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## Towards a Monophyletic Bombyliidae (Diptera): the Removal of the Proratinae (Diptera: Scenopinidae)

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### ABSTRACT

*Prorates* Melander, *Alloxytropus* Bezzi, *Caenotus* Cole, and *Caenotoides* Hall (the *Prorates* group) of the Bombyliidae subfamily Proratinae share the following apomorphies with the Scenopinidae: male eyes divided into regions of large facets dorsally and small facets ventrally, scutum lacking large setae, wing cell bm acute apically, an area of modified setae on abdominal tergite two of both sexes; epandrium divided longitudinally into two sclerites, distiphallus bifid or trifid, and spermathecae reduced from three to two. A cladogram of the *Prorates* group of genera and representative Scenopinidae is presented. The Scenopinidae plus the *Prorates* group of genera form a monophyletic group and the concept of the family is enlarged to

include the *Prorates* group. The Scenopinidae are divided into three subfamilies: The Caenotinae, containing *Caenotus*; the Proratinae containing *Alloxytropus*, *Caenotoides* and *Prorates*; and the Scenopininae containing all the genera placed in the Scenopinidae before this work. The new subfamilies are keyed and described and their constituent genera are listed.

*Apystomyia* Melander has traditionally been classified in the Proratinae. Unlike the *Prorates* group, *Apystomyia* does not exhibit a relationship with the Scenopinidae and it is considered incertae sedis at the family level within the Muscomorpha (sensu Woodley, 1989).

### INTRODUCTION

It is the common opinion of recent authors that the family Bombyliidae is probably paraphyletic (Hennig, 1973; Mühlenberg, 1971;

Bowden, 1980). This opinion is warranted because the family is morphologically diverse and lacks convincing apomorphies. Our ig-

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norance of the phylogenetic relationships of the Bombyliidae hampers attempts to construct a phylogenetic scheme for the Asiloidea. Woodley (1989) hypothesized that the Bombyliidae constitute the most primitive family of the Asiloidea and considered the construction of a phylogenetic scheme for the Bombyliidae a high priority for future work. The work presented here provides testable hypotheses of relationship for four genera comprising 17 species belonging to one subfamily of Bombyliidae, the Proratinae. This subfamily is presently characterized by features which exhibit much homoplasy within the Asiloidea.

During studies on the higher classification of the Bombyliidae, the phylogenetic position of the proratine genera was reexamined using cladistic techniques. A number of synapomorphies were found between *Caenotus* Cole, *Prorates* Melander, *Alloxytropus* Bezzi, *Caenotoides* Hall (here denoted the "Prorates group") and the Scenopinidae. As a consequence the Bombyliidae, as traditionally circumscribed, is polyphyletic. The limits of the Scenopinidae are enlarged to include the *Prorates* group in this paper. The relationships of the remaining genus currently placed in the Proratinae, *Apystomyia* Melander, is less certain, and will be discussed in a forthcoming work. For the time being I consider it incertae sedis at the family level in the Muscomorpha (sensu Woodley, 1989).

Most species of the *Prorates* group of genera are found in xeric habitats of the western Nearctic region, however *Alloxytropus* is Palearctic. They are poorly represented in collections and have been collected on few occasions. Efflatoun (1945) found specimens of *Alloxytropus* hovering sluggishly from 1 p.m. to 4 p.m., the hottest part of the day, in Egypt. Hall (1972) reported that specimens of *Caenotoides* had been collected flying close to the ground in sand dunes in California and Mexico. Often proratines have been collected under circumstances where little can be inferred about their biology. For example, Cole (1923) collected large numbers of *Caenotus* that were attracted to the windows of his trailer in New Mexico. Melander (1950) collected specimens of *Prorates* inside his automobile in California.

## TAXONOMIC HISTORY

The subfamily Proratinae was proposed by Theodor (1983) for *Prorates* Melander (1906), which had been classified in the subfamily Heterotropinae of the Bombyliidae. Theodor (1983) noted similarities in the male genitalia of *Prorates* and a scenopinid *Belosta viticollipennis* Kelsey, and sensory areas on abdominal tergite 2 in both *Prorates* and the Scenopinidae. He speculated that the Proratinae belonged in the Scenopinidae, but Woodley (1989) considered that Theodor's evidence required further corroboration. Evenhuis (1991), in the "World Catalog of Genus-group Names of Bee Flies" removed four additional genera: *Alloxytropus* Bezzi (1925); *Apystomyia* Melander (1950); *Caenotus* Cole (1923); and *Caenotoides* Hall (1972) from the bombyliid subfamily Heterotropinae to the Proratinae. He commented that further phylogenetic work was needed before the correct family placement of the Proratinae could be ascertained.

Heterotropinae was erected in the Bombyliidae by Becker (1913) for *Heterotropus* Loew (1873). Melander (1906) described *Prorates* in the Empididae and included a single species, *P. claripennis* Melander. Cole (1923) described *Caenotus* in the Therevidae for two species, *C. inornatus* (the type species) and *C. minutus*. Cole indicated that *Caenotus* was not closely related to any other North American Therevidae, because the male genitalia differ in general form. Melander (1928) placed *Prorates* and *Caenotus* in the Heterotropinae and considered that the following characteristics warranted the change in placement of *Prorates*: costal vein short, ending at  $R_5$ ; Sc distinct and ending in the costa; antennal style microscopic and anepisternum with pubescence. Hall (1972) redescribed *Prorates* and added five more new species. Many years after he moved *Caenotus* to the Bombyliidae, Melander (1950) described *C. hospes* and *C. canus*.

Melander (1950) also described the monotypic Nearctic genus *Apystomyia*, added it to the Heterotropinae, and described the first Nearctic *Heterotropus*, *H. senex*. This species was later removed to the new genus *Inyo* of the new subfamily Desmatomyiinae by Hall

and Evenhuis (1987). Melander (1950) considered that the enlarged subfamily Heterotropinae could be separated from other Bombyliidae on the basis of the following characters: occiput flattened, eyes of male bisected into smaller (lower) and larger (upper) facets, eyes not indented behind [as in Bezzi's (1924) *Tomophthalmae*], tibiae without serrate spines,  $R_{4+5}$  forked, cell  $r_5$  open, and cell cup closed. Hull (1973) placed the same genera in the Heterotropinae as did Melander (1950). Hall (1972) described *Caenotooides* for three new species from the western United States and Mexico. He added it to the Heterotropinae and noted that the subfamily contained an anomalous group of small bombyliids. Hall amended the following details to the characterization of the subfamily: male usually holoptic, female dichoptic, inner margin of male eyes usually indented opposite antennal bases, anal lobe of wing greatly developed and body not densely hairy. Hall reported that *Caenotooides* was similar to *Caenotus* but differed in the following respects: flagellum with an apical tuft of hair; shorter, one-segmented palpi, and costa terminating at or slightly beyond  $R_4$ .

*Alloxytropus* Bezzi (1925) was described for a single species, *anomala*, from Egypt. Paramonov (1929) subsequently described another species, *A. bezzii*, also from Egypt. Zaitsev (1972a, b) described two more species, one from Mongolia and another from Russia. Bezzi (1925) considered *Alloxytropus* similar to *Heterotropus*, but differing in wing venation and female frons. Melander (1950) considered *Alloxytropus* a synonym of *Prorates*, as did Hall (1972), Hull (1973) and Bowden (1980); however Zaitsev (1989) and Evenhuis (1991) considered the two genera distinct.

Hull (1973) noted that many of the features used to differentiate the Heterotropinae are found in other bombyliids and considered it possible that some of the constituent genera belong in a separate family.

#### METHODS

Genitalia were examined by soaking the terminal segments of the abdomen in cold 10 percent KOH overnight and dissecting out the relevant structures. Drawings were made

using Zeiss binocular dissecting and compound microscopes with camera lucida attachments. Terminology for adults follows McAlpine (1981) except that the complex intromittent organ comprising the aedeagus and surrounding paramere sheath is here termed the phallus (Wood, 1990). The subepandrial plate is an area of sclerotization between segment 9 and the proctiger. In many asiloids it is poorly sclerotized and lies underneath the epandrium. In the *Eremoneura* the plate is completely sclerotized and forms a connection between the proctiger and phallus (Cumming and Sinclair, 1990).

#### ACKNOWLEDGMENTS

This research was completed while DKY held a Roosevelt Postdoctoral Fellowship from the American Museum of Natural History. I am grateful to Bill Barnett and Peling Fong and of the AMNH for technical assistance with scanning electron microscopy. Donald Azuma (Philadelphia Academy of Natural Sciences, Philadelphia) and John Bowden (Colchester, United Kingdom), Jeff Cumming (C.L.B.R.R.-B.R.D., Ottawa, Canada), Neal Evenhuis (B.P. Bishop Museum, Honolulu), Mike Irwin (Illinois Natural History Survey, Champaign, Illinois), Norm Woodley (USDA, Smithsonian Institution, Washington) kindly allowed me to examine and dissect specimens under their care. I am especially grateful to Monty Wood, Jeff Cumming, and Brad Sinclair for sharing with me their ideas on the homologies of the male genitalia of Diptera; their interpretation of *Prorates* is followed here. Neal Evenhuis pointed out to me that Fallén (1817) first used Scenopinidae at the family level. David Grimaldi (AMNH), Norm Woodley, Neal Evenhuis, Jeff Cumming, and Brad Sinclair (C.L.B.R.R.-B.R.D., Ottawa, Canada) provided helpful comments on the manuscript.

#### PHYLOGENETIC CONTEXT

As the phylogenetic relationships of the subfamily Proratinae were uncertain at the outset of this study, the male and female genitalia of the Proratinae were compared with those of other subfamilies of the Bombyliidae and other families of the superfamily Asilo-

idea. This examination revealed that the *Prorates* group of genera shares three features with the Scenopinidae that are never found in the Bombyliidae. These features are: (1) the epandrium of the male genitalia is divided along the midline into two sclerites, (2) the distiphallus is bifid, and (3) only two spermathecae are present in the female. In contrast, all Bombyliidae have an undivided epandrium and none have a bifid distiphallus. The distiphallus of the vast majority of Bombyliidae is undivided, however members of the genus *Heterotropus* and some Mythicomysiinae have a trifid aedeagus. Characteristics of the larvae indicate that *Heterotropus* is primitive within the Asiloidea (Yeates and Irwin, 1992), and the relationship of the Mythicomysiinae to the remaining subfamilies of Bombyliidae remains undetermined. The only bombyliid known to have a reduced number of spermathecae is the highly derived genus *Antonia* which has only one (Theodor, 1983). In addition to the genitalic characters listed above, both sexes of all Scenopinidae and the *Prorates* group of genera (except *Caenotoides*) share a curious small area of modified setae on abdominal tergite two. Theodor (1983) first noticed this character, which is examined in detail here. This paper reports a more detailed cladistic analysis of the relationship between the *Prorates* group of genera and the Scenopinidae.

The Scenopinidae belong to the Asiloidea, and according to the most recent cladistic analysis of that superfamily (Woodley, 1989) they are the sister group of the Therevidae. The relationship between the Scenopinidae and Therevidae is supported by the secondary segmentation of the larval abdomen in both families. This secondary segmentation of the entire abdomen is unknown in other asiloids, and the close relationship between the two families is well established. There is only a single apomorphy for the Therevidae, the larval metacephalic rod being spatulate posteriorly (Malloch, 1917). As few therevids are known in the larval stage, this apomorphy has not been subject to stringent testing. Woodley (1989) noted that because the evidence for the monophyly of the Therevidae is weak, the Scenopinidae may be an apomorphic offshoot of the Therevidae, making the latter paraphyletic.

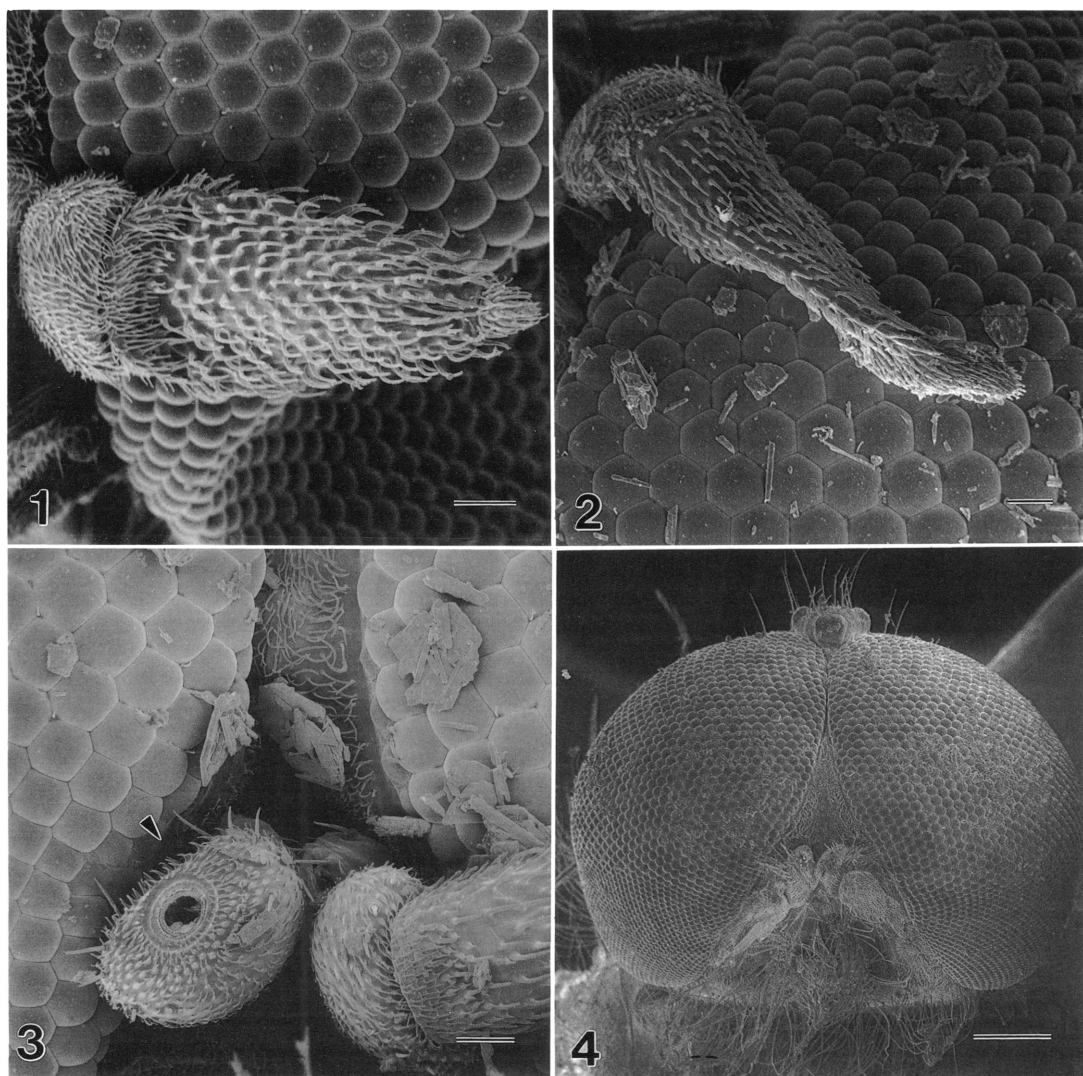
Examination of the male and female genitalia of *Apystomyia* Melander reveals that they lack the similarities which the *Prorates* group of genera shares with the Scenopinidae and they are not included in the study reported below. The relationship of *Apystomyia* to the Bombyliidae and the other families of Asiloidea will be addressed in a forthcoming work. At present it is considered incertae sedis at the family level in the Muscomorpha (sensu Woodley, 1989).

## CLADISTIC ANALYSIS

### OUTGROUP SELECTION

Because of the close relationship between the Scenopinidae and Therevidae, members of the Therevidae were chosen as outgroups in the phylogenetic analysis of the *Prorates* group of genera below. Representative outgroup taxa were chosen from the main clades within the Therevidae as they are currently delineated. Little has been published on the phylogenetic system of the Therevidae. Irwin (1971) hypothesized that there was a dichotomy at the base of the therevid clade, with one branch corresponding to the Therevinae and the other branch corresponding to the Pherocerinae of Irwin and Lyneborg (1981a). Irwin (1976), using characters of the female genitalia and oviposition behavior, proposed a similar basal dichotomy. I have included *Thereva fucata* Loew and *Phycus rufosemoralis* (Kröber) as representatives of both therevid subfamilies.

Irwin (personal commun.) believes that the current therevid subfamily classification, based largely on the Nearctic and Palearctic faunas, will need revision once the fauna of the Southern Hemisphere is better known. With this in mind I have included a representative of the Australian therevid genus *Bonjeania* Irwin, which has bizarre male genitalia exhibiting some plesiomorphic features relative to the therevids of the Nearctic and Palearctic. The male genitalia of *Bonjeania* also have a superficial resemblance to those of *Prorates*, *Alloxytropus* and *Caenotoides*. In all three genera the male genitalia are elongate with the gonocoxal apodemes and distiphallus being long and narrow. In *Prorates* and *Alloxytropus* the gonocoxal apodemes articulate with rods from the aedeagal sheath,



Figs. 1–4. Scanning electron micrographs of heads of members of the *Prorates* group. 1, *Prorates claripennis* male, antenna, scale line = 20  $\mu$ m; 2, *Alloxytropus anomala* male, antenna, scale line = 20  $\mu$ m; 3, *Alloxytropus anomala* male, frons and base of antennae, indentation of inner margin of eyes at level of antennae arrowed, scale line = 20  $\mu$ m; 4, *Caenotus hospes* male head, scale line = 200  $\mu$ m.

whereas in *Bonjeania* the ends of the gonocoxal apodemes are free.

#### INGROUP TAXA

Members of each of the *Prorates* group of genera were coded in the analysis. The type species of *Caenotus*, *C. inornatus*, was included in addition to *C. hospes* because of the plesiomorphic wing venation of *C. inornatus*. Like the outgroup therevids, *C. in-*

*ornatus* has wing vein  $M_3$ , thus suggesting the possibility that *C. inornatus* is more similar to other therevids than the remaining species of *Caenotus*. *Alloxytropus anomala* Bezzi and *Caenotoides californica* Hall, both type species, were coded, as was *Prorates frommeri* Hall. Among the Scenopinidae, the common, widespread, type species of the type genus, *Scenopinus fenestralis* was coded, as was an undescribed species of the genus *Propebrevitrichia* Kelsey. *Scenopinus* lacks acan-

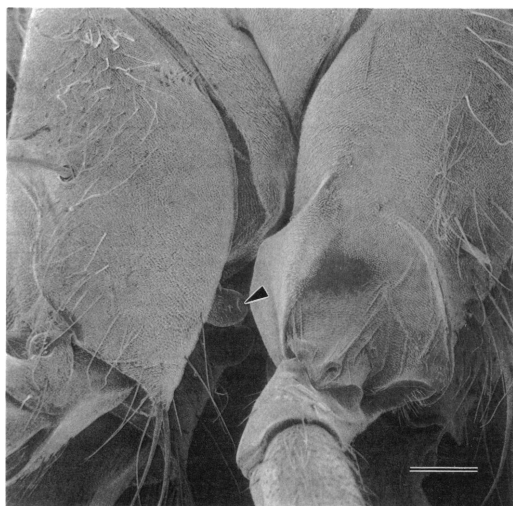


Fig. 5. Scanning electron micrograph of the hind coxa of a therevid showing the rounded knob on anterior face (arrowed), scale line = 200  $\mu$ m.

thopporite spines whereas *Propebrevitrichia* has them. The male genitalia of *Belosta albipilosa* Hardy are illustrated because Theodor noted a similarity between this genus and *Prorates*.

#### CHARACTERS

1. Segmentation of antennal flagellum (excluding the apical or subapical hyaline style): two segments, 0; one segment, 1. Woodley (1989) considered the reduction in segments of the antennal flagellum to four or less an apomorphy of the Muscomorpha (in Woodley's sense). Therevidae have a three- or two-segmented antennal flagellum. Note that figures 37.4 and 37.6 of *Litolinga acuta* (Adams) and *Breviperna placida* (Coquillett) in Irwin and Lyneborg (1981b) are in error; both these species possess three antennal flagellar segments, not four. Members of the Scenopinidae have a single antennal flagellomere. *Caenotus*, *Prorates*, and *Caenotoides* have two-segmented antennal flagella (fig. 1) and *Alloxytropus* has a single segment (fig. 2).

2. Apex of flagellum undifferentiated, without circlet of hairs, 0; second segment of flagellum with circlet of small hairs, 1. The advanced state of this character is an autapomorphy for *Caenotoides*.

3. Eyes of male with dorsal facets similar

in size to ventral facets, 0; eyes of male with facets divided in the horizontal plane into larger dorsal facets and smaller ventral facets, 1. The Therevidae possess the plesiomorphic state of this character. All the remaining taxa under study have the derived state (fig. 4). The derived state is also widespread in the Bombyliidae Homeophthalmae.

4. Eyes of male with inner margin straight, 0; eyes of male with inner margin indented at the level of the antennal bases (fig. 3), 1. The advanced state of this character occurs in *Prorates* and *Alloxytropus*.

5. Mouthparts normal, functional, 0; oral cavity shallow and mouthparts reduced, perhaps nonfunctional, 1. The apomorphic state of this character was found only in *Caenotoides*.

6. Prosternum fused to propleuron forming a precoxal bridge, 0; prosternum separate from propleuron, 1. The plesiomorphic state of this character was found in all the taxa scored here except *Caenotus*.

7. Hind coxa with a rounded knob on the anterior face, 0; knob absent, 1. The plesiomorphic state of this character was found in the Therevidae (fig. 5, also see Irwin and Lyneborg, 1981b: figs. 9 and 10) and all ingroup taxa examined here except *Caenotoides* and the Scenopinidae. A similar rounded knob on the hind coxa is also present on many Rhagionidae and Athericidae (Webb, 1981: fig. 32.5).

8. Costal vein circumambient, extending around wing, 0; costal vein ending in the R field, 1. The advanced state of this character was found in *Prorates* (fig. 6), *Caenotoides* (fig. 10), *Alloxytropus* (fig. 9) and the Scenopinidae (fig. 8).

9. Wing with veins of M and CuA fields reaching the posterior margin of the wing (fig. 7), 0; wing with veins of M and CuA fields not reaching margin (figs. 6, 8–10), 1. The advanced state of this character was found in *Caenotoides*, *Prorates*, *Alloxytropus*, and the Scenopinidae.

10. Vein  $M_3$  present, 0; absent, 1. Wing vein  $M_3$  is lost in various asiloids including the Bombyliidae. All Therevidae have  $M_3$  present. All the ingroup taxa examined here have lost vein  $M_3$  (figs. 6–10) except *Caenotus inornatus*. *C. inornatus* is considered similar to the Therevidae and thus plesiomorphic in

this respect, however it shares an advanced configuration of cell bm (Character 13) with the remaining ingroup taxa.

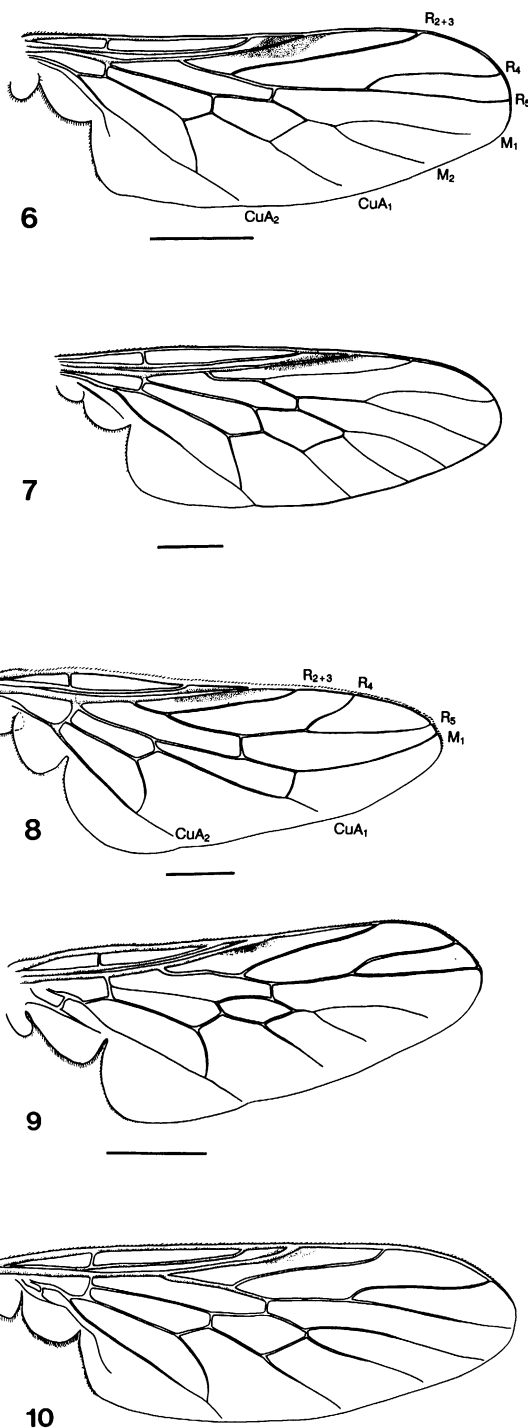
11. Vein  $M_2$  present, 0; absent, 1. Among the ingroup taxa examined only the scenopinids (fig. 8) have the advanced state of this character, and it appears to be an apomorphy for the Scenopinidae.

12. Wing cell m1 not strongly widened distally, 0; strongly widened distally, 1. The peculiarly wide cell m1 was used as an apomorphy of the Scenopinidae (fig. 8) by Woodley (1989), and was only found in the Scenopinidae examined in this study.

13. Cell bm with apex blunt, 0; cell bm with apex acute, 1. The Therevidae have veins  $CuA_1$  and  $M_3$  arising from the apex of cell bm, making the apex of that cell blunt. All the ingroup taxa have only  $CuA_1$  arising from the apex of cell bm (figs. 6–10), making the apex of that cell acute. The apomorphic state of this character is present in *Caenotus inornatus*, which has three branches of M.

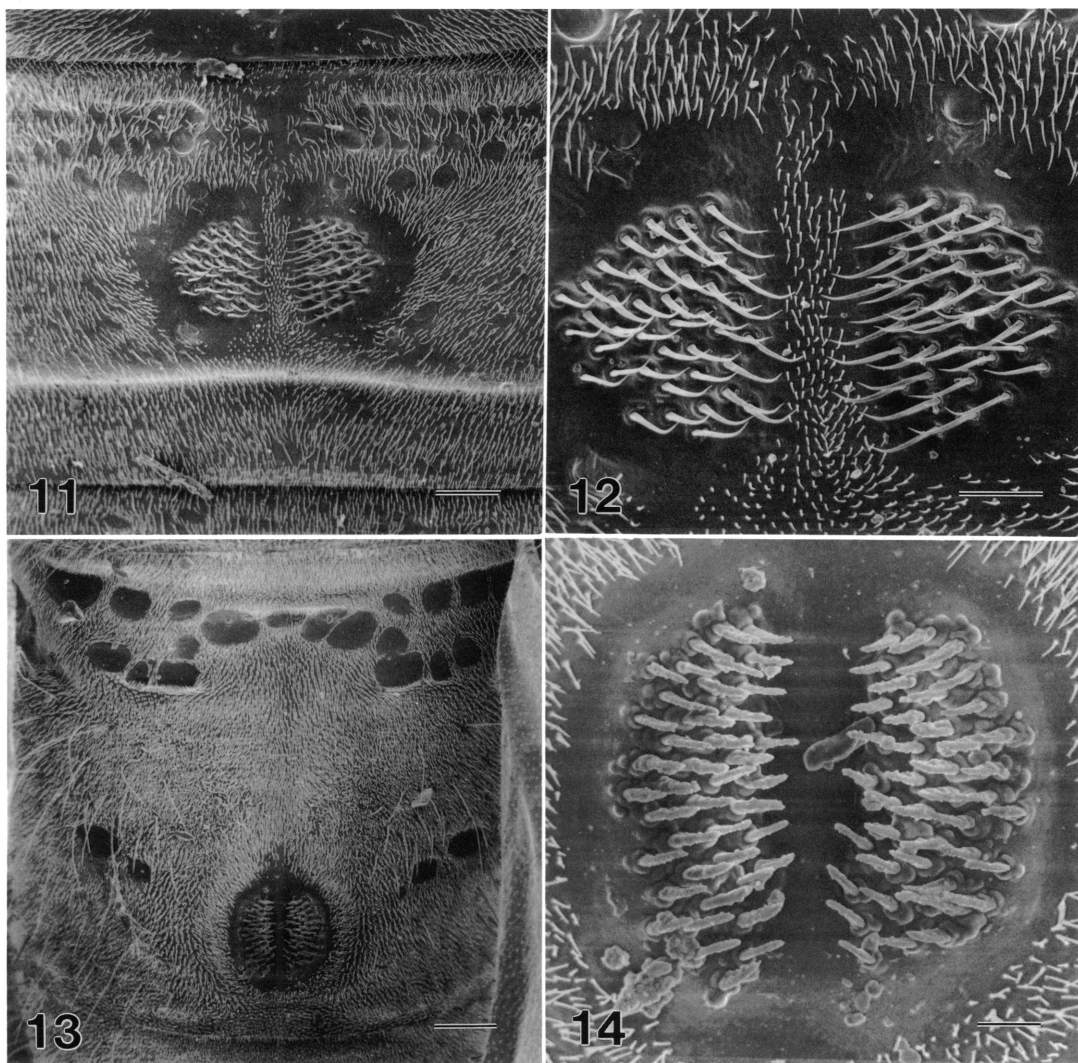
14. Well-developed long setae and short, fine hairs on the scutum, 0; scutum clothed in short, fine hairs only, 1. All therevids have well developed large setae on the scutum, in particular on the notopleuron, supra alar area, and postalar ridge. The ingroup taxa examined lack these large setae, however some *Prorates* have two pairs of small setae on the scutum and one pair on the scutellum. The setae in *Prorates* appear to be homologous with those found in the Therevidae because of their position.

15. Abdominal tergite 2 normal, without modified setae, 0; with two adjoining hemispherical areas of large setae (figs. 11, 13) with acuminate or slightly rounded tips (figs. 12, 14), 1; with a triangular area (figs. 16, 18) of large, truncate setae with flattened (*Prorates*, fig. 17) or slightly rounded apices (*Alloxytropus*, fig. 20) on posterior margin of tergite, 2. Theodor (1983) was the first to bring attention to the occurrence of state 2 of this character in *Prorates* and the scenopinids. The areas of setae described in the advanced states of this character are of unknown function, but I have termed them "sensory areas" because they probably have some sensory function. This character was coded both in additive and nonadditive form but this change had no effect on the topology of the clado-



Figs. 6–10. Right wings, scale lines = 0.5 mm. 6, *Prorates frommeri*; 7, *Caenotus hospes*; 8, *Scenopinus fenestralis*; 9, *Alloxytropus anomala*; 10, *Caenotoides californica*.





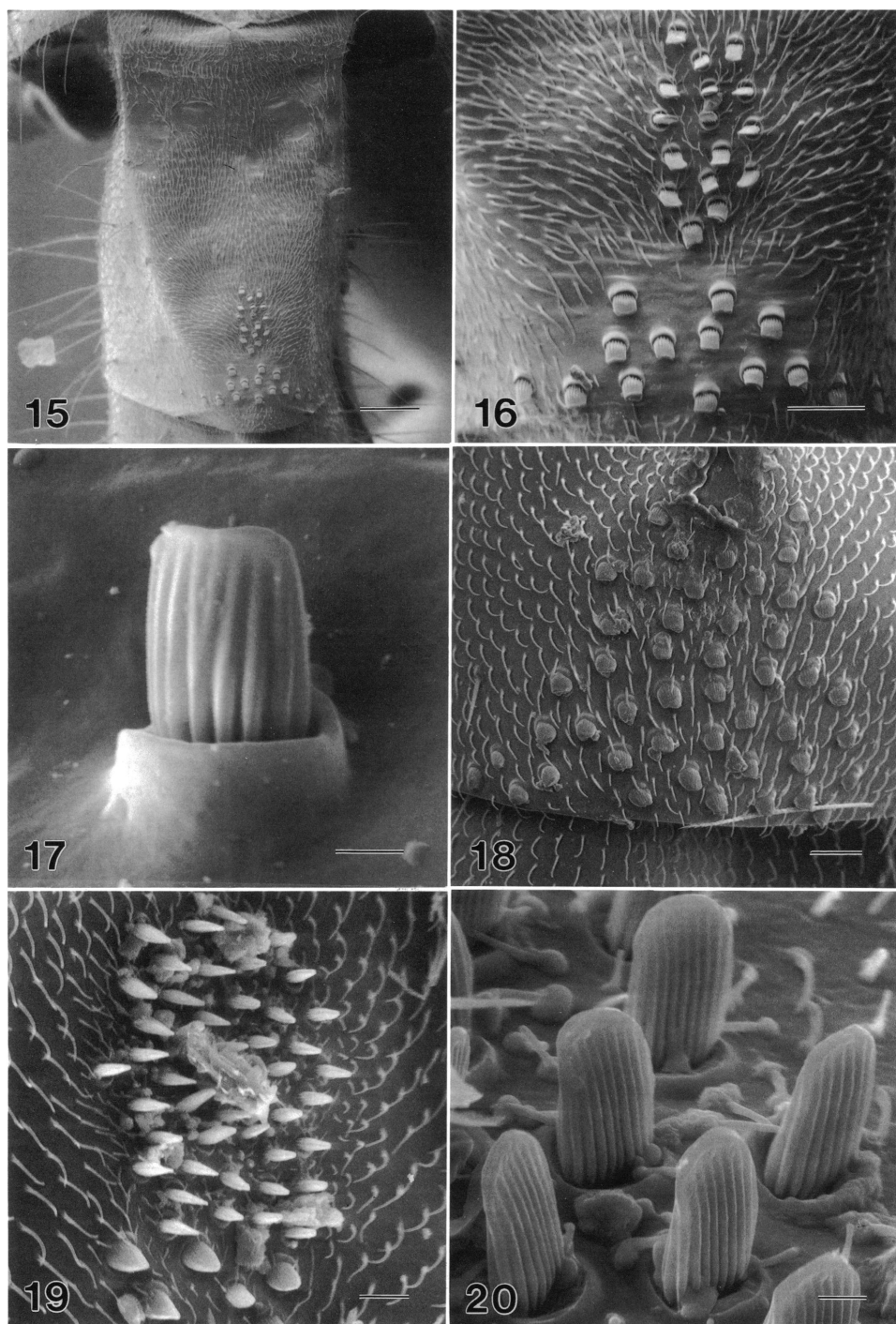
Figs. 11–14. Scanning electron micrographs of sensory areas on tergite 2 of the abdomen. 11, *Scenopinus fenestralis*, scale line = 100  $\mu\text{m}$ ; 12, same, detail, scale line = 50  $\mu\text{m}$ ; 13, *Caenotus hospes*, scale line = 100  $\mu\text{m}$ ; 14, same, detail, scale line = 20  $\mu\text{m}$ .

gram. The optimization of this character, which is equally parsimonious (three steps) in both additive and nonadditive coding, is  $0 > 1 > 2$ . Figure 21 shows the hypothesized transformation series of character 12 from the sensory area on tergite 2 found in *Caenotus* and the Scenopinidae (fig. 21a, state 1) toward the sensory area found in *Alloxytropus* (fig. 21b, state 2) and *Prorates* (fig. 21c). The sensory area in *Alloxytropus* has a posterior triangular region of setae with truncate apices and an adjacent but more anterior re-

gion of setae with rounded apices. In the *Prorates* species examined all the setae in the sensory area had truncate apices. The region of enlarged sensory setae was found in all Scenopinidae examined.

16. Acanthophorites (spine-bearing lobes of female tergite 10) present, 0; absent, 1. Adisoemarto and Wood (1975) considered the presence of acanthophorites to be a groundplan feature of the Asiloidea. These spine-bearing lobes occur in at least some members of each family of the Asiloidea, but





Figs. 15–20. Scanning electron micrographs of sensory areas on tergite 2 of the abdomen. 15, *Prorates claripennis*, scale line = 50  $\mu\text{m}$ ; 16, same, detail, scale line = 20  $\mu\text{m}$ ; 17, same, detail of one of the setae in sensory area showing truncate apex, scale line = 2  $\mu\text{m}$ ; 18, *Alloxystropus anomala*, detail of setae in posterior region of sensory area, scale line = 20  $\mu\text{m}$ ; 19, same, detail of setae in anterior region of sensory area, scale line = 10  $\mu\text{m}$ ; 20, same, detail of setae in fig. 19, scale line = 2  $\mu\text{m}$ .

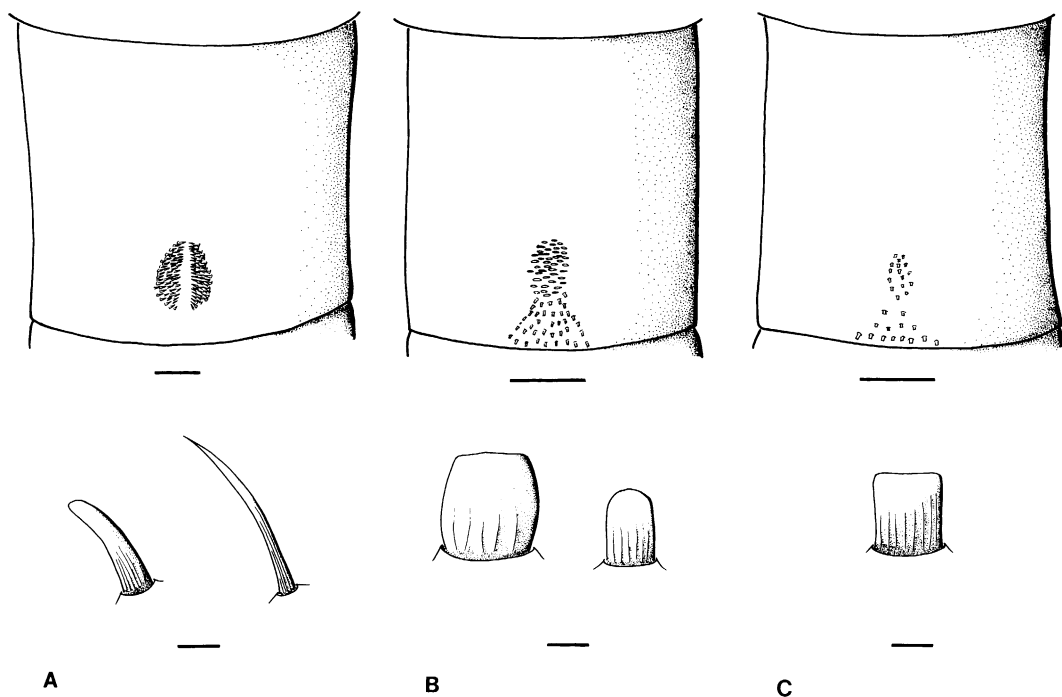


Fig. 21. Drawings of sensory areas on tergite 2 of abdomen taken from scanning electron micrographs. **A.** Position of the sensory areas in *Caenotus* and the Scenopinidae (top, scale line = 0.1 mm) and the shape of the setae in the area in *Caenotus* (bottom left, scale line = 10  $\mu$ m) and *Scenopinus* (bottom right, scale line = 10  $\mu$ m). **B.** Sensory area in *Alloxystropus* (top, scale line = 0.1 mm) and the shape of the setae in the posterior region of the sensory area (bottom left, truncate apex, scale line = 4  $\mu$ m) and the anterior region of the sensory area (bottom right, rounded apex). **C.** Sensory area in *Prorates* (top, scale line = 0.1 mm) and shape of setae in the sensory area (bottom, scale line = 4  $\mu$ m) with truncate apices.

have been lost numerous times, probably in response to changing oviposition habits. They have been retained in all representatives examined here except *Scenopinus* (figs. 34, 35).

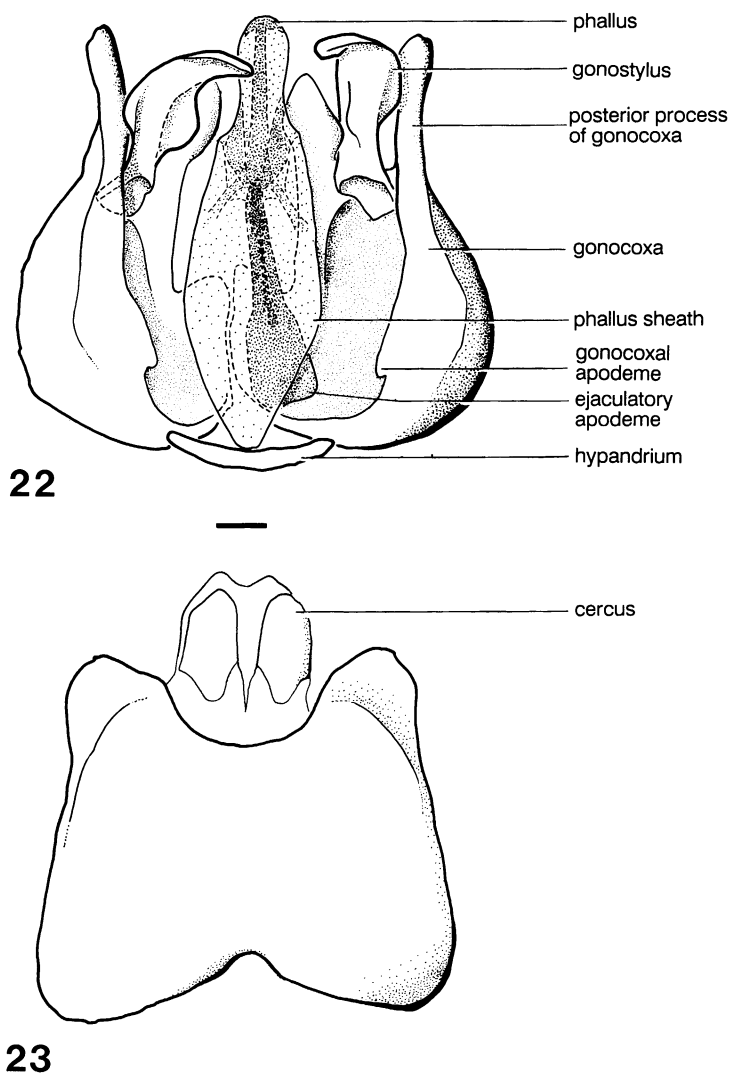
17. Female with sclerotized strip of cuticle running along the midline from the base of tergite 8 to the apex of tergite 9 (e.g., fig. 42), **0**; sclerotized strip lost, **1**. This strip of cuticle was found in all taxa examined except *Phycus*, *Caenotoides*, and *Scenopinus*. Its presence is most probably a groundplan feature of therevids and scenopinids. This character may be correlated with well-developed acanthophorite spines as *Phycus* has very small acanthophorite spines and *Scenopinus* lacks them altogether.

18. Spermathecae three in number, **0**; two, **1**. Three spermathecae are found in therevids, however all the ingroup taxa examined have two spermathecae (figs. 35, 38, 43, 51, 56, 61). Three spermathecae are found com-

monly in all asiloid families except the Scenopinidae. In various genera spermathecae have been lost, for instance *Antonia* Loew (Bombyliidae) has one spermatheca (Theodor, 1983) and *Proctacanthus* Macquart, *Ec-critosis* Schiner, and *Myaptex* Hull (Asilidae: Asilinae) have two (Theodor, 1976).

19. Epandrium consisting of a single sclerite, **0**; divided at the midline into two halves, **1**. The epandrium is whole in the Therevidae (figs. 23, 26) but divided into two in all ingroup taxa (figs. 27, 30, 31, 41, 46, 52, 62). Among other asiloid families the epandrium always consists of one piece in the Bombyliidae but is divided into two in most Asilidae, and in all Apioceridae and Mydidae.

20. Phallus with distiphallus consisting of a single tube with a single apical gonopore, **0**; phallus of two or three tubes with a corresponding number of gonopores, **1**. The Therevidae have the plesiomorphic state of



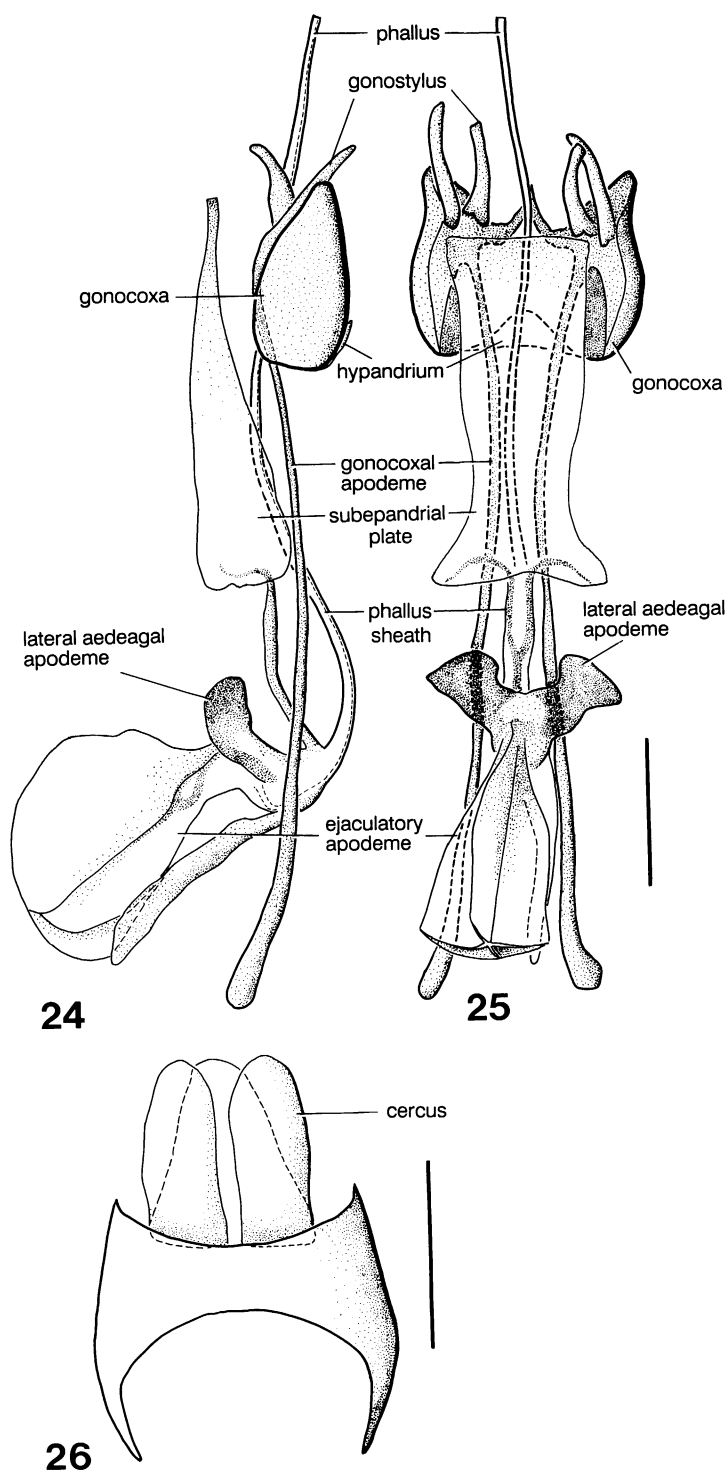
Figs. 22, 23. Terminalia of *Thereva fucata* (Therevidae). 22, Male genitalia; 23, epandrium. Scale line = 0.1 mm.

this character (figs. 22, 24, 25) but all ingroup taxa have the advanced state. *Caenotoides*, *Prorates*, and *Alloxytropus* have two extremely long, narrow distiphallus tubes that are coiled inside the abdomen (figs. 45–46, 54–55, 63–64). *Caenotus* has the phallus divided into two only at the apex (fig. 39). All scenopinids appear to have two or three distiphallus prongs (Kelsey, 1969) (figs. 28, 32) and the species examined here have a gonopore at the apex of each prong.

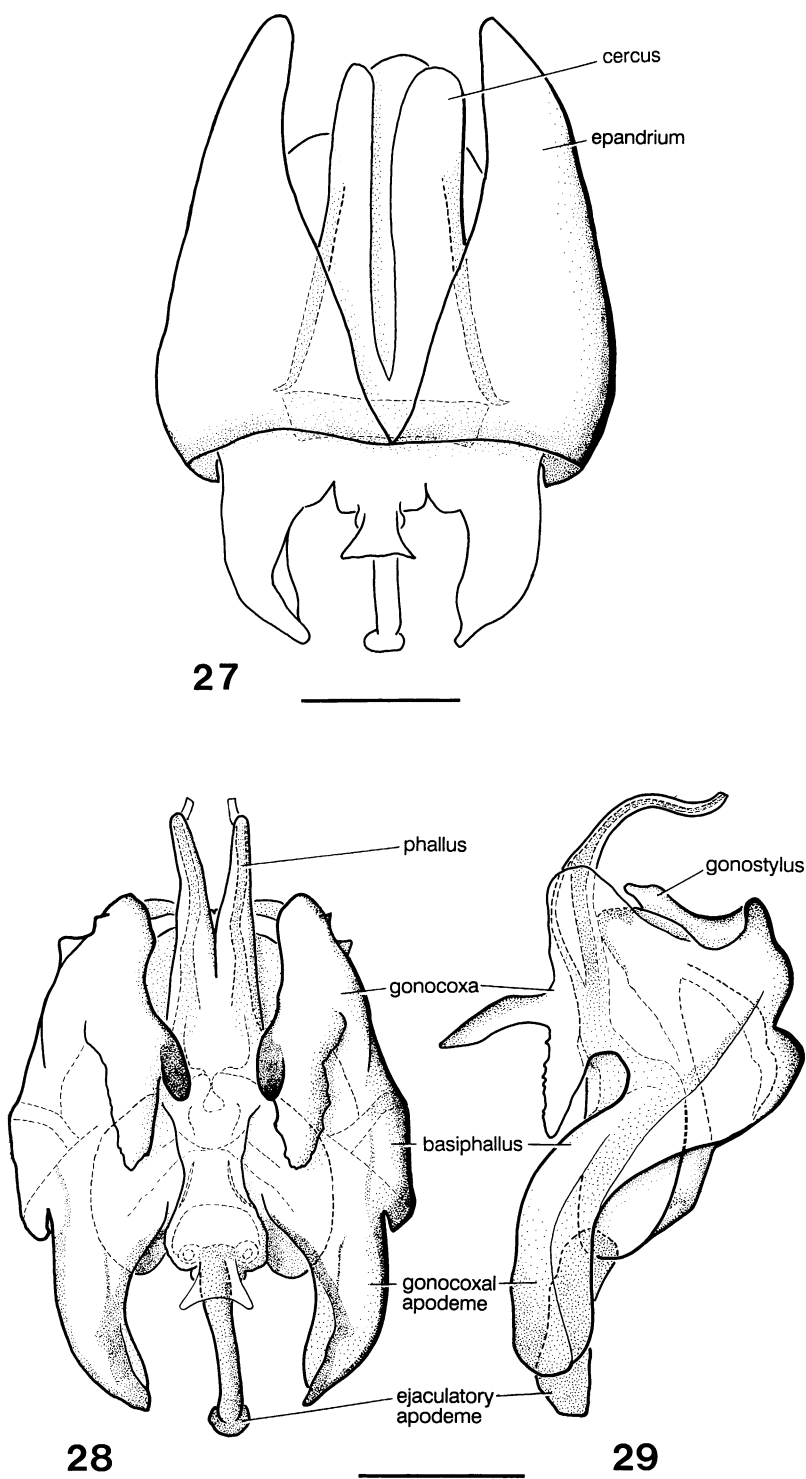
21. Hypandrium separate from gonocoxites, 0; fused to the gonocoxites or absent, 1.

The hypandrium is present as a separate sclerite in some Therevidae examined (*Thereva*, fig. 22; *Bonjeania*, figs. 24, 25), thus this condition is likely to be the groundplan for the family. *Caenotus* has the hypandrium partially separate from the gonocoxites (fig. 40). The remaining ingroup taxa have either lost the hypandrium or it has become fused with the gonocoxites, thus becoming indistinguishable.

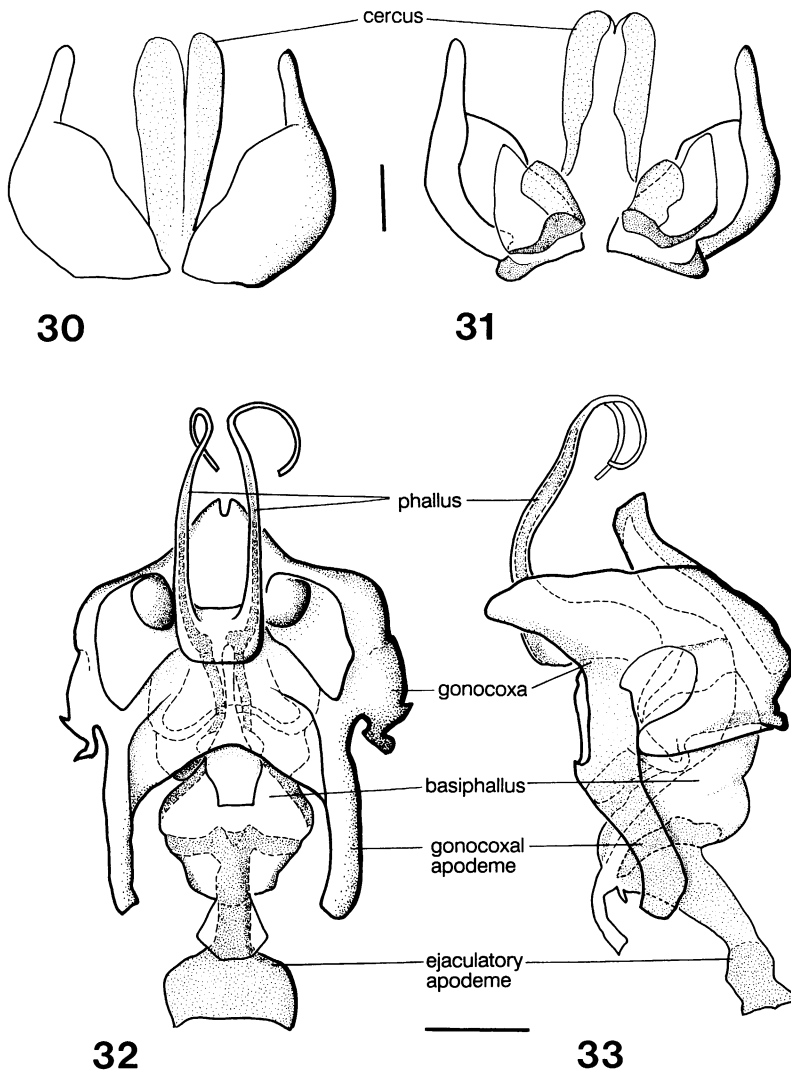
22. Lateral aedeagal apodemes present, 0; reduced or absent, 1. Lateral aedeagal apodemes are present in many asiloid families,



Figs. 24–26. Terminalia of *Bonjeania* sp. (Therevidae). 24, Genitalia, lateral; 25, genitalia, dorsal; 26, epandrium, dorsal. Scale lines = 0.5 mm.



Figs. 27–29. Terminalia of *Propebrevitrichia* sp. (Scenopinidae). 27, Epandrium on outline of genitalia, scale line = 0.1 mm; 28, genitalia, dorsal; 29, genitalia, lateral, scale line = 0.1 mm.

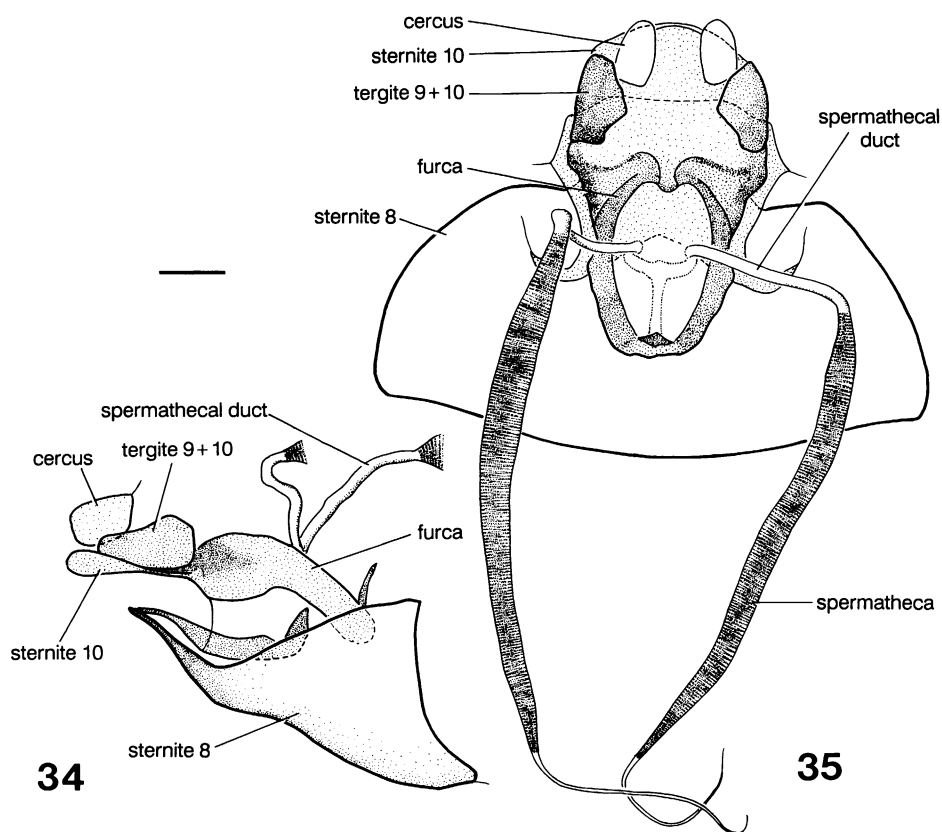


Figs. 30–33. Terminalia of *Belosta albipilosa* (Scenopinidae). 30, Epandrium, dorsal; 31, epandrium, ventral; 32, genitalia, dorsal; 33, genitalia, lateral. Scale lines = 0.1 mm.

however are reduced or absent in Therevidae except *Bonjeania* (figs. 24, 25). Their presence in *Bonjeania* suggests that the lateral aedeagal apodemes are a groundplan feature of the group and were reduced or lost within the Therevidae. All the ingroup taxa examined here have lost the lateral aedeagal apodemes. *Caenotus* has two long apodemes extending dorsally from the aedeagal sheath and parallel to the ejaculatory apodeme and gonocoxal apodemes (see character 26). These

are not considered homologous with the lateral aedeagal apodemes because they do not articulate on the basiphallus.

23. Gonocoxal apodemes of male genitalia either long (*Bonjeania*, figs. 24, 25) or short (figs. 28, 32, 39) with free anterior ends, 0; gonocoxal apodemes produced into long, narrow rods which articulate on sclerotized apodemes from the aedeagal sheath, 1. The apomorphic state was only found in the genera *Caenotoides*, *Prorates*, and *Alloxytropus*



Figs. 34, 35. Female genitalia of *Scenopinus fenestralis* (Scenopinidae). 34, Lateral; 35, dorsal. Scale line = 0.1 mm.

(figs. 45–46, 54–55, 63–64). The configuration of the male genitalia in these genera is very distinctive and indicative of a close relationship.

24. Male genitalia with aedeagal sheath not extending anteriorly beneath the ejaculatory apodeme, 0; male genitalia with aedeagal sheath extending anteriorly beneath the ejaculatory apodeme in a long trough (figs. 45–46, 54–55, 63–64), 1. Only the genera *Caenotoides*, *Prorates*, and *Alloxytropus* had the advanced state of this character.

25. Male genitalia without dorsal, anterior apodeme extending from the phallus sheath, 0; with a long, narrow apodeme extending anteriorly and parallel to the ejaculatory apodeme and gonocoxal apodemes (figs. 39–40), 1. Of the taxa examined only *Caenotus* has the advanced state of this character and it appears to be an autapomorphy for the genus.

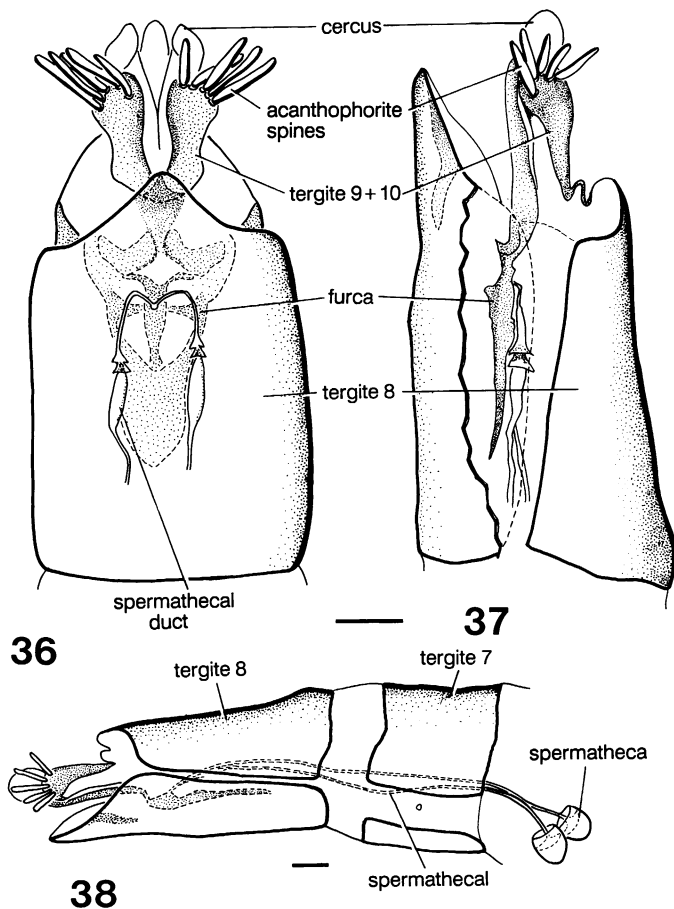
RESULTS

The data matrix (table 1) was analyzed with Hennig86 (Farris, 1988) with the therevids *Thereva fucata* Loew, *Phycus rufofemoralis* (Kröber), and *Bonjeania* sp. specified as out-group taxa. The ie command produced the

TABLE 1  
Data Matrix Input to HENNIG86

| Character no.                  | 1234567890123456789012345    |
|--------------------------------|------------------------------|
| <i>Thereva fucata</i>          | 0000000000000000000001000    |
| <i>Phycus rufofemoralis</i>    | 0000000000000000000100001000 |
| <i>Bonjeania</i> sp.           | 0000000000000000000000000000 |
| <i>Caenotus inornatus</i>      | 0010010000001110011101001    |
| <i>Caenotus hospes</i>         | 0010010001001110011101001    |
| <i>Caenotoides californica</i> | 0110101111001100111111110    |
| <i>Prorates frommeri</i>       | 0011000111001120011111110    |
| <i>Alloxytropus anomala</i>    | 1011000111001120011111110    |
| <i>Scenopinus fenestralis</i>  | 1010001111111111111111000    |
| <i>Propebrevitrichia</i> sp.   | 1010001111111110011111000    |





Figs. 36–38. Female genitalia of *Proprebrevitrichia* sp. (Scenopinidae). 36, Dorsal; 37, 38, lateral. Scale lines = 0.1 mm.

single most parsimonious tree (fig. 65) possible for the data; it had a length of 32 steps, consistency index of 0.81, retention index of 0.86, and a data decisiveness (DD, Goloboff, 1991) of 0.86. The same tree also resulted when successive weighting (Farris, 1969; Carpenter, 1988) was applied to the original tree.

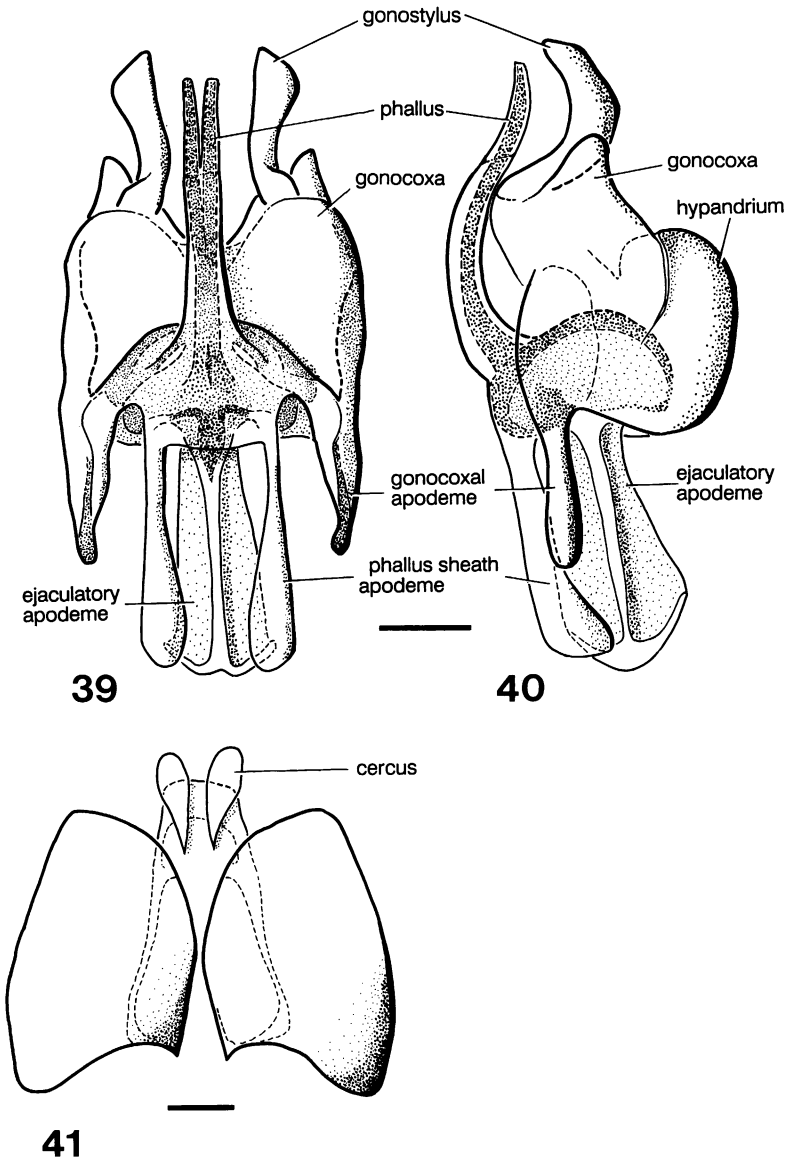
#### MONOPHYLY OF THE SCENOPINIDAE PLUS THE *PRORATES* GROUP OF GENERA

The monophyly of the *Prorates* group + Scenopinidae is supported by seven apomorphies on the most parsimonious tree (fig. 65). Six of these characters exhibit no homoplasy on the tree. Apomorphies that the ingroups share are as follows: character 3,

male eyes divided into regions of large facets dorsally and small facets ventrally; 13, cell *bm* with apex acute; 14, large setae on scutum absent; 18, reduction in number of spermathecae to two; 19, epandrium divided in the midline, and 20, distiphallus divided into two or three apical tubes.

The apomorphic states of two other characters are common to all ingroup taxa examined except one. *Caenotus ornatus* is considered plesiomorphic because it has wing vein *M*<sub>3</sub> (character 10), in common with the Therevidae. *Caenotoides* lacks the area of sensory setae found on tergite 2 of the abdomen (character 15), and this is interpreted as an apomorphic loss on the tree.

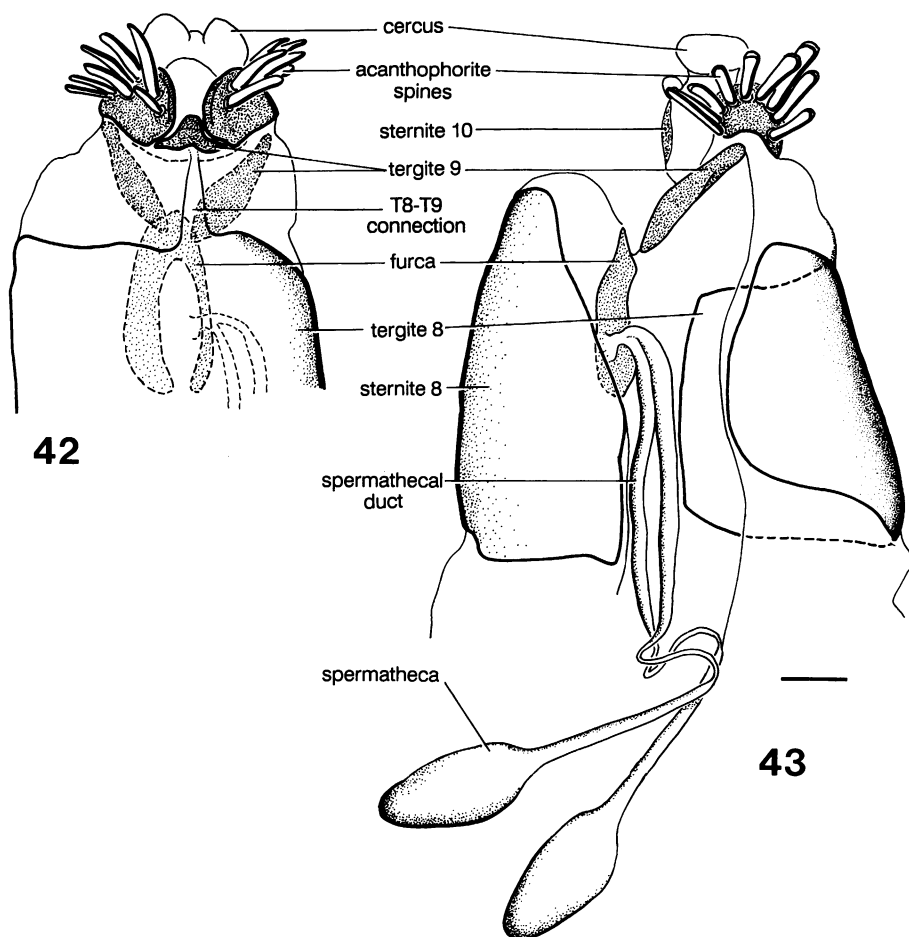
All ingroup taxa except *Caenotus* form a clade based on the apomorphic states of char-



Figs. 39–41. Male terminalia of *Caenotus hospes*. 39, Genitalia, dorsal; 40, genitalia, lateral; 41, epandrium, dorsal. Scale lines = 0.1 mm.

acter 8, the loss of the costal vein beyond the R field of the wing; character 9, the veins of the M and CuA fields not reaching the wing margin and character 21, the hypandrium absent. The Scenopinidae are united by the one-segmented flagellum (character 1), wing vein  $M_2$  absent (character 11) and wing cell  $m_2$  widened distally (character 12). *Caenotoides*, *Prorates*, and *Alloxytropus* are united by two

characters of their male genitalia: the apomorphic states of character 23, gonocoxal apodemes produced into long, narrow rods which articulate on sclerotized apodemes from the aedeagal sheath; and 24, male genitalia with aedeagal sheath extending anteriorly beneath the ejaculatory apodeme in a long trough. *Prorates* and *Alloxytropus* share apomorphic states of character 4, eyes of male



Figs. 42–43. Female genitalia of *Caenotus hospes*. 42, Dorsal; 43, lateral. Scale lines = 0.1 mm.

with inner margin indented at the level of the antennal bases; and state 2 of character 15, a triangular area of large, truncate setae with flattened or slightly rounded apices on posterior margin of tergite.

#### CLASSIFICATION

The results of this study suggest that the *Prorates* group of genera should be classified with the Scenopinidae. Up until now subfamilies have not been used in the Scenopinidae. It is appropriate at this point to use the subfamily rank to reflect the hierarchical information, in the form of a sequenced classification (Nelson, 1974) contained in figure 65. This study corroborates the suggestion of Theodor (1983) that *Prorates* belongs to the Scenopinidae. Below I redescribe the Scen-

opinidae; describe the new subfamily Caenotinae for *Caenotus*; redescribe the Proratinae and limit it to *Prorates*, *Alloxytropus* and *Caenotoides*, and redescribe the subfamily Scenopininae for the genera heretofore placed in the Scenopinidae.

#### Family Scenopinidae

Subfamily Caenotinae, new subfamily

Genus *Caenotus* Cole, 1923

Subfamily Proratinae Theodor, 1983, revised placement

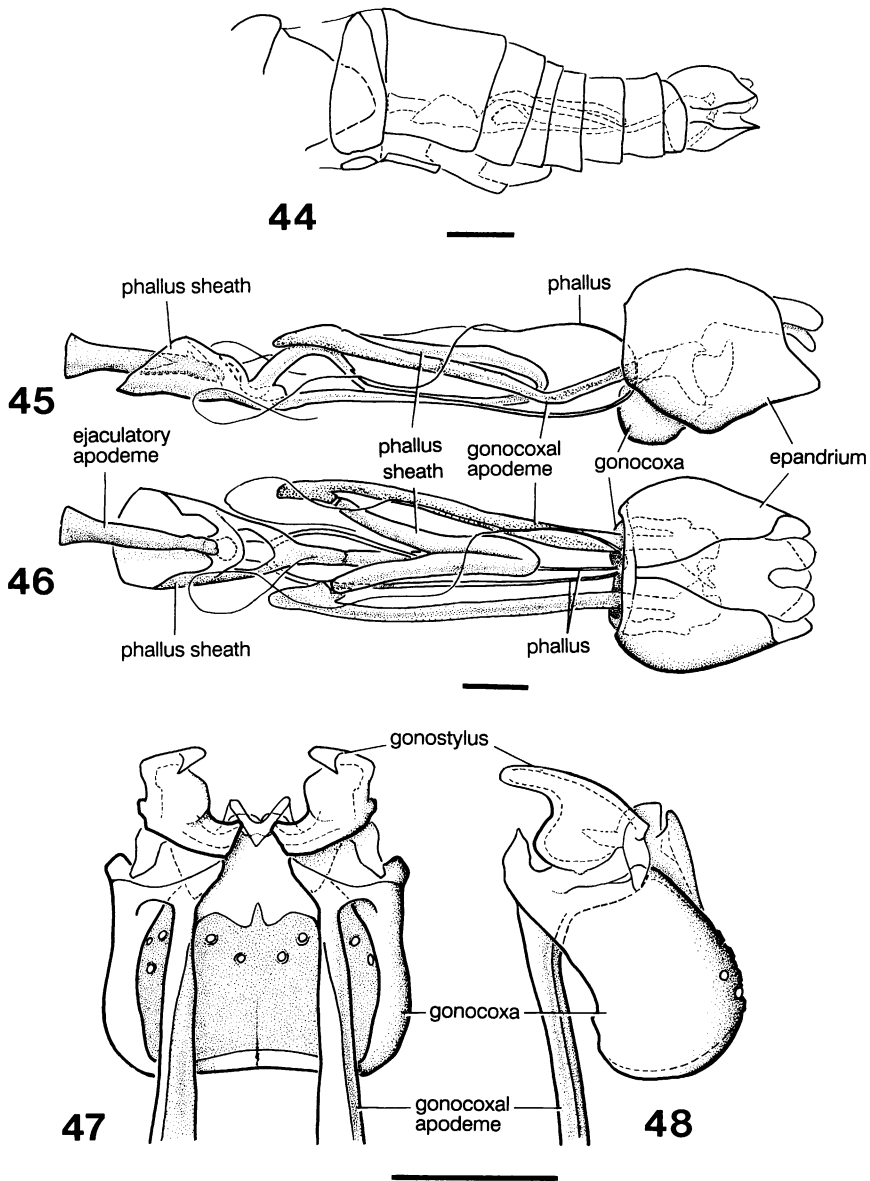
Genus *Prorates* Melander, 1906

Genus *Alloxytropus* Bezzi, 1925

Genus *Caenotoides*, Hall, 1972

Subfamily Scenopininae Fallén, 1917, new status

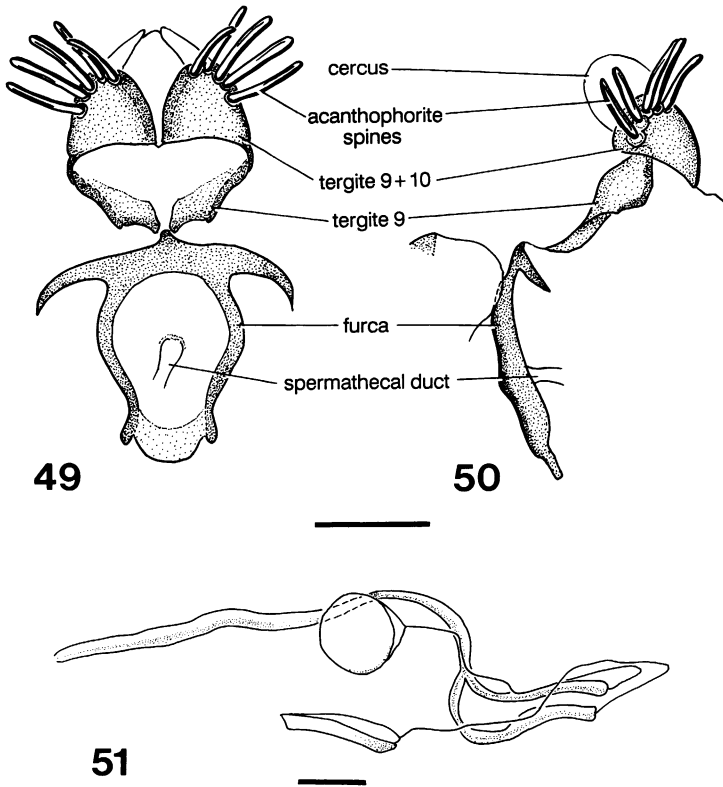
*Scenopinus* Latreille, 1802



Figs. 44–48. Male terminalia of *Prorates claripennis*. 44, Terminalia in abdomen showing anterior extension to tergite 2, scale line = 0.2 mm; 45, terminalia lateral; 46, terminalia dorsal, scale line = 0.1 mm; 47, detail of gonocoxites, dorsal; 48, detail of gonocoxites, lateral, scale line = 0.1 mm.

*Belosta* Hardy, 1944  
*Brevitrichia* Hardy, 1944  
*Caenoneura* Kröber, 1923  
*Heteromphrale* Kröber, 1937  
*Irwiniana* Kelsey, 1971  
*Metatrichia* Coquillett, 1900  
*Neopseudatrichia* Kelsey, 1969  
*Paramonova* Kelsey, 1970

*Paratrichia* Kelsey, 1969  
*Prepseudatrichia* Kelsey, 1969  
*Propebrevitrichia* Kelsey, 1969  
*Pseudatrichia* Osten Sacken, 1877  
*Pseudomphrale* Kröber, 1913  
*Riekiella* Paramonov, 1955  
*Seguyia* Kelsey, 1980  
*Stenomphrale* Kröber, 1937



Figs. 49–51. Female genitalia of *Prorates frommeri*. 49, Dorsal; 50, lateral; 51, spermathecae. Scale lines = 0.1 mm.

#### Key to the Subfamilies of Scenopinidae

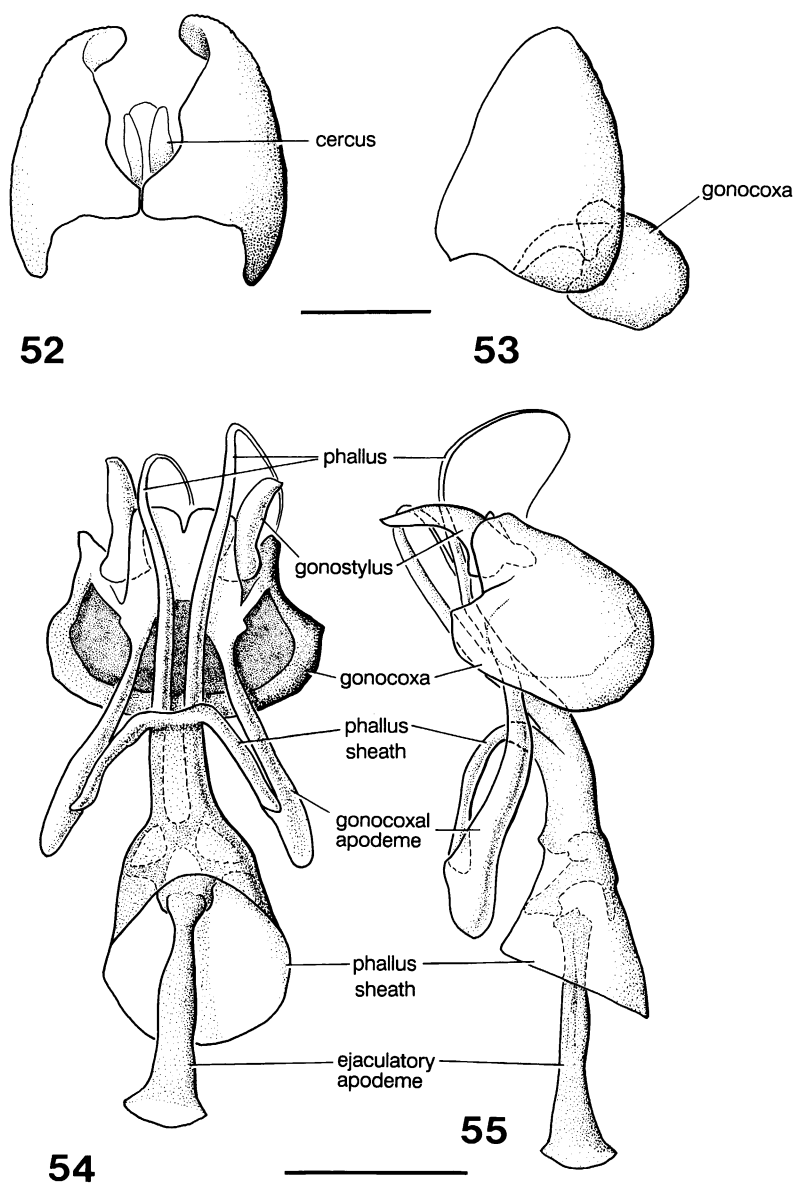
1. Wing with vein  $M_2$  absent (fig. 8) ..... Scenopininae, Fallén, new status
- Wing with vein  $M_2$  present (figs. 6–7, 9–10) ..... 2
2. Costal vein extending around wing (fig. 7); sensory area on tergite 2 made up of two hemispherical regions of enlarged setae (figs. 13–14) ..... Caenotinae, new subfamily
- Costal vein ending at vein  $R_5$  (figs. 6, 9–10); sensory area on tergite two with a triangular region of setae with truncate apices (figs. 16, 18) ..... Proratinae, Theodor, revised placement

#### SCENOPINIDAE

**DIAGNOSIS:** Antennal flagellum of one or two segments; eyes of male distinctly divided into upper large facets and lower small facets; palp one-segmented. Thorax bare, with hairs rather than bristles;  $R_{2+3}$  parallel to  $R_1$ , undivided,  $R_{4+5}$  divided;  $CuA_2$  fused with  $A_1$

before the wing margin. Abdominal tergite 2 of both sexes with a conspicuous area of modified setae medially to the posterior margin (called the sensory area) in all genera except *Caenotoidea*. Male terminalia with epanthrium divided in the sagittal plane into two halves; lateral aedeagal apodemes absent; distiphallus divided into two or three (some Scenopininae) prongs. Female terminalia with or without acanthophorite spines; two spermathecae present.

**REDESCRIPTION:** *Head:* Antennae approximate at base; small scape and pedicel, flagellum of one or two segments, a large basal one covered in pubescence and a smaller apical segment. Scenopininae have a single flagellar segment with an apical style. Eyes of male touching on frons, those of female separated; eyes of male distinctly divided into upper large facets and lower small facets; face small; mouthparts poorly developed (e.g. *Caenotoidea*) to well developed, proboscis

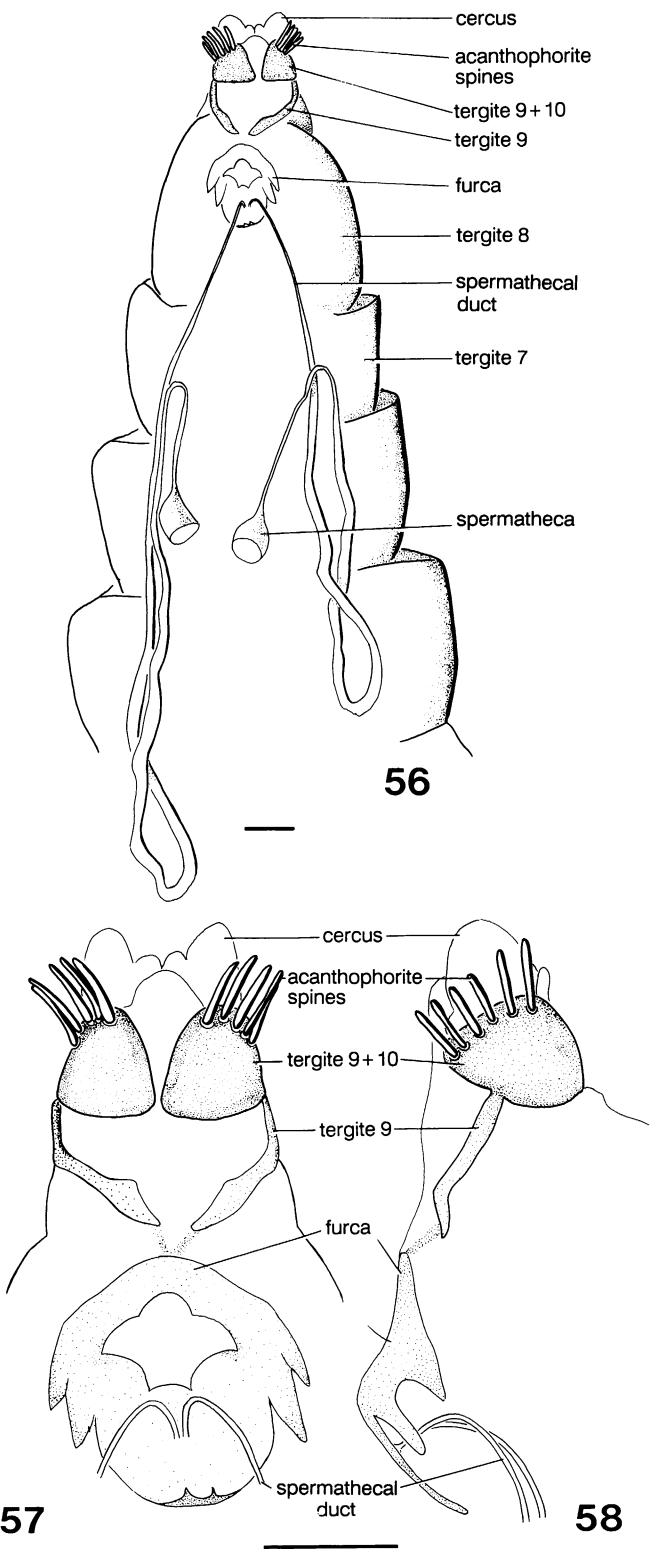


Figs. 52–55. Male terminalia of *Alloxystropus anomala*. 52, Epandrium, dorsal; 53, epandrium, ventral; 54, genitalia, dorsal; 55, genitalia, lateral. Scale lines = 0.2 mm.

extending from oral cavity or held within it; palp one-segmented.

**Thorax:** Bare, with hairs rather than bristles (*Prorates* may have a few weak bristles on the margins of scutum and scutellum); prosternum fused to propleuron forming a precoxal bridge in Scenopininae and Proratinae, prosternum separate in Caenotinae; wings with the costal vein ending at the apex

of the wing except in Caenotinae;  $R_{2+3}$  parallel to  $R_1$ , undivided,  $R_{4+5}$  divided; with  $R_4$  and  $R_5$  extending to wing apex in Caenotinae and Proratinae,  $R_4$  reaching costa well before wing apex in Scenopininae, two branches of M in all Caenotinae and Proratinae except *C. inornatus* where there are three branches of M. Scenopininae with one branch of M.  $CuA_2$  fused with  $A_1$  before the wing margin, cell  $m_1$



Figs. 56–58. Female genitalia of *Alloxytropus anomala*. 56, Dorsal showing spermathecae; 57, dorsal, detail; 58, lateral, detail. Scale lines = 0.1 mm.



closed in some Scenopininae. Legs without prominent setae.

**Abdomen:** Narrow and tapering toward apex, broad in some Scenopininae; tergite 2 of both sexes with a conspicuous area of modified setae mediad to the posterior margin (called the sensory area) in all genera except *Caenotoides*. This region of setae comprising two closely opposed semicircular areas of setae in the Scenopininae and Caenotinae (figs. 10–13) but in the Proratinae it appears as a triangular area of short, apically truncate setae with large sockets (figs. 14–21). Male terminalia: with epandrium divided in the sagittal plane into two halves; hypandrium well developed in the Caenotinae but fused with the gonocoxites or absent in the Proratinae and Scenopininae; gonocoxal apodemes present, very long in Proratinae; basiphallus well developed; lateral aedeagal apodemes absent; distiphallus divided into two or three (some Scenopininae) prongs; gonostyli present in Caenotinae and Proratinae but apparently absent in some Scenopininae. Female terminalia: acanthophorites and acanthophorite spines present in Caenotinae, Proratinae, and some Scenopininae; tergites 9 and 10 fused; furca (sternite 9) u-shaped with arms directed anteriorly or in the form of a ring; two spermathecae.

**DISCUSSION:** A family of diminutive flies found in all zoogeographic regions with almost 400 species described in 21 genera. Body small (length 2–7 mm), rather bare black or brown with hairs or scales rather than bristles. Immature stages are known only for the Scenopininae, salient features of which will be described under that subfamily.

The family is divided into three subfamilies as follows.

#### Caenotinae, new subfamily

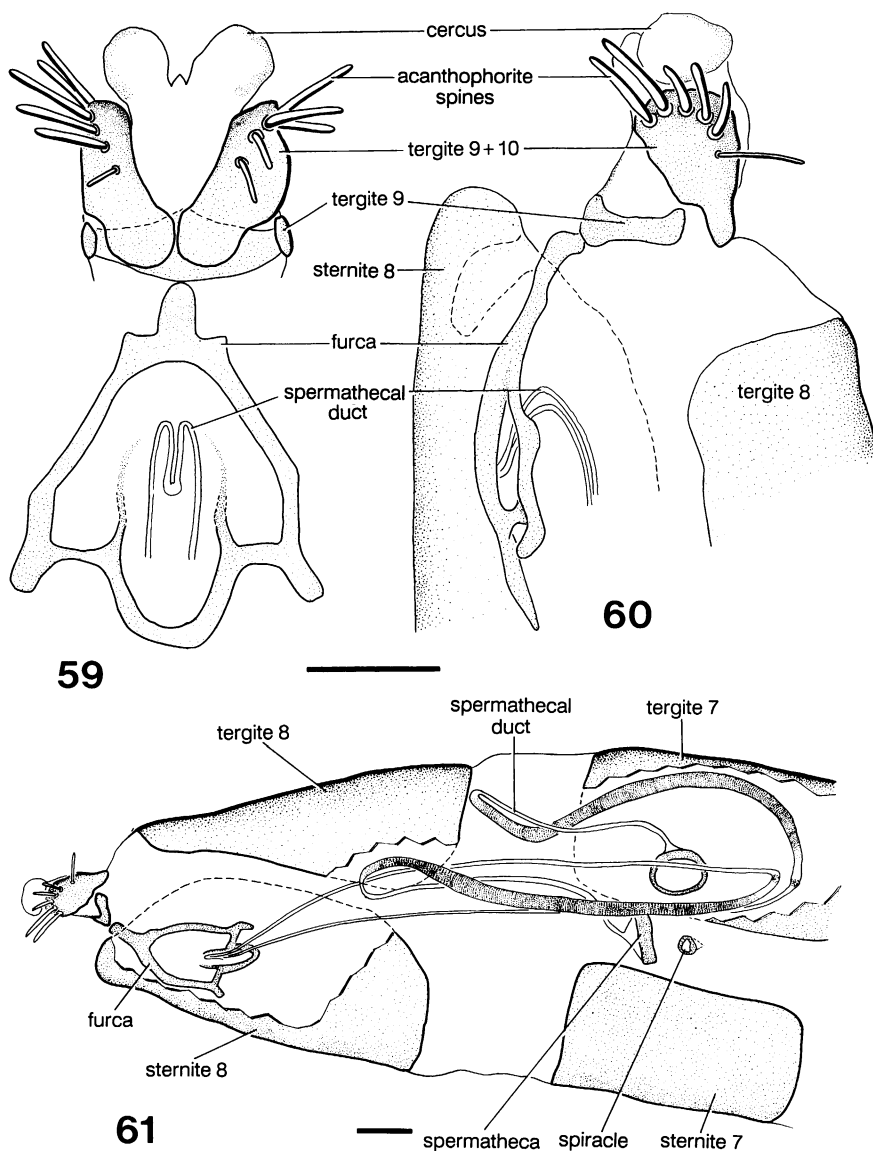
**TYPE GENUS:** *Caenotus* Cole, 1923, the only genus in the subfamily. Characters for the subfamily are those of the genus. The genus has been redescribed by Melander (1950) and Hull (1973).

**DIAGNOSIS:** Antennal flagellum of two segments and an apical style, first segment widened toward middle, second segment as wide as apex of first segment; proboscis and palpi short but well developed; palpi of one segment with constriction at one third of length. Thorax with prosternum free, not connected

to propleuron; hind coxae with poorly developed processes on anterior face. Wings (fig. 6) with costal vein extending around wing; first and second branches of M arising separately from the discal medial cell. Male terminalia with ejaculatory apodeme long, cross-shaped in section; two elongate dorsal processes lying parallel to the ejaculatory apodeme. Female terminalia with spatulate-tipped acanthophorite spines.

**DESCRIPTION:** Antennae short, scape twice as long as wide, pedicel rounded, as long as wide, flagellum of two segments and an apical style, first segment widened toward middle, second segment as wide as apex of first segment. Eyes contiguous in male, well separated in female; male eyes divided into large facets dorsally and small facets ventrally (fig. 3); proboscis and palpi short but well developed; palpi of one segment with constriction at one-third of length. Prosternum free, not connected to propleuron. Hind coxae with poorly developed processes on anterior face. Costal vein extending around wing (fig. 6), stigma present at apex of  $R_1$ ; four posterior cells (five in some *C. inornatus*); first and second branches of M arising separately from the discal medial cell; cell bm with apex acute; anal cell closed with a short stalk. Male genitalia (figs. 39, 40); gonocoxal apodemes long, anteriorly directed; gonocoxites fused medioventrally; gonostylus normal, articulated on gonocoxite; hypandrium large, prominent, rounded, partially fused to gonocoxae; ejaculatory apodeme long, cross-shaped in section; two elongate dorsal processes lying parallel to the ejaculatory apodeme; basiphallus large and rounded, distiphallus short, simple but bifid at apex; phallus well connected to the gonocoxites. Dorsal hump near the apex of each gonocoxite, reminiscent of the distinct dorsal processes found in Scenopininae (figs. 29, 33). Acanthophorites of female genitalia (figs. 42, 43) with spatulate-tipped spines. Sclerotized strips lead from the fused tergites 9 and 10 toward the furca. Furca composed of one u-shaped piece; two moderately sclerotized spermathecae present.

**DISCUSSION:** All species are small, dark-colored flies with reduced vestiture and hyaline wings, found only in the southwestern United States. The type species, *C. inornatus*, differs from all others in having three branch-



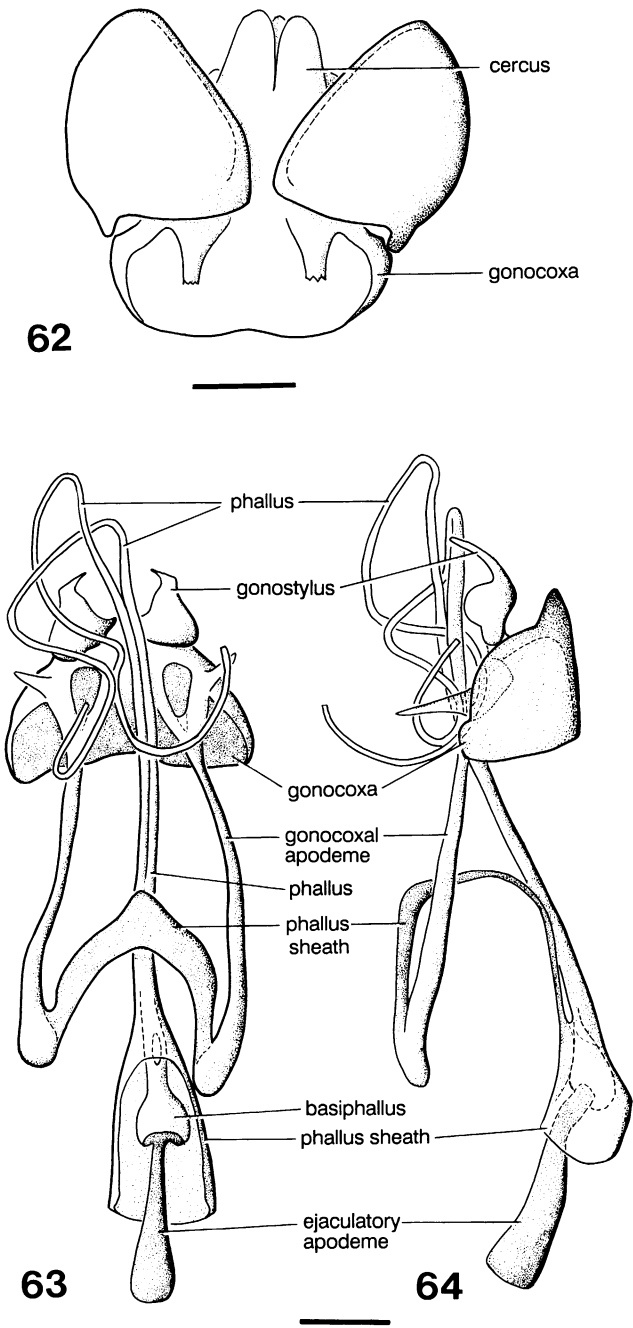
Figs. 59–61. Female genitalia of *Caenotoides californica*. 59, Dorsal; 60, lateral; 61, lateral showing spermathecae. Scale lines = 0.1 mm.

es of  $M$  rather than two. In this respect it is similar to therevids. In *C. inornatus*, however,  $CuA_1$  arises from cell  $dm$ , whereas in therevids it arises on the free section of  $CuA_1$  below cell  $dm$ . Cole mentioned in his original description that there is some variation in this character, with some paratypes having  $M_2$  reduced to a small stub or not reaching the wing margin. In one paratype I examined,  $M_2$  was completely absent in one wing but present and complete in the other wing.

Hull (1973) erroneously recorded three palpal segments. I found only one palpal segment, however each palp has a constriction at one-third the length from the base, which may be interpreted as dividing the palp into two segments.

Subfamily Proratinae Theodor, 1983,  
revised placement

TYPE GENUS: *Prorates* Melander, 1906.



Figs. 62–64. Male terminalia of *Caenotoides californica*. 62, Epandrium, dorsal; 63, genitalia, dorsal; 64, same, lateral. Scale lines = 0.1 mm.

This subfamily is restricted to three genera, *Prorates* Melander (1906) containing six species, *Alloxytropus* Bezzi (1925) containing four species, and *Caenotoides* Hall (1972) containing three species.

Most characteristics of *Prorates* are given in the descriptions by Melander (1906, 1928), Hall (1972), and Hull (1973). The last two authors treat *Alloxytropus* as a synonym of *Prorates*.

**DIAGNOSIS:** Antennal flagellum of one or two segments. Thorax with prosternum fused to propleuron forming a precoxal bridge; wings broad, costa ending at or near  $R_5$ ; posterior veins ending just before wing margin. Abdomen with sensory area present except in *Caenotoides*, sensory area distinctly triangular, each seta apically truncate. Male terminalia highly modified, occupying most of the length of the abdomen; gonocoxal apodemes extremely long; ends of gonocoxal apodemes articulate with y-shaped arms of aedeagal sheath; aedeagal sheath extends anteriorly forming a trough under the ejaculatory apodeme; distiphallus very elongate and narrow. Female terminalia with spines on acanthophorites.

**REDESCRIPTION:** Antenna with scape and pedicel small, (figs. 1, 2); first segment large and wider at base than apex; second segment small and conical, as wide at base as apex of first segment. Proboscis very short (*Caenotoides*) to long, contained within or extending beyond oral cavity. Thorax without large setae or with a reduced pair of prealar, supraalar, and scutellar setae. Prosternum fused with propleuron forming a precoxal bridge. Hind coxal process very small or absent. Legs without prominent setae. Wings (figs. 6, 9, 10) broad, costa ending at or near  $R_5$ ; stigma present at apex of  $R_1$ ; posterior veins ending just before wing margin; cell dm small; sensory area with setae borne in a distinct triangular area, and each seta apically truncate (figs. 15–21); or sensory area absent in *Caenotoides*. Male genitalia (figs. 45–48, 54–55, 62–64) highly modified, occupying much of the length of the abdomen (fig. 44); gonocoxites small, fused ventrally; gonostylus simple, articulating on the gonocoxites; gonocoxal apodemes extremely long, extending anteriorly into abdomen to tergite 2 (*Prorates* and *Alloxytropus*) or 5 (*Caenotoides*); ends of gonocoxal apodemes articulate with y-shaped arms of aedeagal sheath, these arms are firstly directed posteriorly but fuse and curve ventrally and anteriorly; aedeagal sheath also extends anteriorly forming a trough under the ejaculatory apodeme; ejaculatory apodeme long, cylindrical in crosssection; basiphallus small, enclosed by aedeagal sheath; distiphallus very elongate and narrow, twin prongs issuing from the sheath surrounding the bas-

iphallus, extending posteriorly as far as the gonocoxites before curving dorsally and anteriorly again; twin phallus prongs gradually taper and curl around adjacent to the basiphallus. In preparations examined of *Prorates* and *Alloxytropus* the tips of the twin prongs could not be found. Female genitalia (figs. 49–51, 56–58, 59–61) with acanthophorites fused to tergite 9, anterior straps of tergite 9 extending anteriorly toward furca; acanthophorite spines present on each acanthophorite; furca composed of one piece, joined posteriorly; two rounded, disk-shaped spermathecae.

**DISCUSSION:** Theodor (1983) first described this subfamily in the Bombyliidae, but suggested that it may have affinities with the Scenopinidae. Melander (1950) and Hall (1972) and Hull (1973) synonymized *Alloxytropus* with *Prorates*, however Melander had not seen specimens of the former. Zaitsev (1989) and Evenhuis (1991) retained the genus as distinct. The similarity of male genitalia in the two genera indicates that they are closely related. The male genitalia of the species of *Prorates* examined are much more elongate than those of *Alloxytropus anomala*. In addition, the species of *Prorates* examined have two flagellar segments, while *Alloxytropus* has one. *Prorates* is restricted to the Nearctic, whereas *Alloxytropus* is Palearctic. The relationship between the two genera will only be determined when all described and undescribed species of both are revised.

Subfamily Scenopininae Fallén,  
1817, new status

**TYPE GENUS:** *Scenopinus* Latreille, 1802.

This subfamily contains all the flies previously placed in the Scenopinidae.

**DIAGNOSIS:** Antennal flagellum one-segmented with an apical style. Thorax with prosternum and propleuron fused forming a precoxal bridge; wings (fig. 8) with costa ending at  $M_1$ ;  $R_4$  reaching costa on leading edge of wing; cell  $r_5$  open at edge of wing or closed and stalked; one branch of M present. Male terminalia complex; gonocoxites each with a dorsal process; gonostylus present or absent; ejaculatory apodeme rounded or dorsoventrally flattened; distiphallus with two or three prongs. Female terminalia with or without acanthophorite spines.

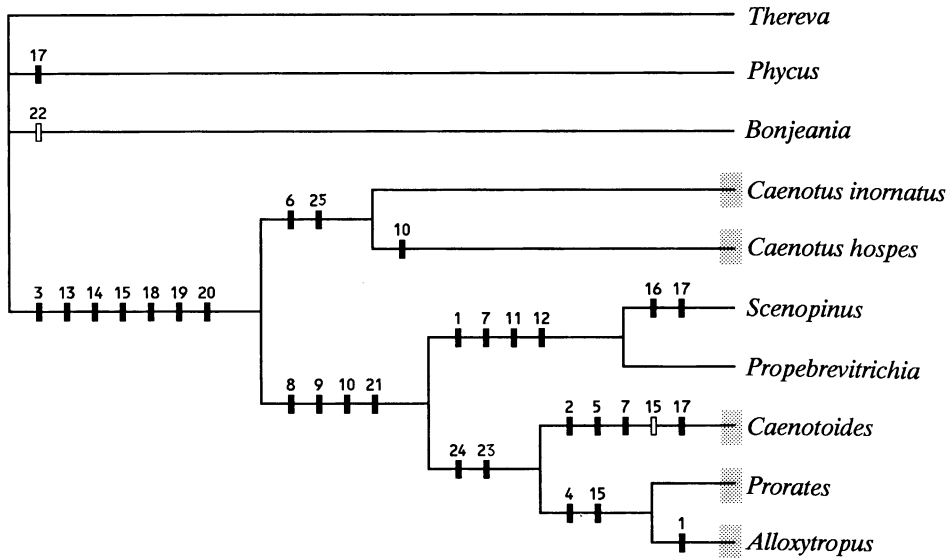


Fig. 65. Cladogram of the *Prorates* group of genera and the Scenopinidae. The Therevidae were chosen as the outgroup. Characters which change along nodes are indicated by their number. All forward character state changes have filled markers, reversals have open markers. Character 15 changes from 0 to 1 on the stem leading to the ingroup and from 1 to 2 on the stem leading to *Prorates* and *Alloxytropus* and reverses from 1 to 0 in *Caenotoides*. Characters 7 and 10 can have alternative optimizations on the tree. Terminals with shaded markers belong to the *Prorates* group of genera.

**DESCRIPTION:** Antennae with scape and pedicel short. Flagellum one-segmented with style present; flagellum varying from long and slender to short and oval. Mouthparts well developed in most. Thorax without bristles but clothed in short, sparse hairs; prosternum and propleuron fused forming a precoxal bridge; legs without prominent setae; empodia reduced or absent. Wings (fig. 8) with costa ending at  $M_1$ ; long stigma at apex of  $R_1$ ;  $R_4$  reaching costa on leading edge of wing; cell  $r_5$  open at edge of wing or closed and stalked; cell  $dm$  long and slender; one branch of  $M$  present. Male genitalia (figs. 27–33) complex, hypandrium fused to gonocoxites or lost; gonocoxites fused in midline and may be reduced, each with a dorsal process; gonostylus present or absent; basiphallus well developed, lateral aedeagal apodemes absent; ejaculatory apodeme rounded or dorsoventrally flattened; distiphallus with two or three prongs. Female terminalia (figs. 34–38) with or without acanthophorite spines; tergites 9 and 10 fused, may be reduced dorsally; two poorly sclerotized spermathecae present.

**DISCUSSION:** By far the largest subfamily

containing over 370 described species in 17 genera found in all zoogeographic regions. *Scenopinus* contains approximately half the species of Scenopininae so far described. Kelsey (1969) monographed the world fauna but did not discuss their phylogeny and Kelsey (1981) diagnosed the subfamily (as Scenopinidae).

The larvae of Scenopininae are predaceous and have been reported from various insect and vertebrate nests and among beetle larvae in wood or other organic substrates. Few scenopinines have been reared and larvae of few species have been described. Kelsey (1981) reported that only the larvae of *S. fenestralis* had been described; Krivosheina (1980) described the larvae and pupae of two Russian species. The first instar larvae have not been described. The mature larvae closely resemble therevids and are vermiform and amphipneustic. The abdominal segments are subdivided and the larvae appear to have 17 segments. This last feature they share with the Therevidae, and Woodley (1989) considered it a synapomorphy for the two families. In contrast to the spatulate metacephalic rod

of therevids, in scenopinines it is parallel-sided (Malloch, 1917).

Krivosheina (1980) and Kelsey (1981) described scenopinid pupae as having the following typical characters: head and thorax fairly smooth, lacking prominent spines or tubercles anteriorly. Antennal sheaths projecting laterally and terminating in a spine. Leg sheaths sometimes extending slightly beyond wing sheath. Spiracles on thorax and abdomen sessile. Abdominal segments each (except first) with a row of short to long spines; terminal abdominal segment with two prominent apical processes.

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