with medial dark strip that projects posteriorly from triangular base, making apex appear three-pronged (Fig. 84); sclerotized loop large, about one-half width of ovipositor, similar in shape to Fig. 107 ..... *A. annulatus* new species  
[host unknown; Costa Rica]
- Preapical sclerite not cleft posteriorly; sternite 7 not appearing three-pronged ..... 54
- 54 Sternite 7 distinctive: anteriorly broad, then narrowed and expanded posteriorly, with numerous marginal setae and with apex of medial black thickening enlarged; posteriorly narrowed and again expanded to width of ovipositor (Fig. 83) ... *A. contortiventris* new species  
[*Pachycondyla impressa*; Ecuador]
- Sternite 7 not as above; medial black thickening, when present, not apically expanded ... 55
- 55 Sternite 7 apically expanded (Fig. 88) ..... *A. eurydomus* new species  
[*Pachycondyla harpax*; Costa Rica, Panama, USA]
- Sternite 7 not expanded apically (Fig. 90) ... *A. conformalis* new species  
[host unknown; Brazil]
- 56 Single preapical sclerite present but attached to anterior end of lateral darkenings by a distinctive sclerotized bar (Figs. 54, 55, 57, 58); most species with lateral postapical sclerites (e.g., Fig. 55) ..... 57
- Preapical sclerites, if present, not attached to anterior end of lateral darkenings (Figs. 91–97, 99–100, 102); lateral postapical sclerites absent ..... 61
- 57 Venter of abdomen with numerous long setae, giving it a “hairy” appearance ..... 58
- Venter of abdomen with shorter and fewer setae, mostly concentrated medially ..... 59
- 58 Preapical sclerite and lateral bars forming relatively smooth anterior margin (Fig. 54); lateral postapical sclerites absent ..... *A. meniscus* new species  
[host unknown; Peru]
- Preapical sclerite projecting anteriorly (Fig. 55); lateral postapical sclerites present ..... *A. barbiventris* new species  
[*Odontomachus barbiventris*; Costa Rica]
- 59 Preapical sclerite extremely large, filling much of space between lateral darkenings (Fig. 57) ..... *A. amplidiscus* new species  
[host unknown; Costa Rica]
- Preapical sclerite small, discrete, with anteriorly directed bars of sclerotization attaching to anterior end of lateral darkenings (Figs. 58, 60) ..... 60
- 60 Sternite 7 broad triangular (Fig. 59) ..... *A. paldiae* new species  
[*Odontomachus chelifer*; Costa Rica]
- Sternite 7 anteriorly rounded, narrowing posteriorly (Fig. 61) .. *A. cyclodiscus* new species  
[host unknown; Panama]
- 61 Ovipositor with oval, window-like clear areas (Fig. 91) ..... *A. fenestratus* new species  
[host unknown; Costa Rica]
- Ovipositor without oval clear areas ..... 62
- 62 Wing vein  $R_{2+3}$  absent; lateral darkenings of ovipositor extremely broad, triangular (Fig. 69); frons short (Fig. 105) ..... *A. brevifrons* new species  
[host unknown; Costa Rica, Mexico]
- Wing vein  $R_{2+3}$  present; lateral darkenings not so broad (except *A. latinsulosus* (Fig. 102), which differs by having small lateral sclerites); frons about as long as wide ..... 63
- 63 Lateral darkenings downturned, projecting posterolaterally, apparently ending free of rest of ovipositor (Fig. 92) ..... *A. asyndetus* new species  
[*Gnamptogenys bispinosus*; widespread in Neotropical lowlands]
- Lateral darkenings not strongly downturned and not ending freely ..... 64
- 64 Lateral darkenings separated by posterior process of ovipositor, which expands posteriorly to fill entire space between them (Fig. 93) ..... *A. catholicus* new species  
[*Pachycondyla crassinoda*, *harpax*, *impressa*, *Odontomachus* spp.]
- Ovipositor not as above ..... 65
- 65 Long, thin sclerite subequal in size to lateral darkenings extending posteriorly between them (Figs. 94–95) ..... 66
- Ovipositor without long, narrow sclerite extending between lateral darkenings ..... 67
- 66 Lateral darkenings lightly sclerotized, yellowish-brown in color, extending posteriorly, so that posterior margin of ovipositor is concave (Fig. 94); posterior margin of tergite 6 with three or more thick setae that are as long as tergite ..... *A. lyratus* Borgmeier  
[host unknown; Brazil, Ecuador]
- Lateral darkenings heavily sclerotized, almost black in color, not extending posteriorly past apex of ovipositor (Fig. 95); posterior margin of tergite 6 with one or two thinner setae that are clearly shorter than length of tergite ..... *A. trifidus* new species

- [*Pachycondyla crassinoda*; Brazil, Colombia, Ecuador, Peru]
- 67 Ovipositor elongate, with long, thin sclerites and a pair of preapical sclerites (Fig. 96); venter of abdominal segment 6 with large patch of several rows of setae that increase in length posteriorly; venter of other abdominal segments bare ..... *A. tanyurus* new species [Paraponera clavata; Colombia, Ecuador]
- Ovipositor and ventral setation not as above ..... 68
- 68 Lateral darkenings strongly expanded posteriorly (Fig. 102); ovipositor with lateral, isolated sclerites (Fig. 103) ..... *A. latinsulosus* new species [Pachycondyla impressa; Costa Rica]
- Lateral darkenings, if slightly expanded posteriorly, without lateral sclerites ..... 69
- 69 Entire ovipositor, including space between lateral darkenings, dark brown, shiny (Fig. 64); ovipositor strongly downturned at midlength (Fig. 65) ..... *A. funditus* new species [host unknown; widespread Neotropical Region]
- At least some portion of ovipositor not dark brown and shiny (Figs. 97, 99, 100); not downturned ..... 70
- 70 Apical portion of ovipositor narrow; lateral darkenings thin, subparallel; space between lateral darkenings subequal to thickness of lateral darkenings (Fig. 97) ..... *A. contracticauda* new species [host unknown; Costa Rica]
- Apical portion of ovipositor relatively broad (Figs. 66, 100) and shaped differently ... 71
- 71 Lateral darkenings apically expanded, separated by rounded sclerite (Fig. 99); venter of ovipositor evenly sclerotized, without distinct sternite ..... *A. indistinctus* new species [host unknown; Ecuador]
- Lateral darkenings not expanded apically, separated by broad, lightly sclerotized region (Fig. 100); ventrally with triangular sternite, expanded posteriorly (Fig. 101) ..... *A. dinoponerae* new species [Dinoponera longipes; Colombia]

# BEHAVIORAL ASPECTS

Females of most species had a stereotyped behavior, similar to that described for *A. paraponerae* (Brown and Feener, 1991a). They were attracted to crushed, injured workers of their host ant species (Table 2 is a list of crushed ants and the flies that have been attracted to them), as were males. Individuals of both sexes approached hosts, but males did not remain for long periods of time. A female will approach the host, walk over it, and follow one of two routines: either she will quickly (within about 15 seconds) begin to probe with her ovipositor and attempt to lay eggs (“layers”) or she will feed on hemolymph from the crushing wounds of

Table 2. List of ant species that, when injured, have attracted *A. miricauda*-group parasitoids (some species, marked with an asterisk, are attracted to healthy, noninjured hosts).

Ant host	Apocephalus parasitoid
<i>Camponotus banghaasi</i>	<i>brochus</i> *
<i>C. rapax</i>	<i>brochus</i> *
<i>C. sericeiventris</i>	<i>emargilatus</i>
<i>C. sericeiventris</i>	<i>magnicauda</i> *
<i>Cephalotes atratus</i>	<i>catholicus</i>
<i>C. atratus</i>	<i>roeschardae</i>
<i>Dinoponera gigantea</i>	<i>gigantivorus</i>
<i>D. gigantea</i>	<i>miricauda</i>
<i>D. longipes</i>	<i>dinoponerae</i>
<i>D. longipes</i>	<i>kungae</i>
<i>Dolichoderus attelaboides</i>	<i>catholicus</i>
<i>D. attelaboides</i>	<i>melinus</i>
<i>D. attelaboides</i>	<i>paraponerae</i>
<i>D. decollatus</i>	<i>melinus</i>
<i>Ectatomma gonionion</i>	<i>catholicus</i>
<i>E. lugens</i>	<i>paraponerae</i>
<i>E. tuberculatum</i>	<i>comosus</i>
<i>E. tuberculatum</i>	<i>lobicauda</i>
<i>E. tuberculatum</i>	<i>paraponerae</i>
<i>Odontomachus bauri</i>	<i>catholicus</i>
<i>O. chelifer</i>	<i>catholicus</i>
<i>O. chelifer</i>	<i>paldiae</i>
<i>O. haematodus</i>	<i>lopesi</i>
<i>O. hastatus</i>	<i>catholicus</i>
<i>Pachycondyla apicalis</i>	<i>crassilatus</i>
<i>P. apicalis</i>	<i>paraponerae</i>
<i>P. commutata</i>	<i>deceptus</i>
<i>P. commutata</i>	<i>melinus</i>
<i>P. crassinoda</i>	<i>catholicus</i>
<i>P. crassinoda</i>	<i>densepilosus</i>
<i>P. crassinoda</i>	<i>paraponerae</i>
<i>P. crassinoda</i>	<i>trifidus</i>
<i>P. harpax</i>	<i>catholicus</i>
<i>P. impressa</i>	<i>catholicus</i>
<i>P. impressa</i>	<i>crassilatus</i>
<i>P. impressa</i>	<i>latinsulosus</i>
<i>P. striata</i>	<i>piliventris</i>
<i>P. unidentata</i>	<i>atrimarginatus</i>
<i>P. unidentata</i>	<i>crassilatus</i>
<i>P. villosa</i>	<i>crassilatus</i>
<i>P. villosa</i>	<i>globosus</i>
<i>P. villosa</i>	<i>paraponerae</i>
<i>Paraponera clavata</i>	<i>paraponerae</i>
<i>P. clavata</i>	<i>tanyurus</i>

the ant (“feeders”). Feeders were not seen to oviposit, and those examined closely were found to be incapable of oviposition because they had no mature eggs in their ovaries. This is reminiscent of an observation by Disney (1994), that most carrion-feeding female phorids were not gravid. After ovipositing, layers often would quickly leave the host but sometimes would also stay to feed.

Little work has been done on the development of

sexual maturity in adult phorid flies, so it is not known if most phorids are able to develop eggs prior to feeding or if they require some sort of protein meal to produce their eggs. Other workers have found that carbohydrate meals (sugar) increased fecundity of *Megaselia halterata* (Wood), but it was not found to be an absolute necessity (Binns, 1980). Difficulties in keeping *Apocephalus* females alive in culture might make similar studies problematic, but there is at least an indication that these flies require a meal of hemolymph before eggs can be matured.

In contrast to other *A. miricauda*-group species, the *A. spatulatus*-subgroup species *A. brochus* and *A. magnicauda* attacked healthy, living hosts. In particular, we saw *A. brochus* appear to be attempting to oviposit in the back of the heads of the host ants. The hosts of both of these species, *Camponotus* spp., are highly divergent from those of other *A. miricauda*-group taxa; therefore, it is possible that the shift in behavior was accompanied by the shift in host. The only specimen of *A. emarginalatus*, the sister-species of *A. magnicauda*, that was collected from a host was attracted to an injured worker of *Camponotus sericeiventris*, however. This lends support to a scenario where, in *A. magnicauda* only, the host shift occurred first, and then the shift to attacking uninjured ants. Much further research is necessary to resolve these issues.

The other species of this group to have radically shifted their hosts, *A. melinus* and *A. roeschardae*, are possibly also each other's closest relatives. Each behaves in a similar manner to *A. paraponerae*, attacking injured hosts exclusively. It would be interesting to compare the chemical components of the mandibular glands of the hosts of these two species with those of *Paraponera clavata*. Apparently the chemicals of *Dolichoderus attelaboides* are similar enough to those of ponerine ants to occasionally attract species such as *A. paraponerae* and *A. catholicus* (Table 2).

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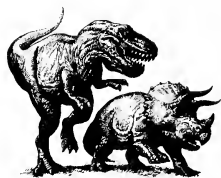
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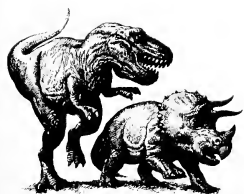
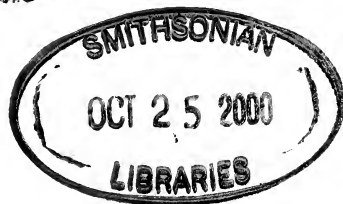
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# CONTRIBUTIONS IN SCIENCE

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# CRANIAL MORPHOLOGY OF *PTERODAUSTRO GUINAZUI* (PTEROSAURIA: PTERODACTYLOIDEA) FROM THE LOWER CRETACEOUS OF ARGENTINA

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AND MARILYN FOX<sup>4</sup>

**ABSTRACT.** With hundreds of filamentlike teeth in its mandibles and several other unique cranial features, the Argentine Early Cretaceous *Pterodaustro guinazui* ranks among the most specialized of pterosaurs. Based on newly collected specimens, this study provides a detailed description of the peculiar skull morphology of *Pterodaustro* and discusses its phylogenetic position within pterosaurs. An overview of the stratigraphy, sedimentology, and chronology of the Lagarcito Formation from which *Pterodaustro* comes is provided, along with an interpretation of the paleoenvironment. Cranial morphology corroborates the sister-taxon relationship between *Pterodaustro* and the Late Jurassic *Ctenochasma* proposed by most previous authors.

**RESUMEN.** Con cientos de dientes filamentosos en sus mandíbulas y varios otros caracteres craneanos distintivos, *Pterodaustro guinazui* del Cretácico temprano de Argentina, es uno de los pterosaurios más especializados. Sobre la base de ejemplares recientemente colectados, este estudio provee una descripción detallada de la peculiar morfología craneana de *Pterodaustro* y analiza sus relaciones filogenéticas dentro de los pterosaurios. También se provee una reseña estratigráfica, sedimentológica, y cronológica de la Formación Lagarcito—la formación portadora de *Pterodaustro*—junto con una interpretación del paleoambiente. La morfología craneana corrobora la relación de grupo hermano entre *Pterodaustro* y *Ctenochasma*, del Jurásico tardío, que fuera propuesta por la mayoría de los autores previos.

## INTRODUCTION

Paleontological expeditions led by J.F. Bonaparte in the late 1960s and early 1970s made a significant contribution to the knowledge of pterosaur evolution with the discovery of the spectacular pterodactyloid *Pterodaustro guinazui* Bonaparte, 1970 (original spelling emended by Wellnhofer [1978] following the guidelines of the ICZN). Collected from the banks of a creek cutting through beds of the Lagarcito Formation at a site known today as Loma del *Pterodaustro*, in what is now the Parque Nacional Sierra de las Quijadas (Fig. 1), *Pterodaustro* was the first pterosaur to be found in Ar-

gentina. When discovered, *Pterodaustro* represented only the second record of pterosaurs from South America (Price, 1971). Most importantly, *Pterodaustro* provided strong evidence that pterosaurs had evolved a filter-feeding morphology uncommon among tetrapods.

Twenty-five years after Bonaparte's exploratory expeditions to the Mesozoic deposits of the central Argentine province of San Luis, three large-scale excavations (in 1994, 1996, and 1998; see Chiappe et al., 1998a, b) were conducted at the quarry in the Loma del *Pterodaustro* where the first specimens of *Pterodaustro* were collected (Fig. 1). These excavations produced hundreds of skeletal remains of this pterosaur, including adult, juvenile, and neonate specimens (Chiappe et al., 1998b).

Despite the availability of material of *Pterodaustro* (even before the newly collected specimens) and the fact that this multitoothed pterosaur has consistently been used as a startling example of morphological specialization within this group (e.g., Benton, 1990; Wellnhofer, 1991; Chiappe and Chinsamy, 1996), the cranial anatomy of *Pterodaustro* has received little attention beyond early descriptions by Bonaparte (1971) and Sanchez (1973). The recent expeditions to Loma del *Ptero-*

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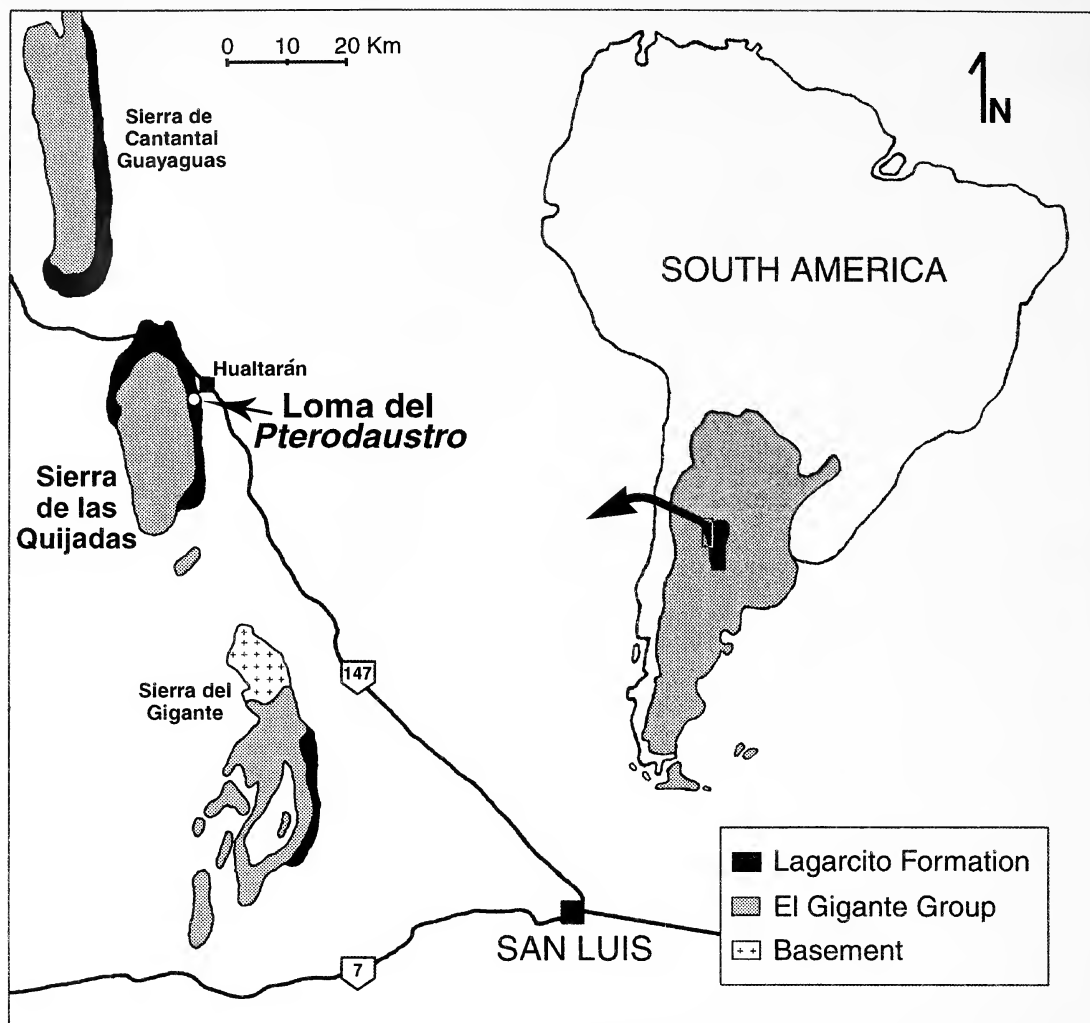


Figure 1 Geographic distribution of the Lagarcito Formation and location of the Loma del *Pterodaustro* fossil site

*daustro* collected several skulls and jaws of adult individuals. These are described here in detail. We also review previous anatomical data on this taxon in light of these specimens and discuss the phylogenetic position of *Pterodaustro* among pterodactyloids.

Institutions are abbreviated as follows: PVL, Sección Paleontología de Vertebrados, Instituto Miguel Lillo (San Miguel de Tucumán, Argentina); and MHIN-UNSL-GEO, Museo de Historia Natural, Universidad Nacional de San Luis (San Luis, Argentina).

## GEOLOGICAL SETTING OF THE LAGARCITO FORMATION

The Lower Cretaceous rocks of the Argentine Province of San Luis form a geotectonic unit known as the San Luis Basin (Flores and Criado Roque, 1972). This basin has been interpreted as a rift basin resulting from cortical stresses generated during

the breakdown of Gondwana (Ramos, 1990). Lithologically, this basin corresponds to a typical continental sequence of red beds exceeding 1,000 meters in thickness. These rocks crop out in several ranges grouped under the name Cordón de Serranías Occidentales, which extend in a north-south direction over roughly 300 kilometers (Fig. 1).

Stratigraphically, the Lower Cretaceous rocks of San Luis are divided into the Gigante Group and the Lagarcito Formation (Flores and Criado Roque, 1972; Fig. 2), which comprise the entire duration of two cycles of infilling of a continental basin (Rivarola, 1994). These cycles represent two depositional megasequences involving environments that range from alluvial fans associated with alluvial plains to fluvial plains and lacustrine environments. Rocks of the Gigante Group form most of the two megasequences, and they are composed of conglomerates, sandstones, claystones, and evaporites. The Lagarcito Formation forms the top section of

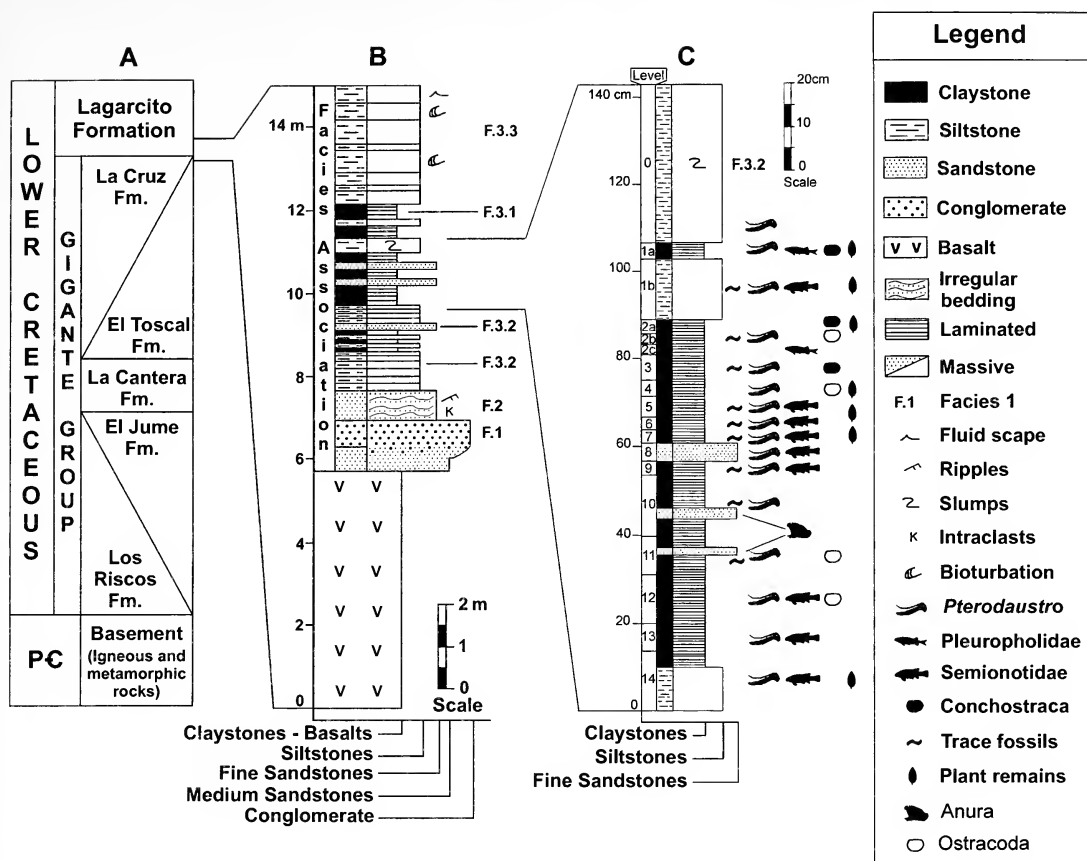


Figure 2 Stratigraphic section and fossil occurrences of the Loma del *Pterodaustro* fossil site (from Chiappe et al., 1998b)

the second megasequence, and it is formed by fine sediments developed under fluvio-lacustrine environments associated with limited development of aeolian dunes.

In the Sierra de Las Quijadas, the Lagarcito Formation is best exposed at Quebrada de Hualtarán (Fig. 1). In this area, 45 meters of continuous sediments of sandstones and mudstones, representing at least three fluvio-lacustrine sequences, rest over a basaltic flow dated between 107.4 and 109.4 Ma (Yrigoyen, 1975).

Most fossils from the Lagarcito Formation have been excavated at a small site (~50 m<sup>2</sup>). This site has become known as Loma del *Pterodaustro* (Chiappe et al., 1995). The Loma del *Pterodaustro* fossil site corresponds to the basal 8 meters of the section of the Lagarcito Formation at Quebrada de Hualtarán (Fig. 2). A detailed sedimentological study of these deposits has been presented elsewhere (Chiappe et al., 1998a). Three lithofacies can be recognized from base to top: Facies 1, inversely graded, massive sandstones to massive, matrix-supported conglomerates with lenticular geometry and disordered fabric; Facies 2, fine-grained sandstone with a flat top and base, and asymmetric ripples; and Facies 3, massive to laminated claystones, silt-

stones, and very fine sandstones, which represent a thickening and coarsening upward sequence. Facies 1–3 have been interpreted as debris flows, sheet-floods deposited in a sand-flat near the shore, and a typical lake sequence, respectively. With very few exceptions, all fossils from Quebrada de Hualtarán come from Facies 3 (Chiappe et al., 1998a, b). This facies has been subdivided into three subfacies of low-energy deposits (Fig. 2). One of them (F3.1; Fig. 2) is composed of laminated, very fine sediments entombing the majority of fossils. This subfacies was interpreted as forming in the offshore portion of a lake.

#### BIOTA, PALEOENVIRONMENT, AND CHRONOLOGY OF THE LAGARCITO FORMATION AT LOMA DEL *PTERODAUSTRO*

The fine sandstones and claystones of the Lagarcito Formation at Loma del *Pterodaustro* have provided abundant fossil remains (Chiappe et al., 1995, 1998a, b). These include a diverse array of trace fossils, plant remains, conchostracans, ostracods, and various vertebrates. Among the vertebrate fauna are semionotid and pleuropholid fishes, anurans,

and abundant pterosaur remains, most of which are probably of *Pterodaustro*. Preservation of delicate structures such as the needlelike mandibular teeth of *Pterodaustro* and the imprints of stems and reproductive plant structures led to the classification of these beds as a Konservat Lagerstätte *sensu* Seilacher et al. (1985) (see also Seilacher, 1990; Chiappe et al., 1995, 1998a).

The facies association of the lower section of the Lagarcito Formation, along with the absence of evidence of subaerial exposure and evaporite levels, suggest that rocks at Loma del *Pterodaustro* correspond to a fluvio-lacustrine sequence of long duration. Preservation of laminations in subfacies 3.1 indicates that the lake was at least periodically thermally stratified, and it may have developed an anoxic bottom that prevented destruction of the laminations and favored preservation of delicate structures.

The lower section of the Lagarcito Formation, at Quebrada de Hualtarán, is interpreted as a complete sequence of transgression and expansion of a perennial lake over an alluvial sandy flat, followed by its gradual infilling and shallowing during a high-stand period of the lacustrine system. The predominant climate during deposition of the Lagarcito Formation is interpreted as semiarid and seasonal (Chiappe et al., 1998a).

Originally, the Lagarcito Formation was placed in the Tertiary (Flores, 1969). After the discovery of *Pterodaustro guinazui*, Bonaparte (1970) placed this unit within the Upper Jurassic on the basis of similarities between this pterosaur and Late Jurassic pterodactyls. Subsequently, with the discovery of an Aptian-Albian palynoflora in the underlying La Cantera Formation (Gigante Group) and the Early Cretaceous dates for the basalts at Quebrada de Hualtarán, Yrigoyen (1975) placed the Lagarcito Formation within the Upper Cretaceous, and Bonaparte (1978) allocated those strata to the Lower Cretaceous. Recent interpretations, combining sedimentological, stratigraphical, and paleontological data, have adjusted the chronology of this lithostratigraphic unit, supporting an Albian age (see Chiappe et al. [1998a] for a more extensive discussion of the age of these beds).

### CRANIAL ANATOMY OF *PTERODAUSTRO GUINAZUI*

This study is mostly based on recently collected material, including a skull and jaw (MHIN-UNSL-GEO-V-57), another skull and jaw missing their rostral halves (MHIN-UNSL-GEO-V-135), and an isolated, nearly complete jaw (MHIN-UNSL-GEO-V-175). As in other known skulls of *Pterodaustro*, the new crania and jaws are flattened, preserved essentially in two dimensions. Many of the bones

are broken, thus complicating identification between sutures. In MHIN-UNSL-GEO-V-57 and MHIN-UNSL-GEO-V-135 the skull is exposed on its left side; only a few right bones are visible. In MHIN-UNSL-GEO-V-57 the left mandible is exposed laterally, whereas in MHIN-UNSL-GEO-V-135 the right one is exposed. MHIN-UNSL-GEO-V-175 exposes its left side.

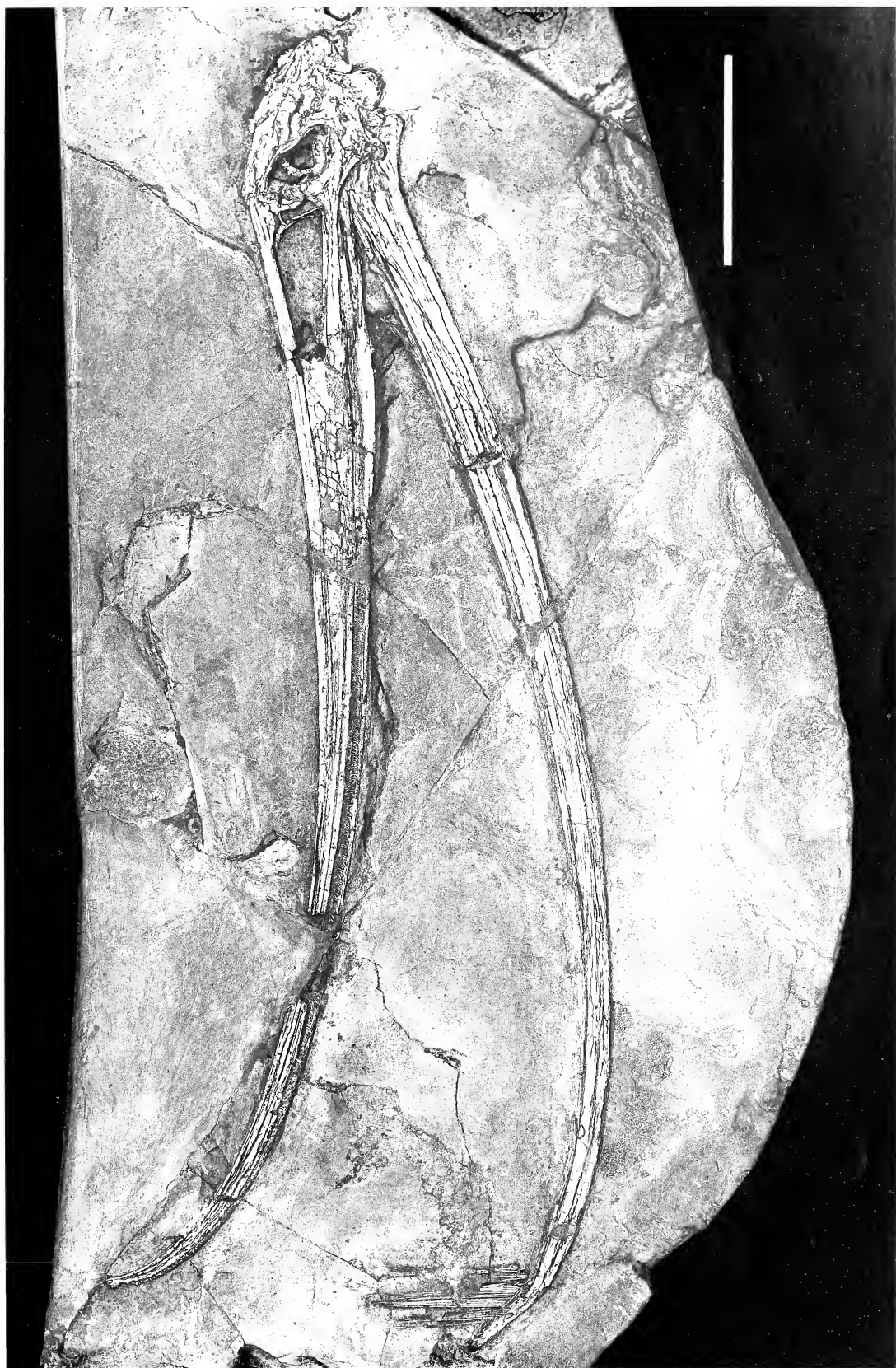
### SKULL

The skull of *Pterodaustro* is characterized by a remarkably long, slender, and upwardly curved preorbital region, which comprises more than 85 percent of the skull length (Figs. 3, 4). MHIN-UNSL-GEO-V-57 (Fig. 3) has a total cranial length of almost 29 cm. This is approximately 20 percent larger than that of PVL-3860, the most commonly figured specimen of *Pterodaustro* (Sanchez, 1973; Bonaparte, 1978; Wellnhofer, 1991). MHIN-UNSL-GEO-V-135 (Fig. 5) is somewhat (~10 percent) larger than MHIN-UNSL-GEO-V-57. The nasoantorbital fenestra in this taxon is comparatively small (Kellner, 1995), reaching between 10 and 12 percent of the total skull length. Because the skull is flattened, no detailed information regarding the temporal openings is available.

In lateral view, the snout curves gently upward (Figs. 3–5). A long premaxilla and maxilla, whose suture is not discernible in any of the available specimens, form the snout. As in other pterosaurs (Wellnhofer, 1978), the slender premaxilla forms the entire dorsal margin of the snout, approaching the rostral margin of the orbit. In MHIN-UNSL-GEO-V-57 it is uncertain whether the premaxilla was toothed or not because the most rostral end of the snout is not preserved. Unfortunately, none of the remaining known skulls clarify this issue. In MHIN-UNSL-GEO-V-57 both premaxillae seem to be fused to each other for most of their length. Sanchez (1973) reported a thin, caudal tongue of the maxilla contacting the nasal and excluding the premaxilla from the nasoantorbital fenestra (Figs. 6A, 7). This condition, which is different from that of most pterosaurs (e.g., Wellnhofer, 1978; Wellnhofer and Kellner, 1991), has not been corroborated by either of the new specimens, in which the premaxilla forms the dorsal margin of the nasoantorbital fenestra (Figs. 6B, 8, 9). Also differing from previous interpretations (Sanchez, 1973), the premaxilla is extended farther caudally over the rostral half of the orbit (cf. Figs. 6A, B, 8).

The maxilla forms most of the lateral surface of the snout (Figs. 3–5, 7). This bone tapers rostrally from the rostral margin of the nasoantorbital fenestra. In all available specimens the suture between this bone and the rostral end of the jugal is not clear. In fact, these two bones appear to be

Figure 3 Skull and jaws of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57) in left lateral view. Scale bar = 5 centimeters



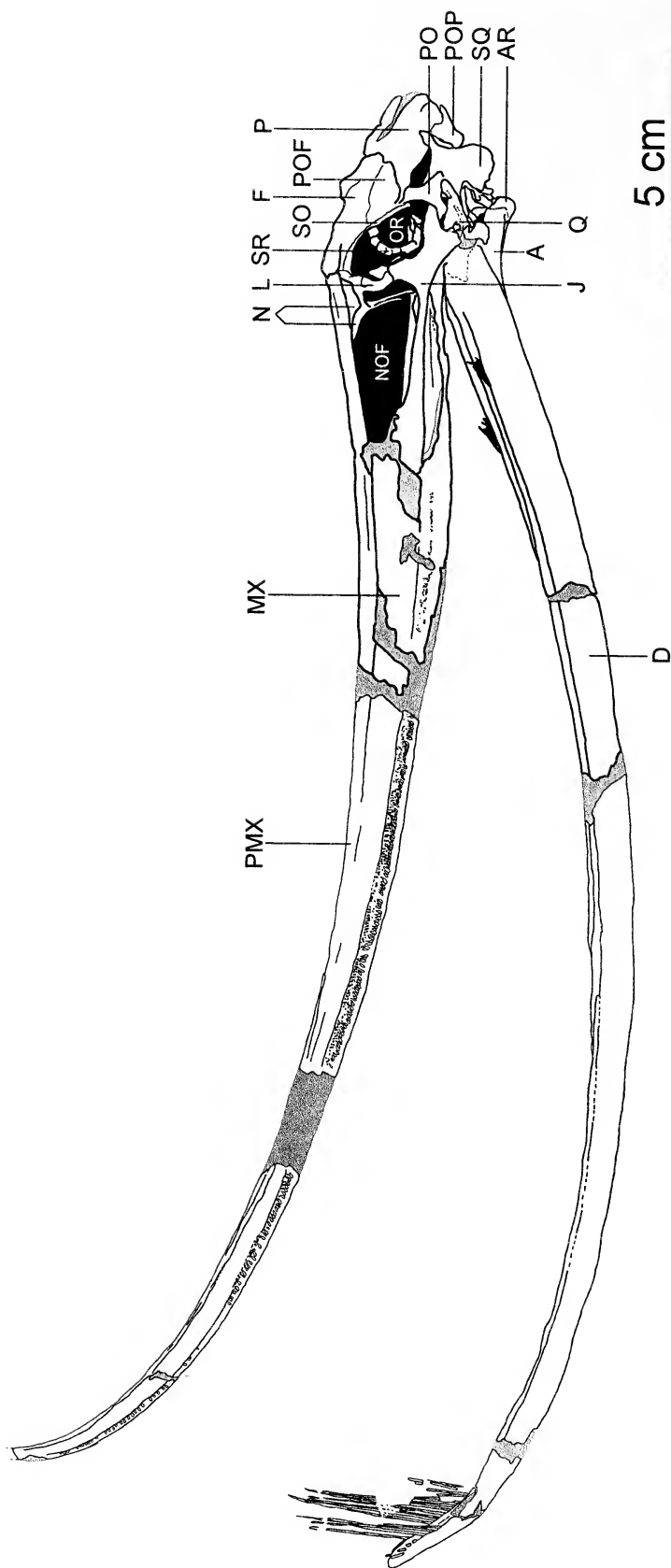
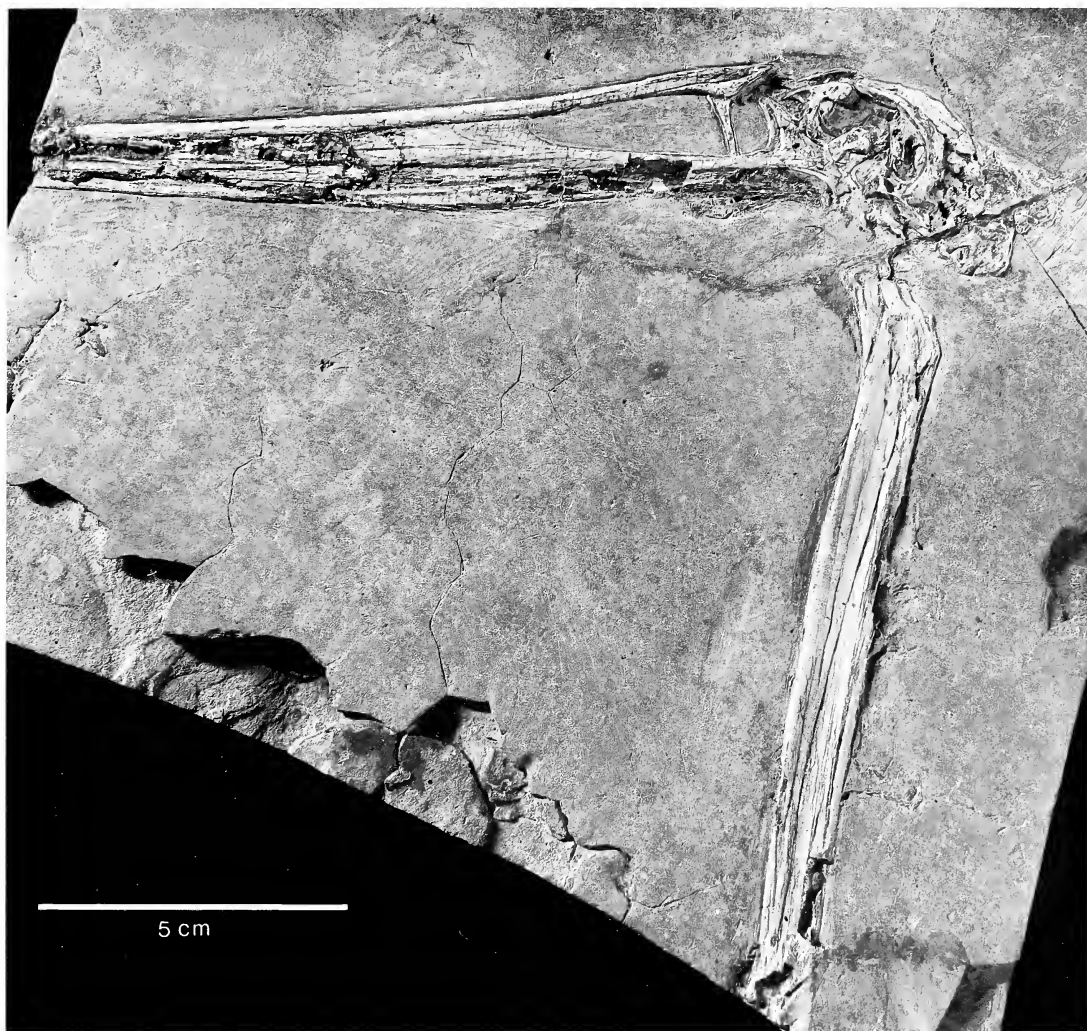


Figure 4 Camera lucida drawing of the skull and jaws of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57) in left lateral view. Abbreviations: A, angular; AR, articular; D, dentary; F, frontal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; NOF, nasolacrimal fenestra; P, parietal; PMX, premaxilla; PO, postorbital; POP, postfrontal; POF, postorbital; POP, postfrontal; SQ, squamosal; SR, sclerotic ring; SO, supraorbital; SQ, squamosal; SR, sclerotic ring





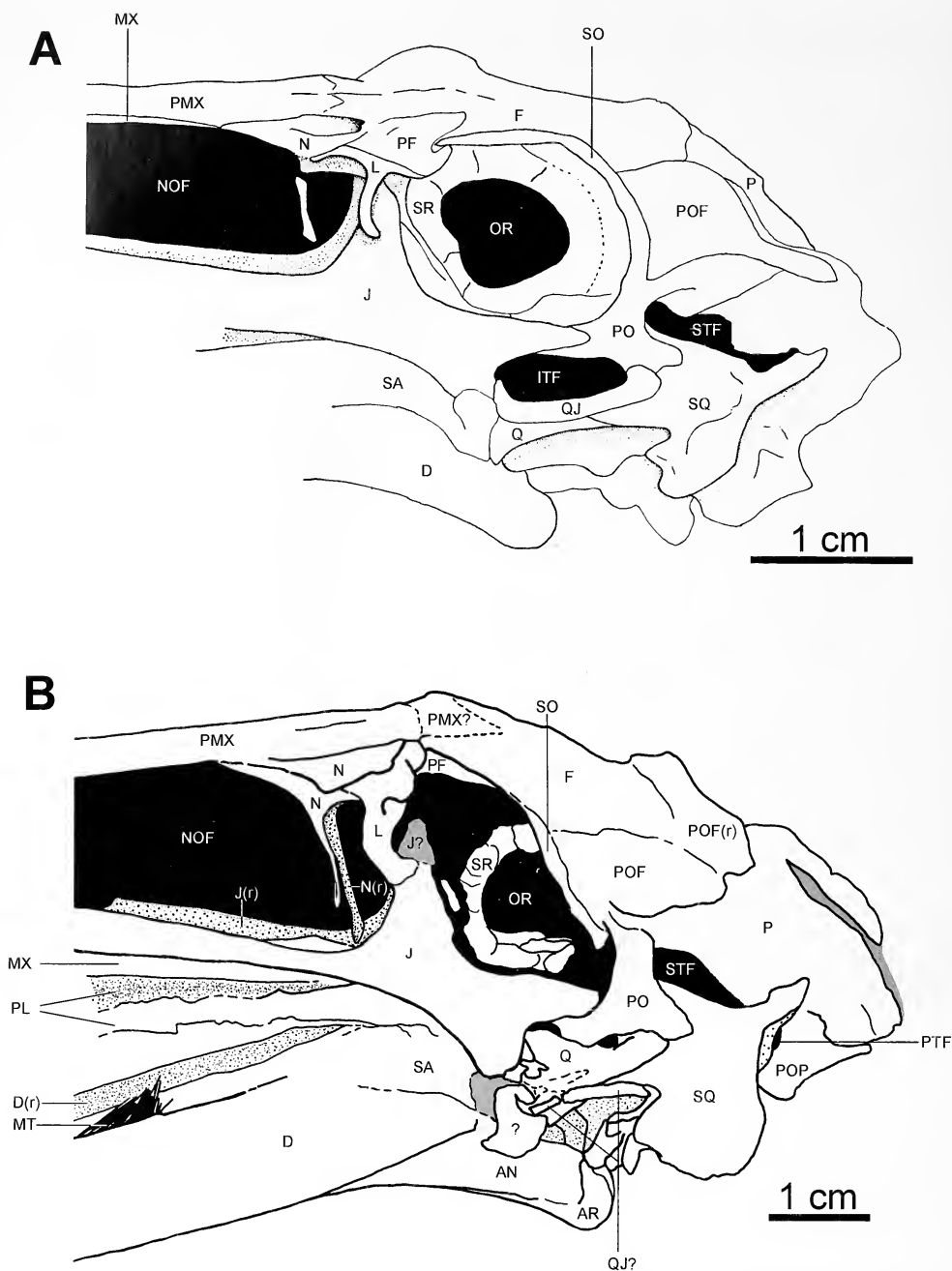
**Figure 5** Skull and jaws of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-135). Skull in left lateral view; mandible in right lateral view

fused to each other. However, a thin tongue of the maxilla projects caudally beneath the jugal, reaching the caudal margin of the nasoantorbital fenestra (Figs. 6B, 8). The maxilla bears hundreds of tiny teeth, which in MHIN-UNSL-GEO-V-57 extend from the rostral end of the maxilla to near the rostral margin of the nasoantorbital fenestra (Fig. 4). Thus, the caudal extension of the maxillary tooth row of this specimen extends much more than that illustrated by Sanchez (1973) in her skull reconstruction (Fig. 7).

The dorsocaudal corner of the nasoantorbital fenestra is formed by a subtriangular nasal (Figs. 6–9). This element has a comparatively long, thin rostral process that reaches the center of the nasoantorbital fenestra, underlying the premaxilla (Figs. 6B, 9). Ventrally, the nasal tapers into a thin process that fails to reach the jugal, although it ends very close to it (Sanchez, 1973). The contact of the

right nasal and jugal in MHIN-UNSL-GEO-V-57 (Fig. 6B) is not natural and can be regarded as a result of deformation during crushing. The morphology of the ventral nasal process is similar to that of archaeopterodactyloids (*sensu* Kellner, 1996, 1997) such as *Pterodactylus* Cuvier, 1809, and *Germanodactylus* Young, 1964. All more derived pterodactyloids, which are members of the Dsungaripteroidea (Young, 1964; Kellner, 1996), have either displaced this nasal process medially (e.g., *Anhanguera* Campos and Kellner, 1985) or have almost lost it (e.g., *Quetzalcoatlus* Lawson, 1975) (see Kellner and Langston, 1996).

The lacrimal of *Pterodaustro* is wedged between the nasal, prefrontal, and jugal. This bone has three distinct processes: a short rostral one, a longer and wider caudal one, and a hook-shaped ventral one (Figs. 6B, 8, 9). Although now flattened, in life the ventral process probably extended slightly lateral to



**Figure 6** Camera lucida drawings of the postorbital region of *Pterodaustro guinazui*. A, from Sanchez (1973) (PVL-3860). B, MHIN-UNSL-GEO-V-57. Abbreviations: ITF, infratemporal fenestra; OR, orbit; PF, prefrontal; QJ, quadra-tojugal; SA, surangular; STF, supratemporal fenestra. Other abbreviations as in Figure 4

the orbit, as seen in some other pterosaurs known from less distorted specimens (e.g., *Anhanguera*). In MHIN-UNSL-GEO-V-57 (Fig. 6B), this process is significantly more robust than the process illustrated by Sanchez (1973; Fig. 6A), which agrees more with that of MHIN-UNSL-GEO-V-135 (Fig. 9). MHIN-UNSL-GEO-V-135 clearly shows that the bone identified as a prefrontal by Sanchez (1973)

is, in fact, the dorsal exposure of the caudal process of the lacrimal (Fig. 9).

Rostrally, both frontals are united by a suture that becomes indistinguishable in the caudal half. Caudally, the frontals are wedged between the post-frontals and parietals (Figs. 6, 8).

The parietals in both specimens are very crushed, making their edges difficult to interpret, particular-

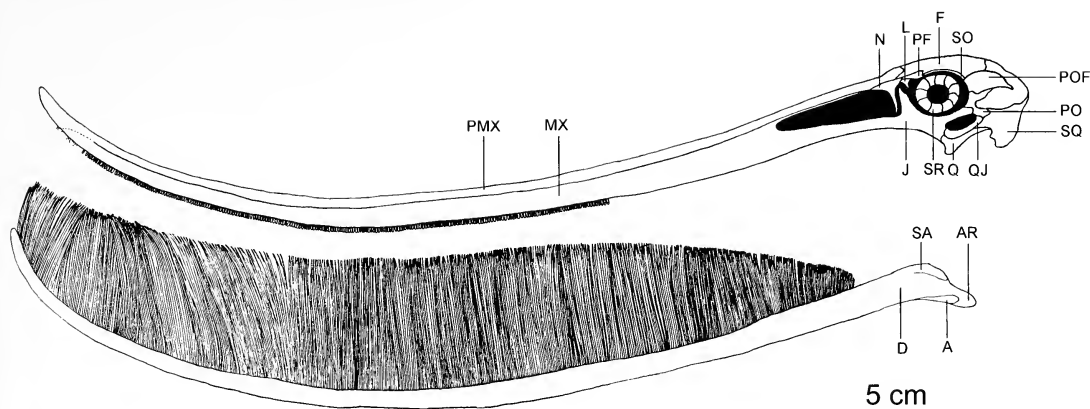


Figure 7 Sanchez's (1973) cranial reconstruction of *Pterodaustro guinazui*. Abbreviations as in Figures 4 and 6

ly in their caudal region. As far as they can be observed, both elements are fused to each other along the midline. Although the boundaries of this bone were not clearly illustrated by Sanchez (1973; Fig. 7), the new specimens indicate that the parietal forms the medial margin of the supratemporal fenestra (Fig. 6B), as in most archosaurs (Romer, 1956). Interestingly, the caudal region of the parietals of all available specimens, including those previously described by Bonaparte (1971) and Sanchez (1973), is slightly extended as a thin bony lamina (Figs. 6, 8, 9). Although some of this appearance results from crushing, it cannot be ruled out that the parietals projected caudally as a small crest. Even if this interpretation is correct, this parietal crest would have been very small and not as developed as in some other pterosaurs (e.g., *Gallodactylus* Fabre, 1974).

Caudal to the lacrimal, there is a flattened bone, here interpreted as the **prefrontal**. Based on MHIN-UNSL-GEO-V-57, this bone would correspond to the rostral portion of what Sanchez (1973) interpreted as the **supraorbital** (Fig. 6A). The slender supraorbital does indeed line the dorsal margin of the orbit and precludes the frontal from the orbital margin (Sanchez, 1973), but it does not appear to extend rostrally to reach the lacrimal (Fig. 6B).

In MHIN-UNSL-GEO-V-57, the **postfrontal** is a suboval element that contacts the frontal medially and the parietal caudally and is partially overlain by the postorbital (Fig. 6B). A caudally oriented process of the postfrontal, as illustrated by Sanchez (1973), was not observed in the new specimens.

The **postorbital** is a triradiate element (Fig. 6B). Its dorsal process is slightly expanded and abuts against the parieto-postfrontal suture. The ventral process overlays the dorsocaudal process of the jugal, whereas the caudal process overlies the lateral surface of the squamosal. The unusual condition of having the postorbital completely separated from the frontal by the postfrontal (Figs. 6B, 8), also indicated by Sanchez (1973; Fig. 6A), distinguishes

*Pterodaustro* from other pterosaurs (Wellnhofer, 1978; Wellnhofer and Kellner, 1991).

The **jugal** is a conspicuous bone that forms the ventrocaudal and ventral margins of the nasoantorbital fenestra and the orbit, respectively, and the rostroventral corner of the infratemporal fenestra (Fig. 6A). The jugal has four distinct processes (Figs. 8, 9). The rostral process forms the ventral margin of the nasoantorbital fenestra and, in MHIN-UNSL-GEO-V-135, projects rostrally beyond the nasoantorbital fenestra for about 9 mm (Fig. 9). This extension is shorter than interpreted by Bonaparte (1971). The dorsal process contacts the lacrimal, forming a bony bar that separates the orbit from the nasoantorbital fenestra. This process is robust and tapers to a sharp point (Fig. 9). Caudally, the jugal forks into dorsocaudal and ventrocaudal processes. The former is overlain by the postorbital and takes part in the rostral margin of the infratemporal fenestra. The second partially overlies the quadrate (displaced in MHIN-UNSL-GEO-V-57).

The tetradactylate jugal of all known *Pterodaustro* specimens (Figs. 6, 9) differs markedly from the tri-radiate shape of the jugal of other pterodactyls, including *Pterodactylus* and *Ctenochasma* Meyer, 1851, resembling more the morphology of the jugal in some basal pterosaurs (Wellnhofer, 1991). The difference appears to be mainly on the ventrocaudal portion, where the jugal of *Pterodaustro* bears an extended process overlying the quadrate (Figs. 6B, 8). This contact between the quadrate and the jugal is known only for this taxon. Furthermore, *Pterodaustro* also differs from some derived pterodactyls (e.g., *Anhanguera*, *Pteranodon* Marsh, 1876) in that its jugal lacks a pronounced caudo-dorsal ridge near the nasoantorbital fenestra.

The **quadratojugal** is very difficult to discern in most specimens. In MHIN-UNSL-GEO-V-57, a thin and incomplete bone, displaced ventrally to the quadrate, is tentatively identified as the left quadratojugal (Fig. 6B). According to Sanchez (1973),

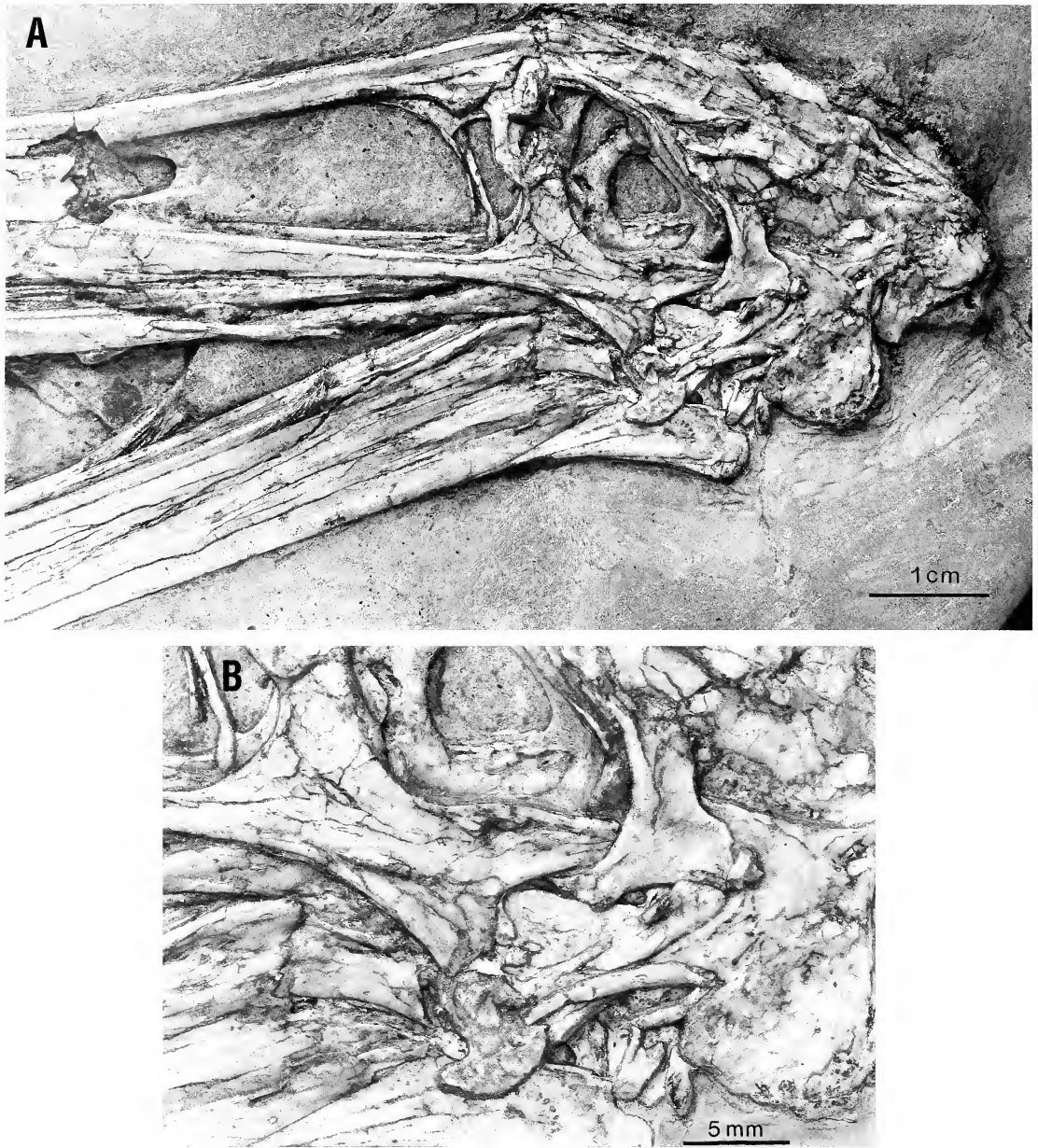


Figure 8 Nasoantorbital, orbital, and postorbital regions of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57), in left lateral view. A, general view. B, detail of the jugal and surrounding bones

this element forms all of the ventral margin of the infratemporal opening. However, such a configuration has not been observed in any other pterodactyloid (Wellnhofer, 1978).

The **quadrate** is not well preserved in any of the new specimens. This bone is rostroventrally tilted (more than  $150^\circ$  relative to the ventral margin of the skull; Fig. 6), a feature common to all Archaeopterodactyloidea (Kellner, 1996, 1997), as well as the Azhdarchidae (Unwin and Junchang, 1997). Rostrally, the main body of the quadrate projects mediad as a broad pterygoid flange. The

proximal end of the quadrate appears to articulate with the squamosal.

The **squamosal** has an expanded, ventrolaterally rounded body (Figs. 6B, 8, 9). As shown by Sanchez (1973), this bone forms the entire ventral margin of the supratemporal fenestra (Fig. 6), restricting the postorbital to the rostral margin of this arcade. The squamosal has a thin, tapering caudomedial process that abuts the braincase (Fig. 6A). Rostroventrally, the squamosal bears a sharp, thin process that runs through the proximal half of the caudal margin of the quadrate.

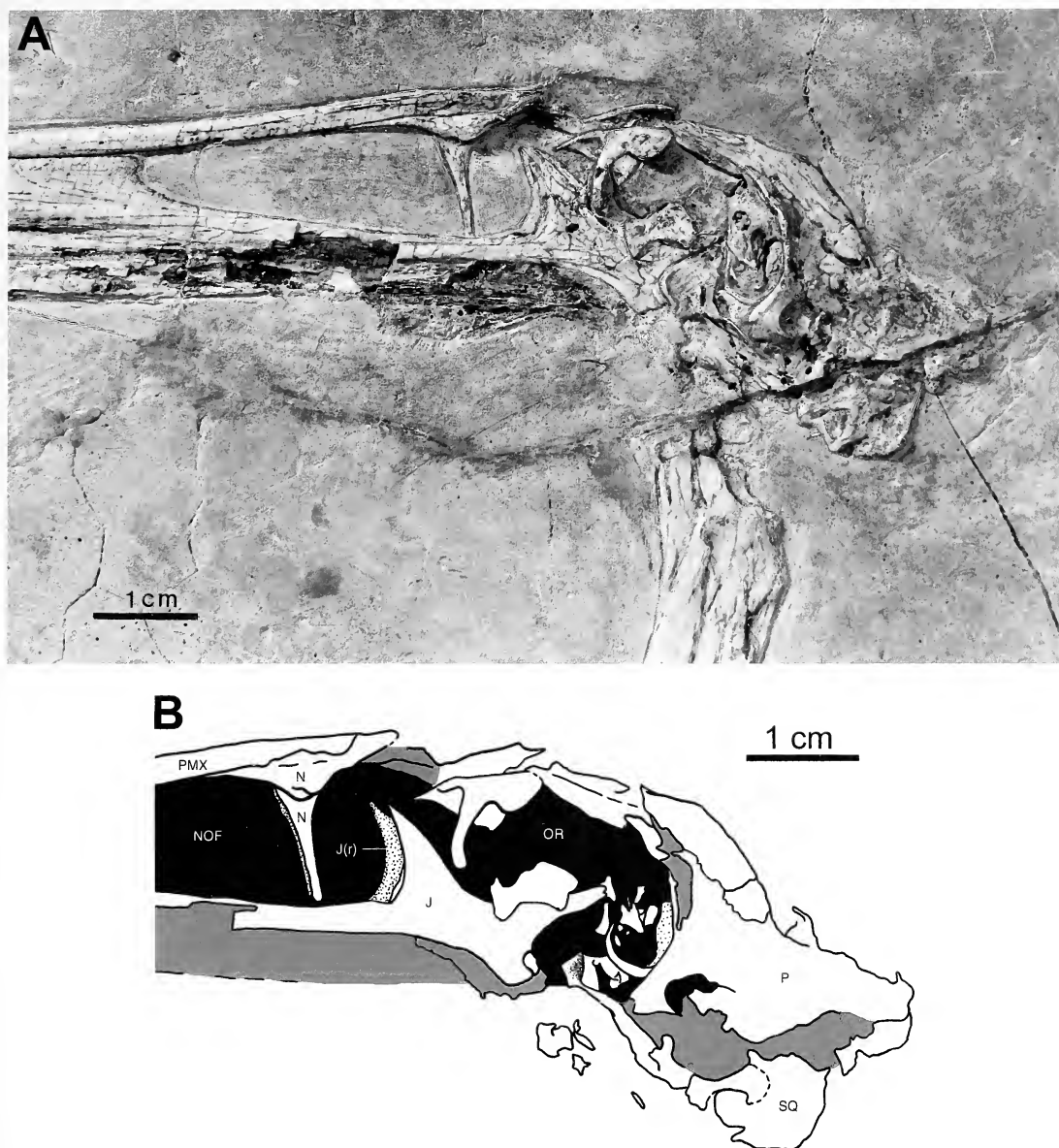


Figure 9 A, nasoantorbital, orbital, and postorbital regions of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-135), in left lateral view. B, interpretive drawing. Abbreviations as in Figures 4 and 6; J(r) refers to the right jugal

Aside from the parietals, the remaining elements of the braincase appear to be completely fused, lacking discrete sutures. Yet a truncated, subtriangular bone extends laterally from the braincase in MHIN-UNSL-GEO-V-57 (Fig. 6B). This is most likely the paraoccipital process of the opisthotic. A small window between this bone and the squamosal may be the posttemporal fenestra (Fig. 6B). Although Sanchez (1973) did not identify this bone, it is very likely that the bone positioned caudoventral to the squamosal in PVL-3860 might also be the opisthotic.

Portions of the palatal bones appear in MHIN-

UNSL-GEO-V-57 and MHIN-UNSL-GEO-V-135, but their compression ventral to the maxilla at the level of the nasoantorbital fenestra prevents recovering any information.

The orbit encloses a sclerotic ring. The number of plates forming the sclerotic ring is uncertain. In MHIN-UNSL-GEO-V-57, at least eight or nine plates can be distinguished (Fig. 6B). Pterosaur sclerotic rings have been reported previously, but complete sclerotic rings are known only for a handful of specimens. In *Rhamphorhynchus* (Meyer, 1847), sclerotic rings are formed by 13 to 15 elements and in *Pterodactylus* by about 20 elements (Wellnhofer,



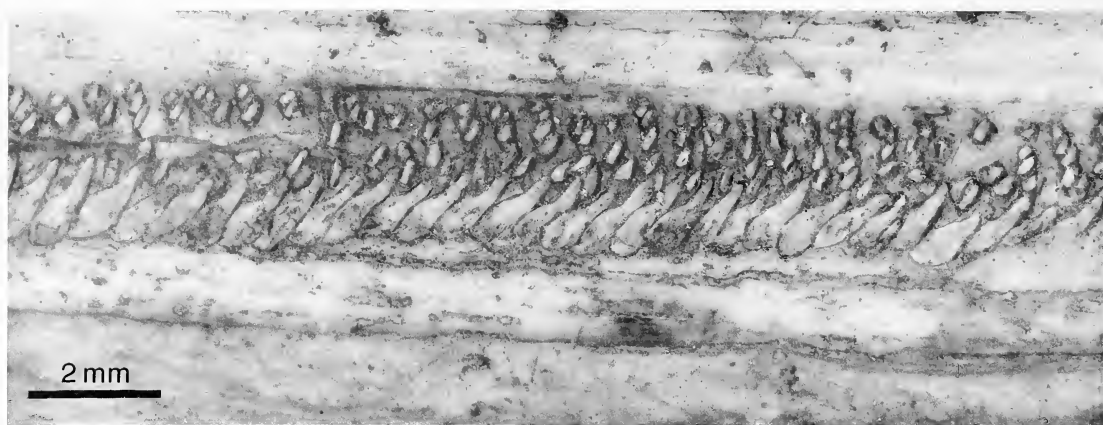


Figure 10 Detail of the midportion of the maxilla of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57), in left lateral view

1978). In more derived forms such as *Pteranodon* (Eaton, 1910; Bennett, 1991) and anhanguerids (specimen in Iwaki Coal and Fossil Museum, Japan), 12 or 13 sclerotic plates are present.

## MANDIBLE

Like the snout, the mandible is curved and slender, tapering rostrally (Figs. 3, 4, 7). Most of the available information is from the lateral surface. The mandible follows the extension of the preorbital region of the skull, making the lower jaw of *Pterodaustro* proportionally longer than in other pterosaurs. The dentary extends almost the entire length of the mandible, and its medial dentigerous margin is higher and thicker than the lateral one. In MHIN-UNSL-GEO-V-57, for example, the dentary margin lateral to the tooth row is one-third to one-quarter shorter than the medial one.

The dentary bears teeth throughout its length (Figs. 4, 6B). This condition differs from that of other archaeopterygoids such as *Ctenochasma*, *Germanodactylus*, *Gallodactylus*, and *Pterodactylus*, in which the dental row ends more rostral to the caudal end of the dentary. For example, whereas *Ctenochasma*, *Gnathosaurus* Meyer, 1834, and *Pterodactylus* have teeth along less than 65 percent of the mandibular length (Wellnhofer, 1978), *Pterodaustro* has teeth along nearly 90 percent of its mandibular length.

The region of the **surangular** is not well preserved in any of the new specimens and the boundary between this bone and the dentary is unclear. In MHIN-UNSL-GEO-V-57, the caudal portion of the surangular is comparatively thick, forming the rostradorsal part of the articular surface for the quadrate. Toward the rostral part, the surangular appears to form a process that contributes to the dorsocaudal margin of the mandibular ramus. This process seems to end before the first mandibular tooth, where it interlocks with the dentary.

The **angular** is exposed laterally (Fig. 6B), but its boundaries with the surrounding bones, particularly with the articular, are difficult to interpret in the available material. Rostrally, this bone tapers under the ventral margin of the dentary. Based on MHIN-UNSL-GEO-V-57 (Fig. 6B), the dorsal extension of the angular is greater than interpreted by Sanchez (1973; Fig. 7).

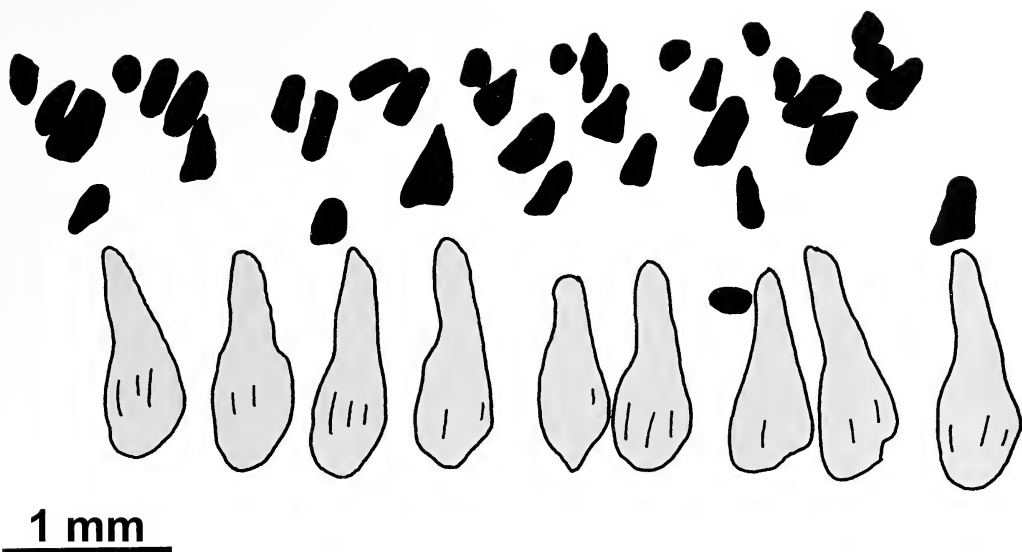
The **articular** forms the caudal tip of the mandible (Figs. 6B, 7). This bone has a long, thin wedge underneath the angular. Unfortunately, the lateral exposure of this bone prevents recovering information about the articular facet of the mandible.

## DENTITION

The upper dentition is formed by hundreds of minute teeth of equal size (Figs. 4, 10, 11). These teeth have spatulate crowns and thin, conical bases. Interestingly, the upper teeth are not set in alveoli (*contra* Sanchez, 1973), nor in a longitudinal groove. Instead, they are joined to the lateral surface of the recessed maxillary dentigerous margin (Figs. 10, 11). Thus, their attachment to the maxilla must have been by means of individual ligaments or, more likely, by a supporting soft-tissue structure that lined the dentigerous margin of the upper jaw. Interestingly, dorsal to most maxillary teeth, a dorso-rostrally oriented row of tiny ossicles is present, usually composed of four elements (Figs. 10, 11).

The mandibular teeth are very close to each other (Figs. 12–14). In cross section, they are oval to subelliptical (Chiappe and Chinsamy, 1996) and considerably thicker rostrally than in the middle and caudal sections of the mandible. The teeth are set in a groove along most of the jaw (Fig. 13), although shallow individual alveoli develop in the rostral end of the dentary (Fig. 12).

The external surface of the mandibular teeth is smooth (Figs. 13, 14). From histological sections we determined that the mandibular teeth are formed by a peripheral, thin layer of nonprismatic



**Figure 11** Camera lucida drawing of the maxillary teeth and associated rows of ossicles of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57), in left lateral view

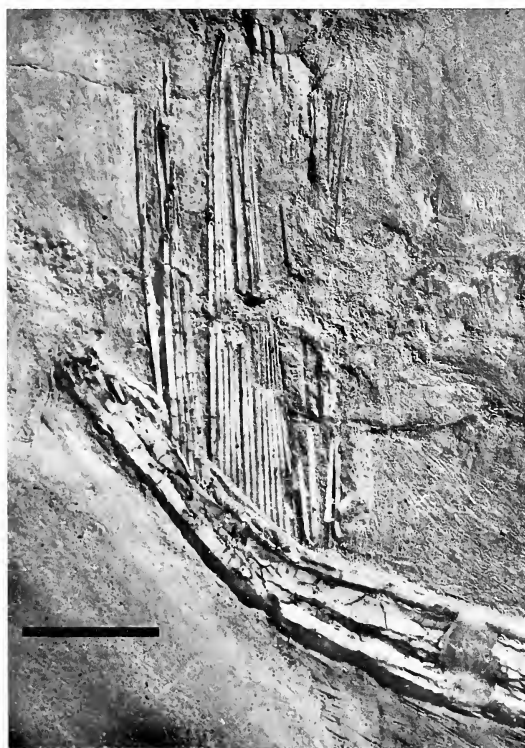
enamel and an inner core of dentine surrounding a central pulp cavity (Chiappe and Chinsamy, 1996). These sections have not shown incremental lines in either the enamel or the dentine, contrary to teeth of *Anhanguera* (Chinsamy and Kellner, 1996).

#### SYSTEMATIC REMARKS

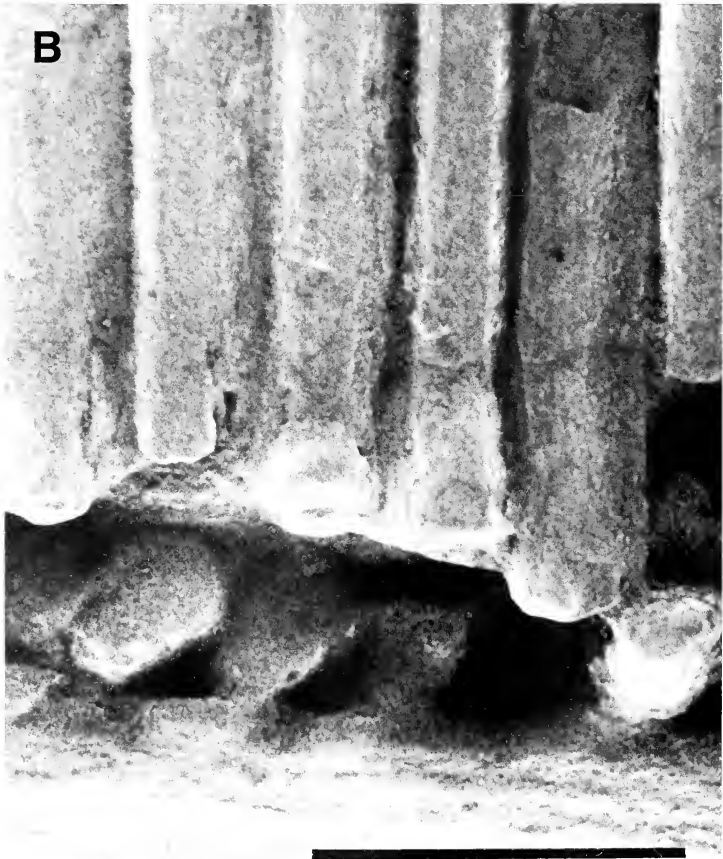
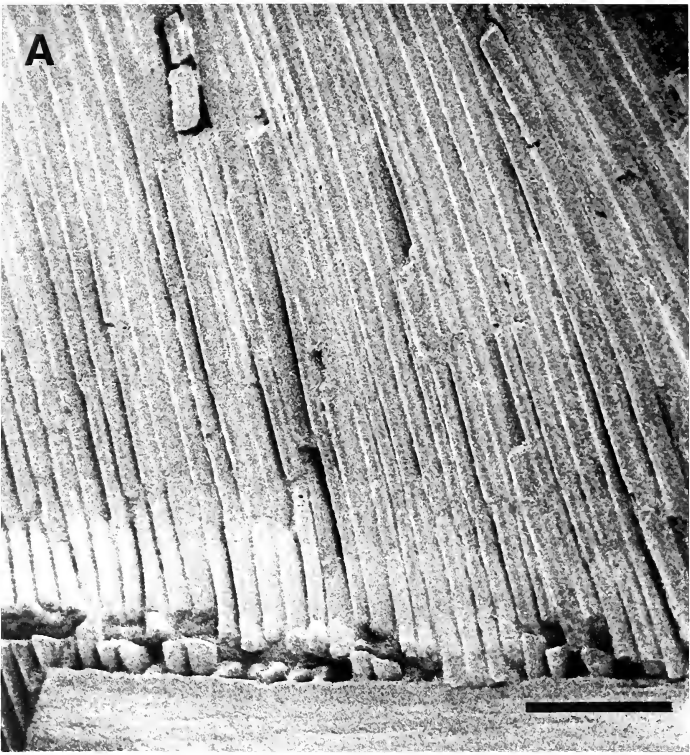
The first remains of *Pterodaustro guinazui* were all isolated specimens providing limited anatomical information about this pterosaur. A humerus (PVL-2571) was established as the holotype and a few other elements as the hypodigm (Bonaparte, 1970). On the basis of the similarity between these elements and those of *Pterodactylus*, Bonaparte (1970) assigned *Pterodaustro* to the Pterodactylidae.

With the discovery of its peculiar skull and mandible, *Pterodaustro* was placed in its own family, Pterodaustriidae (Bonaparte, 1971), particularly because of its unique dentition and extreme extension of its preorbital region. Bonaparte (1971) considered that the Pterodaustriidae was related both to the Pterodactylidae and the Ctenochasmatidae. Further cranial material of *Pterodaustro* was studied by Sanchez (1973), who arrived at the same conclusions as Bonaparte. The systematic relationships proposed by Bonaparte (1971) were adopted by later authors (e.g., Casamiquela and Chong-Diaz, 1980; Wellnhofer, 1991), although Wellnhofer (1978: fig. 32) considered *Pterodaustro* more closely related to *Ctenochasma*.

In a cladistic analysis of pterosaur cervical vertebral morphology, Howse (1986: figs. 11, 12) placed *Pterodaustro* in a polytomy with *Pterodactylus antiquus* Soemmerring, 1812, *Pterodactylus longicollum* Meyer, 1854, and *Ctenochasma*



**Figure 12** Detail of the rostral end of the dentary of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-57), in left lateral view. Scale bar = 1 centimeter





(Fig. 15). Howse (1986) correctly pointed out that all these pterosaurs have elongated midcervical vertebrae with low neural spines, although he failed to acknowledge the presence of this condition in *Germanodactylus* and *Gallodactylus suevicus* (Quenstedt, 1855).

Bennett (1994) regarded *Pterodaustro* as a basal pterodactyloid that formed a trichotomy with *Pterodactylus kochi* Wagner, 1837, and all other pterodactyloids (Fig. 15). This interpretation disagrees with all previous hypotheses by setting *Pterodaustro* apart from *Ctenochasma*, a claim that Bennett (1994) supported by citing the absence of a premaxillary sagittal crest in *Pterodaustro*. *Pterodaustro* does not have a premaxillary sagittal crest, but such a crest is also absent in several other pterodactyloids (e.g., *Gallodactylus*, *Pteranodon*, *Nyctosaurus* Marsh, 1876), which Bennett (1994) included in his grouping of all pterodactyloids other than *Pterodaustro* and *Pterodactylus kochi*. Furthermore, several characters presented by Bennett (1994) that diagnose subsequent, more exclusive nodes cannot be observed in *Pterodaustro* and are therefore equivocal, at least relative to this taxon (e.g., cervicalization of dorsal vertebrae and presence of helical jaw joint).

More recently, Kellner (1996) presented a comprehensive study of pterosaur interrelationships. This author recognized a monophyletic group, the Archaeopterodactyloidea, consisting of a clade formed by *Pterodactylus* and *Germanodactylus*, and its sister-group, an unnamed clade formed by Ctenochasmatidae and Gallodactylidae (Fig. 15). Kellner (1996) included *Pterodaustro* within the Ctenochasmatidae, as the sister-taxon of *Ctenochasma* (Fig. 15). All the synapomorphies diagnosing the Archaeopterodactyloidea (e.g., rounded caudal end of the skull, resulting in a ventral displacement of the squamosal; quadrate strongly inclined caudally, with an angle of about 150° relative to the ventral margin of the skull; elongated mid-cervical vertebrae; neural spines of the midcervical vertebrae low and blade-like; see Kellner, 1996, 1997) are present in *Pterodaustro*.

In Kellner's analysis, the close relationship of *Pterodaustro* and *Ctenochasma* is supported by a single synapomorphy: the presence of a large number of teeth (more than 150; Kellner, 1996, 1997). However, the rostral extension of the surangular of *Pterodaustro* and *Ctenochasma* is smaller than that of other archaeopterodactyloids and may be another synapomorphy of these taxa.

A close relationship between *Pterodaustro* and *Ctenochasma* was also recently supported by Unwin and Junchang (1997), who included these and other Late Jurassic–Early Cretaceous pterosaurs

(e.g., *Gnathosaurus*, *Huanhepterus* Dong, 1982; *Cearadactylus* Leonardi and Borgomanero, 1985) within the Ctenochasmatidae (Fig. 15). However, these authors did not mention any specific synapomorphy uniting these taxa but simply pointed to the filter-feeding specializations usually inferred for them. In contrast to Kellner's (1996) hypothesis, Unwin and Junchang (1997) considered the Ctenochasmatidae to be the sister-group of *Pterodactylus*, regarding *Gallodactylus* as a more basal member of the Ctenochasmatoidea—the higher taxon used by Unwin and Junchang (1997) to group Ctenochasmatidae, *Pterodactylus*, and *Gallodactylus*. Unfortunately, these authors did not provide evidence for the proposed relationships within their Ctenochasmatoidea.

However, support for the sister-group relationship of Ctenochasmatidae and Gallodactylidae is provided by the presence of a concave dorsal margin of the skull (Kellner, 1996, 1997). In all other pterosaurs, the dorsal margin of the skull is either straight or convex. According to the reconstruction presented by Bennett (1991), the dorsal margin of the skull in *Pteranodon* is also concave. However, it must be noted that few complete skulls are known and that in some of these the dorsal margin is essentially straight (Bennett, 1994: fig. 1). If the dorsal margin of the skull of *Pteranodon* was indeed concave, it is probable that this condition was achieved independently (Kellner, 1996).

Kellner (1996) diagnosed the monophyletic group formed by *Pterodactylus* and *Germanodactylus* on the basis of their particular dentition (more than 15 peglike teeth) and the presence of a straight lateral process of the nasal that is not connected to the maxilla. MHIN-UNSL-GEO-V-57 has a straight lateral process of the nasal, suggesting that this apomorphic character may be a synapomorphy of a more inclusive clade, most likely the Archaeopterodactyloidea. Because this process is very delicate, its supposed absence in *Gallodactylus* and *Ctenochasma* (Kellner, 1996) may result from preservational factors.

The skull of *Pterodaustro* exhibits numerous characters of its own that are clear autapomorphies of this taxon. The most obvious are in the dentition. The spatulate teeth of the maxilla of *Pterodaustro* differ from those of all other pterosaurs (Bonaparte, 1971; Sanchez, 1973). In addition, the fact that the maxillary teeth are not set in alveoli and that they are associated with a row of ossicles are other autapomorphic characters. Another distinct autapomorphy of *Pterodaustro* is the remarkable extension of its preorbital region, which is not known in other pterosaurs (Bonaparte, 1971; Sanchez, 1973). As a consequence of this preorbital

←

Figure 13 Stereoelectromicrograph of the mandibular teeth of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-55) showing their insertion in a dentary groove with lower (A) and higher (B) magnification. In A and B, scale bars equal 2 and 1 millimeters, respectively

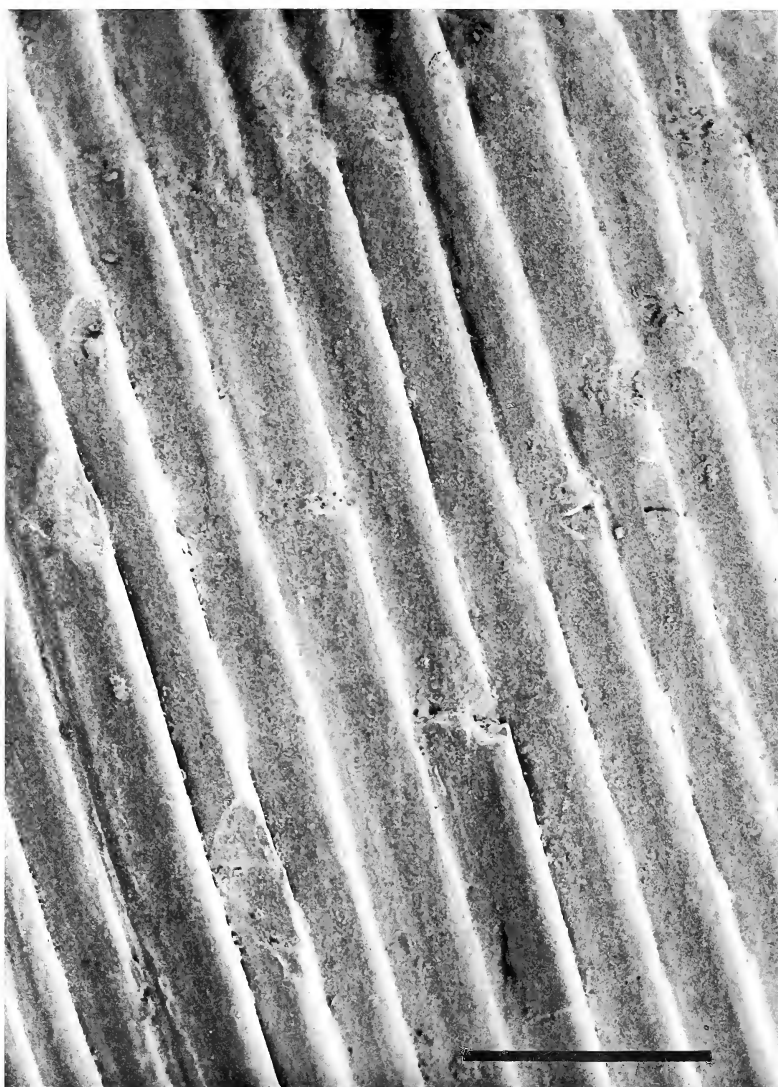


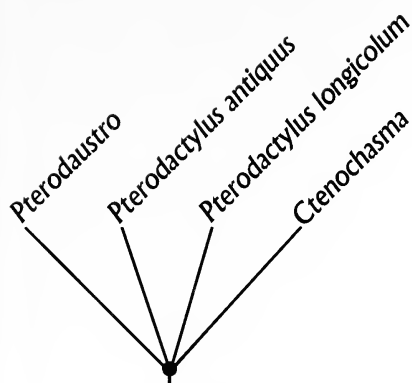
Figure 14 Stereoelectromicrograph of the mandibular teeth of *Pterodaustro guinazui* (MHIN-UNSL-GEO-V-55). Note the smoothness of the enamel's surface. Scale bar = 1 millimeter

extension, the nasoantorbital fenestra of *Pterodaustro* occupies only 10–12 percent of the total length of the skull. In contrast, the nasoantorbital fenestra constitutes 15–16 percent of the length of the skull in *Ctenochasma* and 18–19 percent in *Pteranodon* (excluding the cranial crest; see Bennett, 1991: fig. 2).

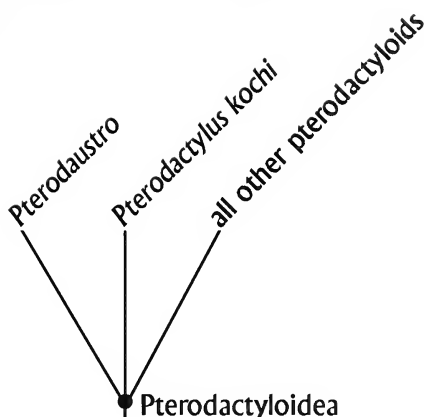
Furthermore, unlike any other pterosaur, in *Pterodaustro* the postorbital is separated from the frontal, and the quadratojugal appears to form the ventral margin of the infratemporal opening (Sanchez, 1973), which in other pterodactyloids is mostly formed by the quadrate (e.g., *Pterodactylus*; Wellnhofer, 1978). Besides, the presence of four jugal processes in *Pterodaustro* may be another autapomorphy. In all pterodactyloids for which the jugal is known, the caudoventral region of this bone is

rounded and does not form an independent process. The apparent contact between the jugal and the quadrate on the lateral surface of the skull (Bonaparte, 1971; Sanchez, 1973) is another potential autapomorphy of *Pterodaustro*, because this feature is not known for other pterodactyloids.

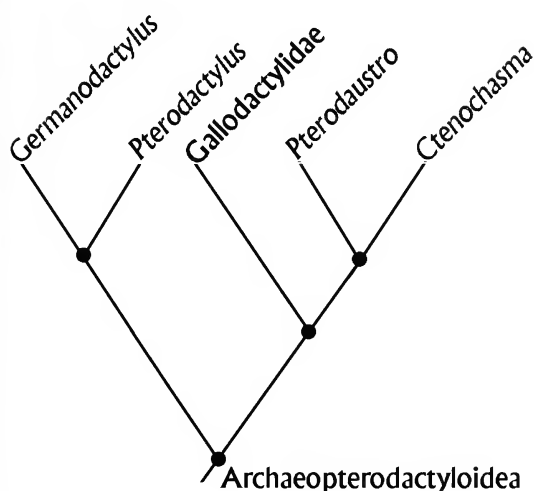
The mandible of *Pterodaustro* also displays several autapomorphic features. The large number of teeth (nearly 500 for each ramus) and their filamentlike aspect are unique among pterosaurs. Also, the extensive length of the mandible, which follows the extension of the preorbital region of the skull, is another autapomorphy of *Pterodaustro*. This condition differs from that in all other pterosaurs, including *Pteranodon*, in which the elongation of the preorbital region is not matched by the lower jaw, which is considerably shorter (Bennett, 1991).



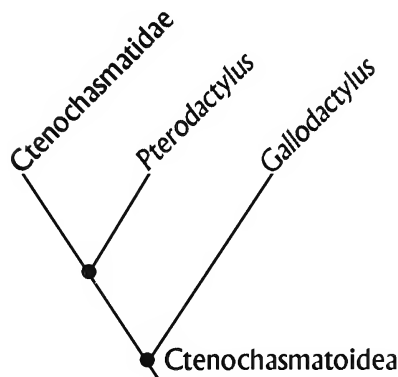
Howse (1986)



Bennett (1994)



Kellner (1996)



Unwin and Junchang (1997)

Figure 15 Different phylogenetic hypotheses of the relationships of *Pterodaustro guinazui* to other pterodactyloids

In sum, although the skull and jaws of *Pterodaustro* are easily distinguishable from those of other pterosaurs by a large number of autapomorphic features, two derived cranial characters (i.e., more than 150 teeth and a reduced rostral projection of the surangular) support the close relationship to *Ctenochasma* advocated by most authors.

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# CONTRIBUTIONS IN SCIENCE

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THE PATTERNED-WING SPECIES OF  
*CONICEROMYIA* (DIPTERA: PHORIDAE)

GIAR-ANN KUNG AND BRIAN V. BROWN



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# THE PATTERNED-WING SPECIES OF CONICEROMYIA (DIPTERA: PHORIDAE)

GIAR-ANN KUNG<sup>1</sup> AND BRIAN V. BROWN<sup>1</sup>

**ABSTRACT.** Fifteen species of patterned-wing *Coniceromyia* are recognized, including the following ten new to science: *Coniceromyia apicalis*, *C. aurantia*, *C. bilineata*, *C. brevivena*, *C. globosa*, *C. impluvia*, *C. impudica*, *C. leucomacula*, *C. setitarsalis*, and *C. truncata*. A key to the identification of males of these species is given.

## INTRODUCTION

The genus *Coniceromyia* Borgmeier (1923) is a group of 32 species confined to the New World. Most species are tropical, with only two reaching the southern U.S.A. (Borgmeier, 1968). Only a small fraction of the true diversity of this genus has been described.

One easily recognizable trait of males of some species of this genus is the presence of patterned wings. Patterned wings are herein defined as the presence of definite pigment in the wing membrane, but some of the patterning found in some species is caused by, or enhanced by, the presence of dense, reduced setae. There is no evidence that species sharing wing-patterning form a monophyletic group, but they are distinctive, attractive, conspicuous taxa whose recognition could inspire studies on the function of such markings.

In this paper we describe ten new species of patterned-wing *Coniceromyia* and present a key to all species known to display this attribute.

## METHODS

Most specimens were collected into 70% ethanol and critical-point dried using hexamethyldisilazane (Brown, 1993) or a standard critical-point drier (Gordh and Hall, 1979).

Terms used are those of McAlpine (1981). Recently, Stuckenberg (1999) has proposed that the large third antennal segment of the Cyclorrhapha should be called the postpedicel, rather than flagellomere 1, as it may comprise a fusion of flagellomere 1 with other flagellomeres. The actual segments that might have been involved in such a fusion are still unidentified, however, and they still are homologous to the flagellomeres of more primitive Diptera. Therefore, we continue to use the term flagellomere 1 for the first visible flagellomere, regardless of its potential composition.

Tarsal ratios are length/width of the tarsal segment.

In addition to regular locality labels, all specimens have

Code-49 barcoded labels, and their information is recorded in a database. The barcode of each holotype is reported in brackets.

Material was deposited in the following museums (codens from Arnett et al., 1993).

- |      |  |
|------|--|
| EAPC | Agroecological Inventory Collection, Departamento de Proteccion Vegetal, Escuela Agrícola Panamericana, Apartado 93, Tegucigalpa, Honduras (R. Cave) |
| EMUS | Department of Biology, Utah State University, Logan, Utah 84322-5305, U.S.A. (W.J. Hanson)   |
| INBC | Instituto Nacional de Biodiversidad, A.P. 22-3100, Santo Domingo, Heredia, Costa Rica (M. Zumbado)   |
| LACM | Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. (B.V. Brown)       |
| MCZC | Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. (on indefinite loan to B.V. Brown)                         |
| MUCR | Museo de Insectos, Universidad de Costa Rica, San Pedro, San José, Costa Rica (P. Hanson)  |
| MUSM | Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Av. Arenales 1267, Apartado 14-0434, Lima-14, Peru (G. Lamas)                   |
| MZLU | Museum of Zoology, Lund University, Helgönav. 3, S-223, 62 Lund, Sweden (R. Danielsson)  |
| ROME | Department of Entomology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario, Canada M5S 2C6 (D.C. Darling)                                     |
| USNM | United States National Museum, Smithsonian Institution, Washington, DC 20560, U.S.A. (on indefinite loan to B.V. Brown)                              |

## SYSTEMATICS

### *Coniceromyia* Borgmeier, 1923

*Coniceromyia* Borgmeier, 1923:338. Type species: *C. epicantha* Borgmeier, by original designation.

**DIAGNOSIS.** Frons with median furrow. One pair of reclinate supra-antennal setae present. Flagellomere 1 elongate, conical in most species. Anepisternum bare or setulose; anepisternal furrow absent. Foremetatarsus of male with elongate, fringed process at apex. Tibiae with large, unpaired setae;

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hind tibia without dorsal, longitudinal rows of enlarged setulae. Costa usually darkened; wing vein  $R_{2+3}$  absent or vestigial. Epandrium with fused surstyli shifted to left side. Hypandrium with bilobed right process. A full list of genus-level characters was given by Borgmeier (1963b).

**PHYLOGENETIC RELATIONSHIPS.** *Coniceromyia* was hypothesized to belong to a newly restricted subfamily Phorinae by Brown (1992a, b), with its closest relative being the Old World genus *Plethysmochaeta* Schmitz (1924). No phylogenetic relationships have been proposed for species within the genus, and no taxonomic subdivisions, such as subgenera, are currently used. The patterned-wing species described herein do not form a monophyletic group but apparently are representatives of a number of lineages that have independently evolved this trait.

**TAXONOMIC NOTES.** Sexual dimorphism in the genus is problematic, as females lack many of the characters that are taxonomically useful in males (including patterned wings). Therefore, most of the 32 described species are known from male specimens, although some have questionably associated females. Most species are known from fewer than five specimens, and twelve species have been recorded from the holotype alone.

Male genitalia, often of great value in determining phorid species (e.g., Brown, 1996, 1998; Disney, 1989), are relatively uniform in *Coniceromyia* and were not illustrated. A full discussion of their structure is given by Brown (1992a).

**WAY OF LIFE.** The natural history of all species is unknown, although one species was collected with army ants. Species of related genera (Brown, 1992b) are scavengers.

The elaborately decorated males of some species, especially *C. stephensoni* Peterson and *C. leucomacula* new species, possibly use their colored wings and brightly marked forefemora in courtship displays or to defend territories against other males. No such observations have been made on these species, however, as specimens of both species have only been collected by traps.

**DISTRIBUTION.** Most species are found in the Neotropical Region, although two species reach the southern U.S.A.

**NOTES ON IDENTIFICATION.** The most recent key to species is that of Borgmeier (1963a); since then, several further species have been described (Borgmeier, 1969a, b; Borgmeier and Prado, 1975; Peterson, 1982; Peterson and Arntfield, 1971; Prado, 1976).

### *Coniceromyia apicalis* new species

(Fig. 1)

**SPECIES RECOGNITION.** This species is most easily recognized by a thickened  $M_1$  vein and the continuation of the wing darkening to the apical margin. A smooth and entire wing margin and the presence of setae on the anepisternum further dif-

ferentiate this species from *C. vespertilio* Schmitz (1927).

**DESCRIPTION.** Male. Body length 1.75 to 2.40 mm. Frons brown. Flagellomere 1 brown, elongate-conical. Arista apical and pubescent. Palpus brown, small, with short, dark setae. Dorsum of thorax brown. Pleural regions brown. Anepisternum with short, fine setae. Scutellum brown. Legs yellowish-brown. Foreleg with two strong setae anterodorsal to posterodorsal on tibia; tarsomeres about twice as long as wide (e.g., in one specimen, tarsal ratio is 2.00:1.75:1.75:1.67:2.00); tarsomere 1 with antero-basal seta, anterior excavation, and anteroapical process, without basal triangular process; posteroventral setae on tarsomere 1 without curved tips. Midcoxa with long, erect setae; tips of setae curved, without thick ventrolateral seta. Hind femur with sparse, tiny, blunt setae on basal half; setae extend dorsally to one-third height of posterior face of femur at basal extremity. Wing with  $M_1$  thickened, about one-half thickness of  $R_{4+5}$ , thicker than  $M_2$  and  $CuA_1$ ; space between  $M_1$  and  $M_2$  narrowed basally, so that the veins are parallel in basal third and divergent in apical two-thirds. Wing with line of darkened pigment and slightly denser setae parallel to and posterior to leading edge. Apical third of wing darkened by pigment from anterior margin to  $CuA_1$  (Fig. 1). Mean costal length 0.42 wing length; range 0.36 to 0.46. Halter white. Tergites brown. Tergite 1 medially constricted, the middle complete to partially split. Abdomen gray ventrally. Terminalia yellowish-brown.

**GEOGRAPHICAL DISTRIBUTION.** Known from two sites in Costa Rica.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for apical, referring to the continuation of the wing pattern to the apical margin.

**HOLOTYPE.** ♂, COSTA RICA: Guanacaste, Estación Pitilla, 11°N, 85.43°W, vi.1989, P. Hanson, Malaise trap, 600 m (LACM) [LACM ENT 029706].

**PARATYPES.** COSTA RICA: Alajuela, Peñas Blancas Valley, 10.32°N, 84.76°W, 1♂, 7.xi.1987, E. Cruz, Malaise trap (LACM), 20 km S Upala, 10.73°N, 85.10°W, 1♂, 1–3.v.1990, F.D. Parker (EMUS); Guanacaste, Estación Pitilla, 11°N, 85.43°W, 3♂, iv.1989, 5♂, v.1989, 1♂, vi.1989, P. Hanson, Malaise trap, 600 m (LACM, MUCR), 2♂, v.1994, P. Rios, Malaise trap, 700 m (INBC).

### *Coniceromyia aurantia* new species

(Fig. 2)

**SPECIES RECOGNITION.** This species is most easily recognized by a basal, oval, orange macula on the anterior face of the forefemur and a posteroventral row of setae on the foretibia.

**DESCRIPTION.** Male. Body length 2.20 to 2.30 mm. Frons reddish-brown. Flagellomere 1 brown, elongate-conical. Arista apical, pubescent. Palpus yellow with short, dark setae. Dorsum of thorax yellowish-brown. Pleural regions yellowish-brown.

Anepisternum with short setae. Scutellum yellowish, brown medially. Legs yellowish-brown. Forefemur with oval, orange macula on basal half of anterior face. Foretibia with dorsal row of short, brown setae anterior to two strong dorsal setae; with posteroventral row of short, thick setae. Foreleg with tarsomeres 2 to 5 one and one-half times as long as wide (e.g., in one specimen, tarsal ratio is 3.29:1.63:1.50:1.50:1.50); tarsomere 1 with anteroapical process and shallow excavation, without basal triangular process; posteroventral setae on tarsomere 1 without curved tips. Setae on midcoxa not long, without curved tips; with thick ventral setae. Hind femur with dense, tiny, blunt posteroventral setae on basal two-fifths; distribution of setae extends dorsally to one-third height of posterior face in basal half, tapers to ventral margin in apical half. Wing (Fig. 2) with darkened pigment along  $M_1$  and  $M_2$ , line of dense setae posterior to anteroapical margin. Apical three-fourths of wing darkened by dense setae. Mean costal length 0.34 wing length. Halter yellowish-white. Tergites dark brown. Tergite 1 medially constricted, middle entirely split. Abdomen yellowish-white ventrally. Terminalia light brown.

**PHYLOGENETIC RELATIONSHIPS.** We consider this species to be part of a monophyletic group, along with *C. leucomacula* new species and *C. stephensoni* Peterson (1982), based on the presence of posteroventral setae on the foretibia and a differentiated macula on the anterior face of the forefemur.

**GEOGRAPHIC DISTRIBUTION.** Amazonian Peru.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for orange, referring to the orange macula on the forefemur.

**HOLOTYPE.** ♂, PERU: Madre de Dios, Manu N.P., Cocha Cashu Station, 23–30.viii.1986, D.C. Darling, Malaise trap, 380 m (MUSM) [LACM ENT 137646].

**PARATYPES.** PERU: Madre de Dios, Manu N.P., Cocha Cashu Station, 1♂, 18–22.viii.1986, 1♂, 22–27.viii.1986, 1♂, 23–30.viii.1986, 1♂, 31.viii–1.ix.1986, D.C. Darling, Malaise trap, 380 m (LACM, ROME), Pakitza, 11.94°S, 71.28°W, 1♂, 13–18.ii.1992, D. Quintero, Malaise trap (LACM), 1♂, 10.vi–6.vii.1993, R. Cambra, yellow pans (LACM).

### *Coniceromyia bilineata* new species

(Fig. 3)

**SPECIES RECOGNITION.** This species is most recognizable by the two striae on the wing at the anterior margin and along  $M_1$ . The most similar species is *C. striativena* Borgmeier (Borgmeier, 1963a), which has darkening along  $M_2$ .

**DESCRIPTION.** Male. Body length 2.15 to 2.35 mm. Frons dark brown. Flagellomere 1 dark brown with long pubescence, elongate-conical. Arista apical, pubescent. Palpus yellow. Dorsum of thorax

dark brown. Pleural regions same color as dorsum of thorax dorsally, lighter in color ventrally. Anepisternum without setae. Scutellum dark brown. Foreleg dark brown, yellowish-brown from apical region of femora to apex; midleg slightly lighter brown from tip of femur to apex; hind leg dark brown. Foreleg with three dorsal setae on tibia; tarsal ratio of tarsomeres 2 to 4 subequal (e.g., in one specimen, ratio is 1.80:0.89:1.00:1.14:2.00); tarsomere 1 with basal triangular process, anterior excavation, and anteroapical process; posteroventral setae on tarsomere 1 without curved tips. Foreleg with pulvilli slightly enlarged. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with dense, tiny, blunt posteroventral setae on basal third, distribution of setae tapered apically toward ventral margin. Wing with darkened pigment along anteroapical margin and  $M_1$ ; subcostal cell darkened by pigment at apex (Fig. 3). Mean costal length 0.48 wing length. Halter yellow. Tergites dark brown, almost black. Tergite 1 shortened or not shortened medially. Abdomen gray ventrally. Terminalia light brown.

**GEOGRAPHICAL DISTRIBUTION.** Known from one site in Costa Rica.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for two-lined, referring to the two striae on the wing.

**HOLOTYPE.** ♂, COSTA RICA: Guanacaste, Volcan Cacao, Cerro Pedregal, 10.93°N, 85.48°W, ii–iv.1989, I. Gauld, D. Janzen, Malaise trap, 1000 m (LACM) [LACM ENT 053782].

**PARATYPES.** COSTA RICA: Guanacaste, Santa Rosa National Park, 10.95°N, 85.62°W, 1♂, 21.ii–14.iii.1987, I. Gauld, D. Janzen, Malaise trap (LACM), Volcan Cacao, Cerro Pedregal, 10.93°N, 85.48°W, 4♂, ii–iv.1989, I. Gauld, D. Janzen, Malaise trap, 1000 m (INBC, LACM), 1♂, ii–iv.1989, P. Hanson, Malaise trap, 1000 m (LACM).

*Coniceromyia blomae* Peterson and Arntfield, 1971

*Coniceromyia blomae* Peterson and Arntfield, 1971:395–398, fig. 1.

**NEW MATERIAL EXAMINED.** MEXICO: Chiapas, Yerba Buena, 16.35°N, 96.07°W, 1♂, 8.vi.1969, W. Mason, 1760 m (LACM).

### *Coniceromyia brevivena* new species

(Fig. 4)

**SPECIES RECOGNITION.** This species differs from all other patterned-wing *Coniceromyia* by the presence of the apical half of  $R_{2+3}$ . This species is further differentiated from *C. maculipennis* Borgmeier (1969b) by the lack of darkening along the posterior wing margin.

**DESCRIPTION.** Male. Body length 3.1 mm. Frons dark brown. Flagellomere 1 dark brown, elongate-conical. Arista apical and pubescent. Palpus light brown with short, dark setae. Dorsum of

thorax dark brown. Pleural regions same color as dorsum of thorax. Anepisternum with short, fine setae. Scutellum dark brown. Legs brown, lighter apically. Foreleg with three dorsal setae on tibia; tarsomeres 2 to 4 twice as long as wide, tarsal ratio is 3.50:2.00:2.00:2.00:1.60; tarsomere 1 with three thick anterobasal setae ventral to anterior excavation, without basal triangular process; posteroventral setae on tarsomere 1 without curved tips. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with tiny, blunt posteroventral setae on basal half; distribution of setae tapered apically toward ventral margin. Apical third of wing, except for apex, darkened by pigment; costal and subcostal cells darkened by pigment. Apical half of  $R_{2+3}$  present (Fig. 4). Costal length 0.43 wing length. Halter yellow. Tergites dark brown. Tergite 1 medially constricted. Abdomen dark gray ventrally. Terminalia dark brown.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in Peru.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for short vein, referring to the presence of the apical half of  $R_{2+3}$ .

**HOLOTYPE.** ♂, PERU: Madre de Dios, Rio Tambopata Reserve, 12.83°S, 69.28°W, 8.xi.1983, T. Erwin, canopy fogging, 290 m (USNM) [LACM ENT 028082].

### *Coniceromyia globosa* new species

(Fig. 5)

**SPECIES RECOGNITION.** This species is most easily recognized by the round macula on the wing between the anteroapical margin and  $M_1$ . The most similar species are *C. setitarsalis* new species and *C. impluvia* new species, in which the darkening on the wing between the anteroapical margin and  $M_1$  is not distinctly round.

**DESCRIPTION.** Male. Body length 1.8 to 1.9 mm. Frons brown. Flagellomere 1 brown, elongate-conical. Arista apical, pubescent. Palpus brown. Dorsum of thorax brown. Pleural regions same color as dorsum of thorax. Anepisternum without setae. Scutellum brown. Legs yellowish-brown. Foreleg with two anterodorsal setae on tibia; tarsal ratio of tarsomeres 2 to 4 subequal (e.g., in one specimen, ratio is 2.29:1.00:1.14:1.33:2.00); tarsomere 1 with anteroventral excavation and anteroapical process, without basal triangular process; posteroventral setae on tarsomere 1 without curved tips. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with dense, tiny, blunt posteroventral setae in basal third; setae slightly tapered apically. Wing with pigment darkened along  $R_{4+5}$ , anteroapical margin,  $M_1$ ,  $M_2$ ; darkened pigment forming round macula between  $M_1$  and anteroapical margin (Fig. 5). Mean costal length 0.48 wing length; range 0.46 to 0.50. Halter yellowish-brown. Tergites dark brown. Tergite 1 shortened medially. Abdomen gray ventrally. Terminalia light brown.

**GEOGRAPHICAL DISTRIBUTION.** Costa Rica and Panama.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for spherical, referring to the round macula on the wing.

**HOLOTYPE.** ♂, COSTA RICA: San José, Braulio Carrillo NP, 10.17°N, 84.12°W, 10.iv.1985, H. Goulet, L. Masner, 500 m (LACM) [LACM ENT 003289].

**PARATYPES.** COSTA RICA: San José, Braulio Carrillo NP, 8.2 km NE Tunel, 10.12°N, 83.97°W, 1♂, 15.v.1988, P. Hanson, 1500 m (LACM). PANAMA: Panama Prov., Cerro Jefe, 1♂, 31.vii.1978, N.E. Woodley, 975 m (MCZC).

### *Coniceromyia impluvia* new species

(Fig. 6)

**SPECIES RECOGNITION.** This species is most similar to *C. setitarsalis* new species but differs by a shorter flagellomere, presence of darkening along  $CuA_1$ , and absence of curved tips on ventral setae of tarsomere 1 on the foreleg. The clear window in the darkening of the wing, between the apical margin and  $M_1$ , is twice as long as wide, further differentiating this species from *C. setitarsalis*.

**DESCRIPTION.** Male. Body length 1.7 to 2.0 mm. Frons dark brown. Flagellomere 1 brown, elongate-conical, length of tapered portion less than length of untapered portion. Arista apical, pubescent. Palpus yellow. Dorsum of thorax brown. Pleural regions same color as dorsum of thorax. Anepisternum without setae. Scutellum brown. Legs brown to yellowish-brown. Foreleg with two dorsal setae on tibia; tarsal ratio of tarsomeres 2 to 4 subequal (e.g., in one specimen, ratio is 2.29:0.88:1.00:1.00:1.16); tarsomere 1 with anterior excavation and anteroapical process; posteroventral setae on tarsomere 1 without curved tips. Tarsomere 1 without triangular process. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with dense, tiny, blunt posteroventral setae in basal third; distribution of setae slightly tapered apically. Line of pigment and dense setae parallel to and posterior to leading edge of wing. Wing darkened by pigment near tip of  $R_{4+5}$  along anteroapical margin,  $M_1$ ,  $M_2$ , and, faintly, along  $CuA_1$ ; darkened pigment present between  $M_1$  and anteroapical margin in apical half, but not extending to apical margin (Fig. 6). Mean costal length 0.45 wing length; range 0.42 to 0.47. Halter white. Tergites dark brown. Abdomen gray ventrally. Terminalia light brown.

**GEOGRAPHICAL DISTRIBUTION.** Lowland Costa Rica.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for window, referring to the presence of a clear window in the wing darkening.

**HOLOTYPE.** ♂, COSTA RICA: Puntarenas, 24 km W Piedras Blancas, 8.77°N, 83.4°W, xii.1990, P. Hanson, Malaise trap, 200 m (LACM) [LACM ENT 040466].

**PARATYPES.** COSTA RICA: Limon, 16 km W

Guapiles, 10.15°N, 83.92°W, 1♂, iii–v.1990, P. Hanson, Malaise trap, 400 m (LACM); Puntarenas, Road to Rincon, 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♂, iii–iv.1989, P. Hanson, I. Gauld, Malaise trap, 200 m (LACM), 1♂, xi.1990, P. Hanson, Malaise trap, 200 m (INBC), 3 km S Rincon, 8.68°N, 83.48°W, 1♂, ix–xi.1989, 1♂, xii.1989, P. Hanson, Malaise trap, 10 m (LACM). PANAMA: Darien, Cana Pirre Trail, 7.72°N, 77.7°W, 1♂, 7.vi.1996, A. Gillogly, FIT, 1250 m (LACM).

### *Coniceromyia impudica* new species

(Fig. 7)

**SPECIES RECOGNITION.** This species is most easily recognized by its dark coloration, distinctive wing pattern, and the presence of curved tips on the ventral setae on tarsomere 1 of the foreleg.

**DESCRIPTION.** Male. Body length 2.35 to 2.85 mm. Frons blackish-brown. Flagellomere 1 dark brown with long pubescence, elongate-conical. Arista apical, pubescent. Palpus yellow. Dorsum of thorax and pleural regions dark brown. Anepisternum without setae. Scutellum dark brown. Legs with femora dark brown, yellow-orange apically; tibiae dark brown, yellow-orange basally and apically; tarsi yellowish-brown. Foreleg with three to four dorsal to anterodorsal setae on tibia; tarsal ratio of tarsomeres 2 to 5 subequal (e.g., in one specimen, ratio is 2.00:1.25:1.25:1.33:1.33); tarsomere 1 with basal triangular process, anterior excavation, and anteroapical process; tarsomere 1 with curved tips on some posteroventral setae. Foreleg with pulvilli slightly enlarged. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with dense, tiny, blunt posteroventral setae on basal third, setae tapered apically toward ventral margin. Wing with darkened pigment along, and in membrane posterior to,  $M_1$ , with enlarged areas at tip of  $R_{4+5}$  and mid- $M_1$ . Macula darkened by pigment on middle of  $M_2$  present to absent,  $R_{4+5}$  slightly darkened by pigment and narrow line of darkened pigment parallel to and posterior to the leading edge of the wing (Fig. 7). Mean costal length 0.50 wing length; range 0.47 to 0.53. Halter yellow. Tergites dark brown, almost black. Tergite 1 shortened or lightened medially. Abdomen dark, almost black, ventrally. Terminalia dark brown.

**GEOGRAPHICAL DISTRIBUTION.** Honduras.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for bold, referring to the dark and distinctive wing pattern.

**HOLOTYPE.** ♂, HONDURAS: Francisco Morazan, San Antonio de Oriente, Cerra Uyuca, 14.03°N, 87.07°W, 12–18.ii.1990, R. Cave, Malaise trap in cloud forest (LACM) [LACM ENT 061908].

**PARATYPES.** HONDURAS: Cortés, Parque Nacional Cusuco, 15.48°N, 88.22°W, 2♂, 2.iii.1995, R. Cordero, Malaise trap (LACM), 1600 m, 6♂, 30.ix.1995, 3♂, 15.x.1995, R. Cave, Malaise trap in oak/pine cloud forest, 1600 m (EAPC, MZLU);

Francisco Morazan, Parque Nacional La Tigra, 14.25°N, 87.08°W, 1♂, 29.iii.1995, 1♂, 13.vi.1995, R. Cave, Malaise trap in oak/pine cloud forest (MZLU); San Antonio de Oriente, Cerra Uyuca, 14.03°N, 87.07°W, 2♂, 12–18.ii.1990, 1♂, 7–13.v.1990, R. Cave, Malaise trap in cloud forest (LACM).

### *Coniceromyia leucomacula* new species

(Figs. 8, 9)

**SPECIES RECOGNITION.** This species is most easily recognized by a large white patch on the forefemur and an oval macula between  $M_2$  and  $CuA_1$ . A second darkening on the wing, between  $M_1$  and  $M_2$ , may be present or absent.

**DESCRIPTION.** Male. Body length 2.3 to 2.9 mm. Frons brown. Flagellomere 1 with various degrees of orange and brown, elongate-conical. Arista apical, pubescent. Palpus yellow-orange. Dorsum of thorax brown with yellowish margins. Pleural regions yellowish-brown to brown. Anepisternum with short, fine setae. Scutellum brown, darker than pleural regions. Legs mostly yellow. Foreleg with anterior of femur black apically with white patch about three-quarters length of femur, posterior side brown. Midfemur brown basally and yellowish-brown apically. Hind femur with apical anteroventral black spot. Foretibia with dorsal row of orange setae anterior to one to four black dorsal setae, with row of posterior spine-like setae, row extending ventrally along apical margin; tarsal segments clearly longer than wide (e.g., in one specimen, tarsal ratio is 5.20:3.60:4.00:3.00:2.67); tarsomere 1 with thick basal seta, ventral to anterior excavation, and anteroapical process, without basal triangular process; posteroventral setae on tarsomere 1 without curved tips. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with tiny, blunt posteroventral setae on basal half; setae extend slightly higher at basal extremity. Wing with costal cell slightly darkened by pigment, anteroapical margin with faint darkening of pigment and dense, fine setae. Apical half with large, oval, darkening of pigment between  $M_2$  and  $CuA_1$  and smaller and lighter spot between  $M_1$  and  $M_2$  (Fig. 8). Mean costal length 0.44 wing length; range 0.41 to 0.47. Halter white. Tergites brown. Tergite 1 medially constricted; middle entirely to partially split. Tergites 3 through 6 with lighter anterior margin. Abdomen gray ventrally. Terminalia yellowish. Hypandrium brown.

**VARIATION.** Specimens from Estación Cacao differ from the holotype and other specimens by overall lighter coloration, including the lack of darkening between  $M_1$  and  $M_2$  and smaller macula between  $M_2$  and  $CuA_1$  (Fig. 9).

**PHYLOGENETIC RELATIONSHIPS.** See *C. aurantia*, above.

**GEOGRAPHICAL DISTRIBUTION.** Known from three midelevation sites in Costa Rica.

**DERIVATION OF SPECIFIC EPITHET.** The

name is a combination of the Greek word for white, *leukos*, and Latin word *macula*, referring to the white patch of the forefemur.

**HOLOTYPE.** ♂, COSTA RICA: Puntarenas, Monteverde Biological Station, 10.33°N, 84.79°W, 9–18.iii.1995, B. V. Brown, Malaise trap, 1700 m (LACM) [LACM ENT 051936].

**PARATYPES.** COSTA RICA: Cartago, La Cangreja, 9.8°N, 83.47°W, 7♂, vii.1991, 1♂, viii–ix.1991, 2♂, xi.1991, 4♂, xii.1991, 10♂, vi–vii.1992, 9♂, ix–xii.1992, P. Hanson, Malaise trap, 1950 m (INBC, LACM, MCZC, MUCR, USNM); Guanacaste, Cerro Pedregal, 10.93°N, 85.48°W, 3♂, ii–iv.1989, I. Gauld, D. Janzen, Malaise trap, 1000 m (LACM), Estación Cacao, 10.93°N, 85.47°W, 2♂, ii.1989, I. Gauld, D. Janzen, Malaise trap, 900 m (LACM); Puntarenas, Monteverde Biological Station, 10.33°N, 84.79°W, 1♂, 9–18.iii.1995, B. V. Brown, Malaise trap, 1700 m (LACM).

### *Coniceromyia setitarsalis* new species (Fig. 10)

**SPECIES RECOGNITION.** This species is most similar to *C. impluvia* but differs by a longer flagellomere, absence of darkening along CuA<sub>1</sub>, and presence of curved tips on the ventral setae of tarsomere 1 on the foreleg. The clear window in the darkening of the wing, between the apical margin and M<sub>1</sub>, is about as long as wide, further differentiating this species from *C. impluvia*.

**DESCRIPTION.** Male. Body length 1.9 to 2.6 mm. Frons dark brown. Flagellomere 1 dark brown with long pubescence, elongate-conical, with tapered portion longer than untapered portion. Arista apical, plumose. Palpus brown. Dorsum of thorax dark brown. Pleural regions same color as dorsum of thorax. Anepisternum without setae. Scutellum dark brown. Legs brown to yellowish-brown, lighter apical of femora. Foretibia and tarsus with long, fine, erect, ventral setae. Foreleg with two dorsal setae on tibia; tarsal ratio of tarsomeres 2 to 4 subequal (e.g., in one specimen, ratio is 2.67:1.11:0.89:1.00:2.00); tarsomere 1 with anterior excavation and anteroapical process. Excavation bordered with setae, ventrobasal margin of excavation with dense, fine setae. Tarsomere 1 without basal triangular process; some posteroventral setae on tarsomere 1 long, thin, curve-tipped, and erect. Midcoxa with fine setae and thick ventrolateral seta. Hind femur with dense, tiny, blunt setae on basal third; distribution of setae tapered apically toward ventral margin. Wing darkened with pigment at apex of costa, base of M<sub>1</sub>, with macula anterior to M<sub>1</sub> at midpoint of M<sub>1</sub>, pigment lighter at apex; pigment darkened along anteroapical margin and apex of M<sub>2</sub>, M<sub>2</sub> faintly darkened by pigment (Fig. 10). Mean costal length 0.52 wing length; range 0.49 to 0.54. Halter yellow. Tergites dark brown. Tergite 1 shortened medially. Abdomen gray ventrally Terminalia light brown.

**GEOGRAPHICAL DISTRIBUTION.** Known from four midelevation sites in Costa Rica.

**DERIVATION OF SPECIFIC EPITHET.** The name is a combination of the Latin word *seta* and Greek word *tarsus*, referring to the setose tarsomere 1 of the foreleg.

**HOLOTYPE.** ♂, COSTA RICA: Cartago, La Cangreja, 9.8°N, 83.97°W, vi–vii.1992, P. Hanson, Malaise trap, 1950 m (LACM) [LACM ENT 062665].

**PARATYPES.** COSTA RICA: Cartago, La Cangreja, 9.8°N, 83.97°W, 1♂, vii.1991, 1♂, viii–ix.1991, 2♂, xi.1991, 1♂, vi–vii.1992, 1♂, ix–xii.1992, P. Hanson, Malaise trap, 1950 m (LACM); Puntarenas, Monteverde, 10.10°N, 83.43°W, 1♂, 1–5.vi.1988, B. V. Brown, Malaise trap in stunted forest, 1700 m (LACM), 1♂, 1–10.iii.1992, D. M. Wood, Malaise trap, 1500 m (LACM); San José, Braulio Carrillo National Park, 8.2 km NE Tunel, 10.12°N, 83.97°W, 1♂, 15.v.1988, P. Hanson, Malaise trap, 1500 m (LACM), Zurquí de Moravia, 10.05°N, 84.02°W, 1♂, vii.1990, 5♂, ix–x.1990, 2♂, x–xii.1990, 1♂, iii.1991, 2♂, v.1991, 1♂, vi.1991, 3♂, vii.1991, 1♂, ix.1991, 1♂, v.1992, 2♂, iii–iv.1993, 2♂, iv–v.1993, 7♂, 1–15.vi.1993, 3♂, ix–x.1993, 1♂, v.1995, 1♂, vi.1995, 1♂, i.1996, P. Hanson, Malaise trap, 1600 m (INBC, LACM, MUCR).

### *Coniceromyia stephensoni* Peterson, 1982

*Coniceromyia stephensoni* Peterson, 1982:136–138, figs. 1–2.

**PHYLOGENETIC RELATIONSHIPS:** See *C. aurantia*, above.

**NEW MATERIAL EXAMINED.** COSTA RICA: Puntarenas, Las Alturas, 8.95°N, 82.83°W, 1♂, 10–13.vi.1998, B. Brown, V. Berezovskiy, Malaise trap #1, 1600 m (LACM).

### *Coniceromyia striativena* Borgmeier, 1963a (Fig. 11)

*Coniceromyia striativena* Borgmeier, 1963a:457–458, fig. 3.

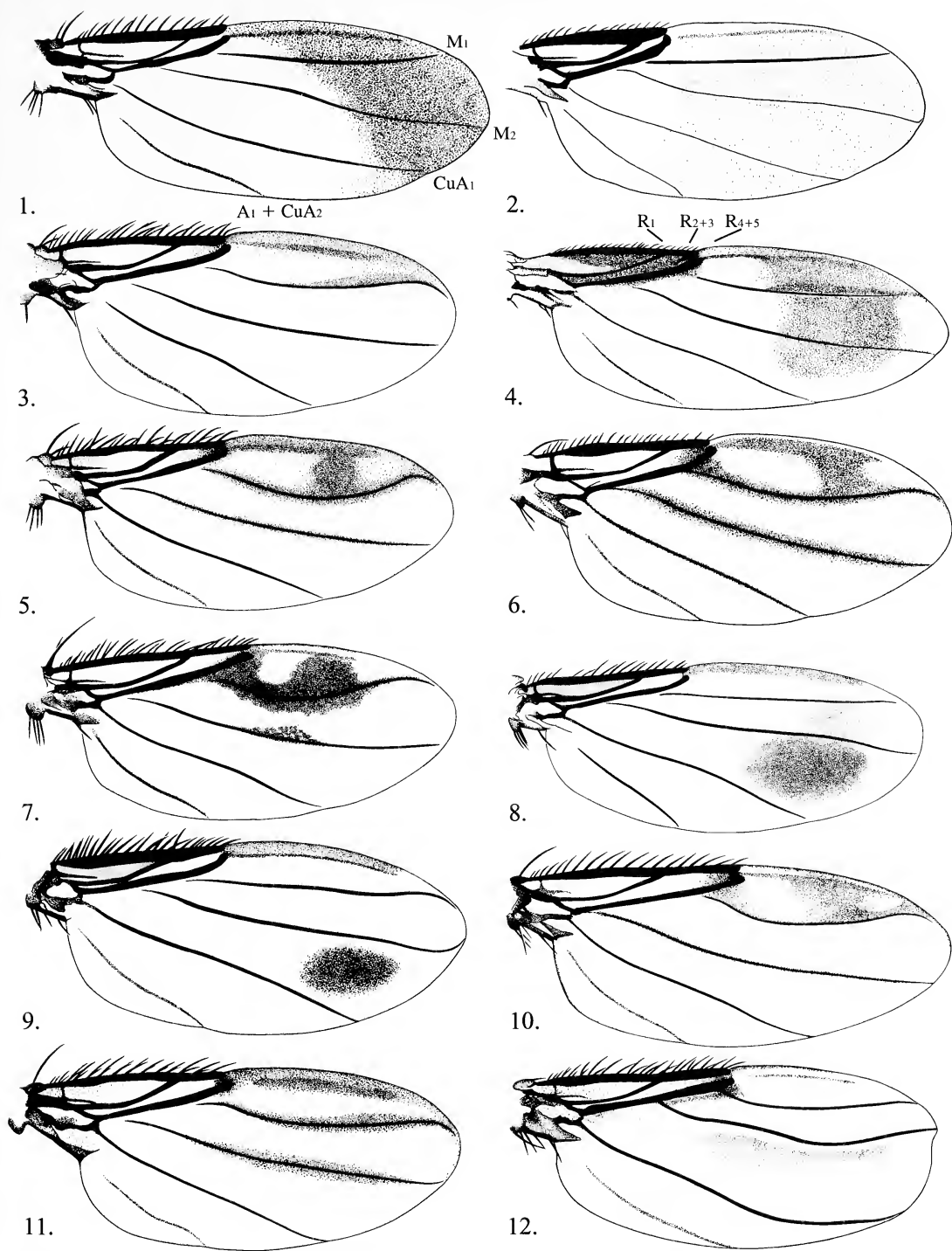
**EMENDED DESCRIPTION.** We examined the holotype of this species and found an error in the original description: the halter is whitish-yellow, not black as stated by Borgmeier.

**NEW MATERIAL EXAMINED.** COSTA RICA: Alajuela, 5 km W San Ramon, 10.05°N, 84.05°W, 2♂, i.1997, 3♂, iv.1997, O. Castro, Malaise trap, 1200 m (LACM); Cartago, Turrialba, 9.93°N, 83.67°W, 1♂, 15–19.vii.1966, P. Spangler, Malaise trap, 600 m (USNM). MEXICO: Chiapas, San Cristobal, 16.75°N, 92.67°W, 1♂, 20.vii.1969, W. Mason, Malaise trap, 2000 m (LACM).

### *Coniceromyia truncata* new species (Fig. 12)

**SPECIES RECOGNITION.** This species is most easily distinguished from the other patterned-wing





Figures 1–12 Wings. 1. *Coniceromyia apicalis* new species. 2. *Coniceromyia aurantia* new species. 3. *Coniceromyia bilineata* new species. 4. *Coniceromyia brevivena* new species. 5. *Coniceromyia globosa* new species. 6. *Coniceromyia impluvia* new species. 7. *Coniceromyia impudica* new species. 8. *Coniceromyia leucomacula* new species [La Cangreja]. 9. *Coniceromyia leucomacula* new species [Estación Cacao]. 10. *Coniceromyia setitarsalis* new species. 11. *Coniceromyia striativena* Borgmeier. 12. *Coniceromyia truncata* new species

*Coniceromyia* by the sinuous, widely spaced  $M_2$  and  $CuA_1$  and the truncate apical margin of the wing.

**DESCRIPTION.** Male. Body length 2.40 to 2.75 mm. Frons dark brown. Flagellomere 1 oval, brown. Arista subapical, pubescent. Palpus yellow with long, dark setae. Dorsum of thorax dark brown. Pleural regions brown. Anepisternum without setae. Scutellum dark brown. Legs yellowish-brown to dark brown. Forefemur with more than one row of long, thin setae on anteroventral margin and one row of long, thin setae on posteroventral margin. Foreleg with two strong dorsal or near-dorsal setae on tibia; tarsomere 1 with triangular process, ventral excavation, and apical process. Basal margin of triangular process with dense, short, fine setae. Posteroventral setae on tarsomere 1 without curved tips. Tarsal segments twice as long as wide (e.g., in one specimen, tarsal ratio is 2.00:1.87:1.83:1.80:1.88). Midcoxa with fine setae and thick ventrolateral seta. Hind femur with tiny, blunt posteroventral setae on basal half; distribution of setae slightly tapered apically. Wing with apical margin truncate.  $M_2$  and  $CuA_1$  slightly sinuous, with the space between these two veins markedly large. Dense setae and darkened pigment anteriorly and posteriorly parallel to  $R_{4+5}$ , between  $M_1$  and  $M_2$ , extending slightly apical of  $M_1$ . Costal and subcostal cells slightly darkened by pigment. Dense patch of fine setae between  $M_2$  and  $CuA_1$ , producing a faint darkening (Fig. 12). Mean costal length 0.50 wing length; range 0.48 to 0.52. Halter yellow. Tergites dark brown; tergite 1 lightened medially. Abdomen gray ventrally. Terminalia light brown.

**GEOGRAPHICAL DISTRIBUTION.** Known from four midelevation sites in Costa Rica.

**DERIVATION OF SPECIFIC EPITHET.** The name is Latin for truncate, referring to the apical margin of the wing.

**HOLOTYPE.** ♂, COSTA RICA: San José, 6 km N San Gerardo, 9.55°N, 83.8°W, xi.1992, P. Hanson, Malaise trap, 2800 m (LACM) [LACM ENT 050221].

**PARATYPES.** COSTA RICA: Cartago, 4 km NE Canon, 9.71°N, 83.94°W, 1♂, vi.1995, P. Hanson, Malaise trap, 2350 m (LACM), Genesis II, 9.71°N, 83.91°W, 1♂, ii.1995, 1♂, viii.1995, 1♂, vii.1996, P. Hanson, Malaise trap, 2350 m (LACM), Villa Mills, 9.57°N, 83.73°W, 1♂, xi–xii.1989, 1♂, iii–iv.1990, P. Hanson, Malaise trap, 3000 m (LACM); Puntarenas, Las Alturas, 8.95°N, 82.83°W, 1♂, iii–v.1995, P. Hanson, Malaise trap, 2100 m (LACM); San José, 2 km W Empalme, 9.72°N, 83.97°W, 1♂, vi.1995, 1♂, vii.1995, P. Hanson, Malaise trap, 2300 m (LACM), 20 km S Empalme, 9.63°N, 83.85°W, 2♂, viii.1988, 1♂, iii–iv.1990, P. Hanson, Malaise trap, 2800 m (LACM), Sendero el Carbon, Estación Cuerici, 5 km E Villa Mills, 9.57°N, 83.73°W, 1♂, 16.iii.1996, A. Picado, 2600 m (INBC), 6 km N San Gerardo, 9.55°N, 83.8°W, 3♂, vi.1992, 1♂, ix.1992, 1♂, xi.1992, P. Hanson, Malaise trap, 2800 m (LACM, MUCR).

**KEY TO PATTERNED-WING CONICEROMYIA MALES**

- 1 Anepisternum with setae ..... 2
- Anepisternum without setae ..... 7
- 2 Anterior of forefemur black with distinct white markings ..... 3
- Anterior of forefemur not black with distinct white markings ..... 4
- 3 Anterior of forefemur with large white patch extending three-quarters length of femur. Wing with oval darkening between  $M_2$  and  $CuA_1$ . Wing with or without lighter darkening between  $M_1$  and  $M_2$  (Figs. 8, 9) ..... *C. leucomaculata* new species [Costa Rica]
- Anterior of forefemur mostly black with narrow white markings. Wing with large double-lobed darkening, one lobe between anterior margin and  $M_2$ , other lobe between  $M_2$  and  $CuA_1$  ..... *C. stephensoni* Peterson [Costa Rica, Panama]
- 4 Apical half of  $R_{2+3}$  present. Costal and subcostal cell entirely darkened. Apical third of wing, except for apex, darkened. Darkening not extending to  $CuA_1$  (Fig. 4) ..... *C. brevivena* new species [Peru]
- Apical half of  $R_{2+3}$  not present. Both costal and subcostal cells not entirely darkened. Apex of wing darkened to  $CuA_1$ , or not darkened. .... 5
- 5 Forefemur with anterior, oval, orange macula on basal half. Tarsomere 1 of foreleg without basal seta. Foretibia with posteroventral row of setae in apical half ..... *C. aurantia* new species [Peru]
- Forefemur without orange macula. Tarsomere 1 of foreleg with basal seta. Foretibia without posteroventral row of setae in apical half ..... 6
- 6 Darkening of wing not extending to apical margin.  $M_1$  not thickened. Space between  $M_1$  and  $M_2$  not narrowed basally. Apical two-fifths of wing, except for apex, darkened ... *C. blomae* Peterson and Arntfield [Mexico]
- Darkening of wing extending to apical margin.  $M_1$  thickened. Space between  $M_1$  and  $M_2$  narrowed basally so that veins are parallel in basal third and divergent in apical two-thirds. Apical third of wing darkened (Fig. 1) ..... *C. apicalis* new species [Costa Rica]
- 7 Flagellomere 1 oval.  $M_2$  and  $CuA_1$  widely spaced and sinuous. Apical margin of wing truncate (Fig. 12) .. *C. truncata* new species [Costa Rica]
- Flagellomere 1 elongate-conical.  $M_2$  and  $CuA_1$  not widely spaced and sinuous. Apical margin of wing not truncate ..... 8

- 8 Wing with darkening in membrane posterior to  $M_1$  ..... 9
- Wing without darkening in membrane posterior to  $M_1$ ; darkening, if present, restricted to wing veins ..... 11
- 9 Foretibia without excavation with three to four dorsal to anterodorsal setae. Wing patterning along  $M_2$ -enlarged midvein so that the darkening extends into membrane posterior to  $M_2$ . Patterning does not extend posteriorly to  $CuA_1$  ..... *C. impudica* new species [Honduras]
- Foretibia excavate with one long seta. Wing patterning extends posteriorly to  $CuA_1$  .. 10
- 10 Wing margin emarginate at  $M_2$  and  $CuA_1$ . Costal and subcostal cells not darkened. Darkening present in apical half of wing. Darkening not present on posterior margin ..... *C. vespertilio* Schmitz [Brazil]
- Wing margin not emarginate; smooth and entire. Costal and subcostal cells darkened. Posterior half and apical two-fifths of wing darkened ..... *C. maculipennis* Borgmeier [Brazil]
- 11 Wing pattern restricted to two lines of darkening: anterior margin and  $M_1$  (Fig. 3); wing without distinct darkening between these two lines. Ventral setae on tarsomere 1 of foreleg without curved tips ..... *C. bilineata* new species [Costa Rica]
- Wing pattern not restricted to two lines of darkening along anterior margin and  $M_1$ . Ventral setae on tarsomere 1 with or without curved tips ..... 12
- 12 Anterior margin of wing darkened, but membrane between anterior margin and  $M_1$  not darkened. Wing darkened in three striae: anteroapical margin,  $M_1$ , and  $M_2$  (Fig. 11) .... *C. striativena* Borgmeier [Costa Rica, Mexico]
- Wing with membrane between anterior margin and  $M_1$  darkened; darkening on  $M_2$  present or absent ..... 13
- 13 Foreleg with basal triangular process on tarsomere 1. Wing with darkened pigment along  $M_1$ , with enlarged areas at tip of  $R_{4+5}$  and mid- $M_1$ . Darkening mid- $M_2$  present or absent. Without darkening along  $CuA_1$  (Fig. 7) .... *C. impudica* new species [Honduras]
- Foreleg without basal triangular process on tarsomere 1. Wing with darkened pigment between anteroapical margin and  $M_1$ ; along anteroapical margin,  $M_1$ , and  $M_2$ . Darkening along  $M_2$  sometimes faint. Darkening along  $CuA_1$  present or absent ..... 14
- 14 Wing with a distinct round macula between anterior margin and  $M_1$ ; darkening present along  $M_2$ , although sometimes faint (Fig. 5) ..... *C. globosa* new species

[Costa Rica, Panama]

- Darkening between anterior margin and  $M_1$  not distinctly round; darkening on  $M_2$  present, although sometimes faint (Figs. 6, 10) .. 15
- 15 Tapered portion of flagellomere 1 longer than untapered portion. Tarsomere 1 of foreleg with long, thin, curve-tipped, erect, posterior setae.  $CuA_1$  without darkening (Fig. 10) .... *C. setitarsalis* new species [Costa Rica]
- Tapered portion of flagellomere 1 shorter than untapered portion. Setae on posterior of tarsomere 1 of foreleg short, not curve-tipped or erect.  $CuA_1$  faintly darkened (Fig. 6) ..... *C. impluvia* new species [Costa Rica]

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