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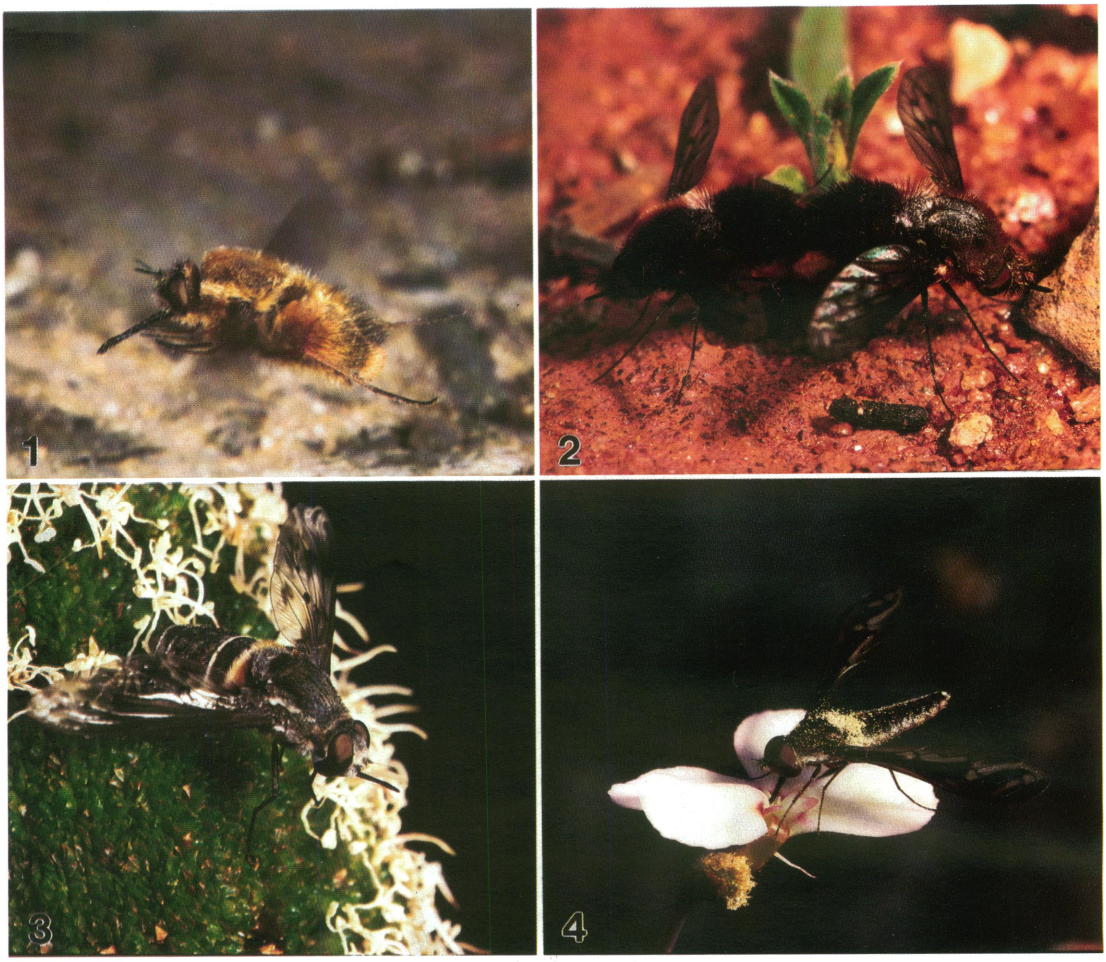

Australian Bombyliidae of the subfamilies Bombyliinae (above) and Lomatiinae (below), by Jiri Lochman: (1) *Staurostichus limbipennis* (Macquart); (2) *Staurostichus* sp.; (3) *Oncodosia ampla* (Walker); (4) *Aleucosia tridentata* Yeates.

Sweet is the lore which nature brings;
  Our meddling intellect
Misshapes the beauteous forms of things:-
  We murder to dissect.

William Wordsworth, "The Tables Turned," 1798

CONTENTS

ABSTRACT

Previous classifications and phylogenetic trees of the Asiloidea and the Bombyliidae are reviewed. Data from male genital musculature presented by Ovchinnikova (1989) and female genitalia by Mühlenberg (1971b) are reanalyzed within a numerical cladistic framework. A cladogram of the Bombyliidae and their relatives is constructed based on a data matrix containing 87 taxa and 154 characters. This study includes 24 non-Bombyliidae taxa used as outgroups, from the families Rhagionidae, Nemestrinidae, Acroceridae, Asilidae, Therevidae, Apioceridae, Mydidae, Scenopinidae, Hilarimorphidae, and Apsilocephalidae. I chose 63 ingroup species representing all the currently accepted subfamilies and tribes except the Xenoprosopinae and Villoestrini. 147 of the characters used were derived from adult morphology and 7 were from larval morphology. The data set was analyzed using the parsimony program Hennig86 which identified 8 most parsimonious trees, each with a length of 716 steps, consistency index of 0.25, and retention index of 0.71.

All characters are described and almost all are illustrated using line drawings, photographs, and scanning electron micrographs. Previously used characters are reanalyzed and new character systems are introduced, especially features of the postcranium and cibarium.

The Acroceridae and Nemestrinidae do not form a monophyletic group and each should be recognized at superfamily level. The Asiloidea is also weakly monophyletic, based largely on larval features. The Apioceridae is found not to be monophyletic, some included genera being more closely related to the Mydidae. The Hilarimorphidae, including the proratine *Apystomyia* Melander, form the sister-group to the Bombyliidae. The remaining Proratinae form a clade with the Scenopinidae, confirming recent work on the subfamily.

Bombyliidae, as here defined to exclude genera traditionally placed in the Proratinae, is found to be monophyletic, however the evidence for its monophyly is weak. The subfamily Heterotropinae was found to be nested within the Bombyliidae, thus the free-living, predatory habits of *Heterotropus* Loew larvae are interpreted as reversals from a parasitoid lifestyle rather than a primary plesiomorphic condition.

In a reclassification of the Bombyliidae, 15 subfamilies are recognized: the Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae, Lordotinae NEW SUBFAMILY, Heterotropinae, Bombyliinae, Crocidiinae NEW STATUS, Mariobezziinae, Oniromyiinae, Cythereinae, Lomatiinae, Anthracinae, Tomomyzinae, and Antoniinae. The position of *Sericosoma* Macquart requires further research; it exhibits closest affinity with the Mariobezziinae. The proposed classification is conservative and reflects much of the structure of previous classifications. Chief differences include the recognition of the Gerontini and Systropodini as tribes of the Toxophorinae rather than separate subfamilies and the synonomy of the Cylleniinae within the Cythereinae. Crocidiinae is recognized as a subfamily, rather than a tribe of the Bombyliinae. Lordotinae is the only new family-level taxon proposed, characterized by the highly modified, telescoping female genitalia which are adapted for inserting the eggs into the substrate. Tribal divisions within the Bombyliinae, Lomatiinae, and Anthracinae are discussed. A key to the subfamilies of Bombyliidae is presented, and all subfamilies are diagnosed, synapomorphies listed, and their taxonomic scope, distribution, and biogeography briefly discussed.

The fossil history of the Bombyliidae is discussed in relation to the cladogram. Bombyliidae probably originated in the Jurassic and had undergone much diversification at subfamily level by the end of the Cretaceous. The evolution of the bombyliid postcranium and female sand chamber is discussed in light of the cladogram. The evolution of the acanthophorites within the Bombyliidae is discussed in relation to the occurrence of this feature in other families of Asiloidea.

INTRODUCTION

Now, at the close of the 20th century, we are beginning to fathom how many different species have evolved on this planet and coexist with us (Wilson, 1992). The primary aim of systematists is to organize these products of evolution into hierarchical order expressed as a classification.

With around 4,500 species currently described, the Bombyliidae (bee flies) is numerically one of the largest families in one of the largest orders (Diptera) in by far the largest class of living things. Sheer species number is only one dimension of the entire concept of diversity (Vane-Wright et al., 1991;

Williams et al., 1991). The degree of difference (however measured) between these species is another dimension, and the Bombyliidae have many groups of high phylogenetic uniqueness (Nixon and Wheeler, 1992). The bombyliids are a treasure trove of very different structural types. The morphological diversity included in the family can be illustrated by comparing two species: the enormous *Exoprosopa marginicollis* Gray, with iridescent green-blue body scales recalling those found on the wings of a Morpho butterfly, and striking black and hyaline wings spanning 45 mm; and the tiny, delicate, humpbacked yellow and black species of *Glabellula* Bezzi with hyaline wings and a body length about 1 mm.

While almost all adult bee flies are fast-flying anthophiles, their larvae are clandestine and feed on other insect immatures, making a living as predators or parasitoids. The systematic comparison of the larvae of Bombyliidae is in its infancy due primarily to the paucity of preserved material; comparisons of pupae are little further advanced. This study is based almost exclusively on adult characteristics, and the few larval characters used are taken from the literature.

Bombyliidae occur around the world except at the poles, and during this study I examined specimens from each zoogeographic region except the Oriental. The bee flies reach their highest diversity (species and structures) in and around the five regions of Mediterranean climate: the area surrounding the Mediterranean Sea itself, southwestern U.S.A., and the southern regions of the three large land masses found in the Southern Hemisphere—South America, Africa, and Australia (Hull, 1973). These areas are home to very speciose, endemic floras and support a vast array of pollinators including bee flies. As we shall see, the morphology and behavior of Bombyliidae have been modified in response to the aridity of the habitats in which these flies are most numerous. Although recent attention has been directed toward the preservation of biodiversity in tropical rainforests, the areas of Mediterranean climate are also of critical concern in the preservation of biodiversity, as Wilson (1992) has stressed.

The structural diversity of the Bombyliidae provides a wealth of morphological characters, but at the same time presents an enormous challenge to our methods. The technique of choice for organizing the hierarchy of living organisms is cladistics, and I use this method explicitly.

My interest in the higher classification of the Bombyliidae arose after conducting revisionary work on one subfamily (Yeates, 1988, 1989, 1991a, 1991b). I realized that phylogenetic reconstruction within this subfamily was hampered because of our inadequate knowledge of the relationships between the subfamilies, thus rendering character polarity by outgroup choice a largely arbitrary procedure. In addition, the poly- or paraphyletic nature of the Bombyliidae is an obstacle in attempts to reconstruct the phylogeny of the Asiloidea. Clearly, only a detailed cladistic analysis of the entire family Bombyliidae, including the problematic groups, using many other asiloids as outgroups, could provide answers to these problems.

One aim of this study is to examine the relationships of the Bombyliidae to other families of Asiloidea. I will reexamine the characters used to support the monophyly of the family and to search for additional synapomorphies. Mühlenberg (1971b) cited the loss of vein M_3 of the wing as an apomorphy of the family, however this vein is also lost in closely related groups such as the Therevidae and Scenopinidae. Woodley (1989) cited the parasitic nature of the larvae and hypermetamorphosis as apomorphies of the Bombyliidae, however these features also occur in closely related families and are not universally present in the Bombyliidae (Andersson, 1974; Yeates and Irwin, 1992). Thus neither of these characters present conclusive evidence for bombyliid monophyly. During the course of this work I found it necessary to remove the Proratinae, traditionally classified in the Bombyliidae, and divide it between two other families of the Asiloidea in order to keep the remaining Bombyliidae monophyletic.

The division of the Bombyliidae into subfamilies is based on classifications formulated early this century, and there is little evidence that these subfamily divisions reflect the cladistic relationships within the family. The main aim of this study is to provide a framework for the cladistic classification of the Bombyliidae by elucidating the sister-group relationships between the subfamilies.

My third aim is to provide a comprehensive review of bombyliid adult morphology. Hull (1973) and Hall (1976) have provided overviews of adult morphology as it relates to classification, and other workers such as Mühlenberg (1971a), Theodor (1983), and Zaytsev (1986) have provided surveys of particular character systems. I reexamine characters used to support previous classifications and introduce new character systems which I have found informative.

FAMILY-LEVEL CLASSIFICATION OF THE BOMBYLIIDAE

In recent decades the Bombyliidae have either been united in a superfamily with the Nemestrinidae and Acroceridae, or alternatively in a superfamily with the Asilidae, Therevidae and related families. The differences between these schemes are the result of the different emphasis placed on the various supporting characters.

Hennig (1952) placed the Bombyliidae in a superfamily with the Acroceridae (as Cyrtidae) and Nemestrinidae. Hennig referred to Bezzi's (1924) division Tomophthalmae as a homogeneous phylogenetic group, however the Homeophthalmae he regarded as the "leftovers." This is the first indication, echoed by Hennig and subsequent workers in later years, of the poly- or paraphyletic nature of the Homeophthalmae and thereby the entire family.

In his review of wing venation in the Diptera, Hennig (1954) retained his Bombyliidae-Acroceridae-Nemestrinidae grouping used in 1952. He considered that the bristle-like empodium of Bombyliidae may have been derived independently from those of other flies with this feature (Heterodactyla Brauer) and the similarities in the larvae of the three families may go beyond the convergences due to their parasitic way of life.

Hennig (1972, 1973) united the Acroceridae, Nemestrinidae, and Bombyliidae in the superfamily Nemestrinoidea. He noted that this was one of the most problematic groups of of Diptera and cited only the parasitism and hypermetamorphosis of the larvae as a derived characteristic, implying a close relationship between the families. Hennig (1973) cited the acanthophorite spines as evidence that the Bombyliidae may in fact share a closer relationship with the Asiloidea than the Nemestrinoidea.

Rohdendorf (1974) divided the Bombyliidae of previous authors into four family-level subgroups, the Bombyliidae, Cyrtosiidae, Usiidae, and Systropodidae. These four families thus made up their own superfamily, the Bombyliidea. This reclassification was not supported by character evidence, and to quote Rhodendorf (1974: 77) "The scheme of division of the bombyliids into four families, as I have proposed, is purely preliminary and must be reasoned out in detail by a special investigation." After a general discussion of the superfamily (p. 89), Rhodendorf commented that the "Bombyliidea have not been studied sufficiently to allow discussion of the phylogeny of its individual groups in more detail". Hall and Evenhuis (1980) and Evenhuis (1982) unfortunately followed Rhodendorf's suggestion in part and treated the Systropodinae as a separate family.

Hennig (1976) made only passing comments concerning the Bombyliidae but (p. 24) considered them distinct from the Asiliformia [= Asiloidea of Woodley (1989)] and Homeodactyla [= Stratiomyiformia, Tabaniformia, and Xylophagomorpha of Woodley (1989)]. He considered that the endophallus and phallus sheath are solidly fused in the Asiliformia and Cyclorrhapha but separate and independant in the Bombyliidae and Homeodactyla. This led him to conclude that evidence may be forthcoming that the Asiliformia, Empidiformia and the Cyclorrhapha form the monophyletic "Heterodactyla," excluding the Bombyliidae.

Griffiths (1986) included the Nemestrinidae and doubtfully the Acroceridae in the Tabaniformia, united by the dorsal and lateral/ventral sheathing processes around the aedeagus and gonites (= parameres). He placed the Bombyliidae, Asilidae, Apioceri-

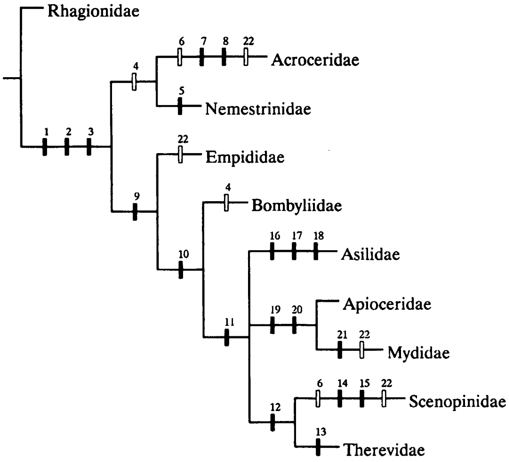

Fig. 1. The single cladogram which resulted after reanalysis of the data in Woodley (1989). The correspondence of the character numbers used here to those in Woodley's work, and the data matrix can be found in Appendix 1. Characters showing homoplasy have open hash marks, those without homoplasy have filled hash marks.

dae, Mydidae, Bombyliidae, Therevidae and Scenopinidae in the Pleroneura (= Asiliformia of Hennig) of the Heterodactyla. According to Griffiths (1986), the Pleroneura have the following synapomorphies: (1) The aedeagal sheath is formed by the fusion of the gonites, (2) Lateral aedeagal apodemes present, and (3), Female tergite 10 divided into a pair of acanthophorites. Griffiths made clear the distinction between this gonite sheath and the sheath of the Tabaniformia which is formed by lobes enclosing the aedeagus and gonites. These features will be discussed further in the character analysis.

Woodley (1989) presented the most clearly argued hypothesis of relationships among the "Orthorrhaphous" Brachycera within a cladistic framework. I reanalyzed Woodley's characters using Hennig86 (data matrix in Appendix 1) and his topology was the only cladogram produced (fig. 1). Woodley united the Acroceridae and Nemestrinidae in the Nemestrinoidea because the parasitic larvae were hypermetamorphic (character 4). The Nemestrinoidea formed the sister group to the remainder of the Asiloidea, Empidoidea, and Muscoidea (the latter = Muscomorpha of McAlpine, 1989, "Cyclorrhapha" of other authors). These last three superfamilies were united by their bristlelike empodium (character 9). Woodley placed the Bombyliidae in the Asiloidea, and this superfamily was united by an apomorphic characteristic of the larvae: the position of the posterior spiracle in the apparent penultimate segment of the abdomen (character 10). The Bombyliidae formed the sister group for the remainder of the Asiloidea, retaining the primitive characteristic of the larval head capsule: the cranium is formed of a single sclerite that shows no evidence of subdivision (character 11). All remaining asiloid larvae have the cranium modified into a hinged metacephalic rod. Woodley considered that larval parasitism and hypermetamorphosis were an autapomorphy of the Bombyliidae and arose independently of the Nemestrinoidea (p. 1385). According to the topology of Woodley's cladogram (fig. 1), hypermetamorphosis and parasitism may have arisen in the ancestral Muscomorpha (sensu Woodley), and been primitively retained in the Bombyliidae, while being apomorphically lost in the remaining Asiloidea, the Empidoidea, and his Muscoidea. Nagatomi (1992) recently commented on Woodley's scheme, and united the Asilidae with the Apioceridae + Mydidae in a diagram, without discussing the evidential support for this clade.

Of the 20 characters Woodley (1989) used to classify the Nemestrinoidea and Asiloidea, 13 are from adults and 7 are larval. Of the adult characters, only 3 specify relationships between families; the remaining 10 are autapomorphic at the family level. Of the larval characters, 3 are autapomorphic at the family level and 4 specify relationships between families.

The genus *Hilarimorpha* has a confusing systematic history summarized by Webb (1974). Webb concluded that *Hilarimorpha* belonged in a family of its own, but could not determine its phylogenetic position within the lower Brachycera. Woodley (1989) relegated *Hilarimorpha* to the Bombyliidae; however, as the larvae of *Hilarimorpha* are unknown, the classification of the genus remains conjectural.

Krivosheina (1991) proposed a classification of the lower Brachycera which included the Acroceridae, Nemestrinidae, and Bombyliidae in the Bombylioidea. She also rec-

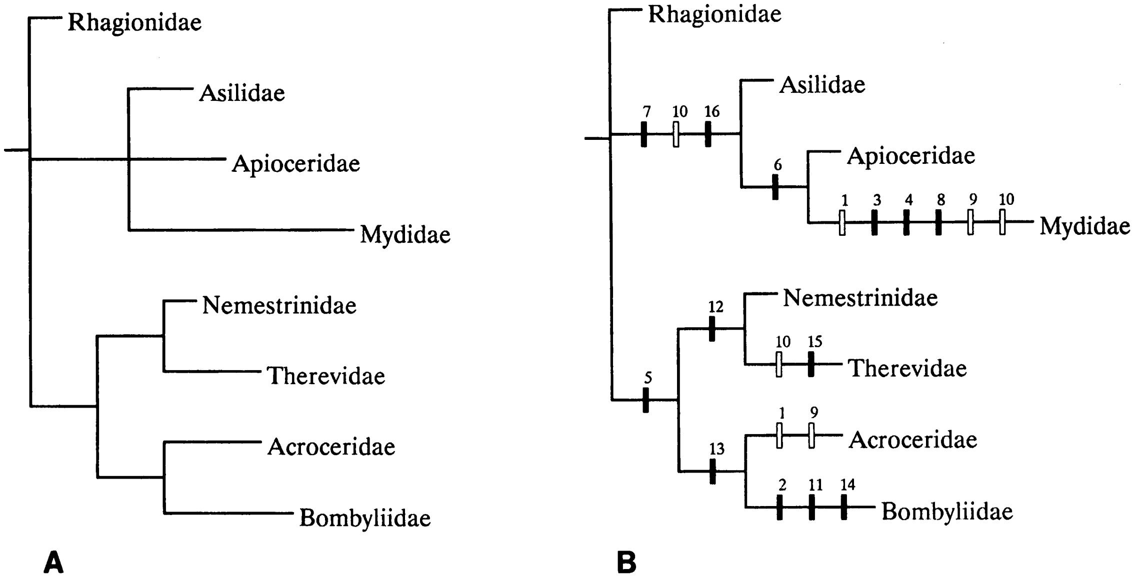

Fig. 2. Reanalysis of data presented in Ovchinnikova (1989), see Appendix 2 for details. **A.** Strict consensus tree of the two most parsimonious trees found. The two trees differ only in their resolution of the clade Asilidae + Apioceridae + Mydidae. **B.** One of the two most parsimonious trees found with characters mapped under ACCTRAN optimization (Swofford and Maddison, 1987). Characters showing homoplasy have open hash marks, those without homoplasy have filled hash marks. The other most parsimonious tree differed in that it included a clade comprising the Mydidae and Asilidae.

ognized the Systropodidae, Cyrtosiidae, and Usiidae as distinct families rather than subfamilies of Bombyliidae where they are usually placed. This classification of the Bombyliidae appears to owe much to Rhodendorf's (1974) scheme and Krivosheina does not discuss the Bombylioidea in the text. Krivosheina (1991) placed the Hilarimorphidae in the Empidoidea and treated the Leptogastridae as separate from the Asilidae, following Martin (1968) and Rhodendorf (1974).

Ovchinnikova (1989) made a detailed study of the male genital musculature of the "Orthorrhapha." She found that the Bombyliidae, Nemestrinidae, and Acroceridae were quite different from one another and questioned their classification into one superfamily. Of the three families, nemestrinids were closest to the primitive condition found in rhagionids. The Acroceridae were found to possess highly modified musculature with a reduction in mobility of the aedeagal sheath. The Bombyliidae examined (*Villa*, *Hemipenthes*, and *Anastoechus*) showed little differentiation and had retained all the muscles present in more primitive forms, with some modification. Ovchinnikova found that the Asilidae, Therevidae, and Apioceridae share an apomorphic pair of tergosternal muscles ($M5^3$) which service the aedeagal complex. In contrast, the Mydidae had muscle $M5^3$ absent and a decreasing mobility of the phallus.

Ovchinnikova's (1989) study deserves further attention because it details the distribution of character states that clearly contain cladistic information, however she did not subject her data to cladistic analysis. Cladistic analysis of data compiled in her tables 2–5 (details in Appendix 2) produces two most parsimonious solutions. Their consensus is shown in figure 2a, and the characters are mapped onto one of the most parsimonious cladograms (fig. 2b). The other most parsimonious cladogram differs only in that it unites the Asilidae and Apioceridae, supported by character 10. Thus characters of the male genitalic musculature clearly support a clade containing Asilidae, Apioceridae and Mydidae, with M38 (Char. 7) and M20 (Char. 16) present. Muscles M20 also occur in some Stratiomyidae and Tabanidae, and the polarization of this character is open to reinterpretation. The sister-group relationship between these three families is unresolved by this data, character 6 supporting (Apioceridae + Mydidae) and character 10 supporting (Asilidae + Apioceridae). Of particular note is the finding that $M5^3$ in therevids is not considered homologous with the $M5^3$ found in asilids and apiocerids (Char. 10). This is in contrast to the conclusions of Ovchinnikova; the different insertion points of the muscle in these groups may corroborate their separate evolutionary origins. The remaining ingroup families form a clade based on the loss of muscle M33 (Char. 5). M33 has also been lost in some rhagionids and the stratiomyids. The Nemestrinidae and Therevidae form a clade based on the division of M19 into 2 pairs (Char. 12), however M19 has also divided into two pairs in some asilids, xylomyids and stratiomyids. The Acroceridae and Bombyliidae are united by the common presence of M36 (Char. 13). The homology of M36 in Acroceridae and Bombyliidae is questionable because there is one pair of muscles in Bombyliidae but two in Acroceridae.

In summary, male genital musculature does not support the monophyly of the Asiloidea, Nemestrinoidea (sensu Woodley, 1989), or Bombylioidea. It does support, however, the monophyly of three families currently placed in the Asiloidea. Woodley (1989) was unsure as to the sister-group relationship of the Asilidae. These data argue in favor of the (Asilidae + Apioceridae + Mydidae) clade over a (Asilidae + Scenopinidae + Therevidae) clade. At family level characters 10 and 15 support the monophyly of the Therevidae, however, the distribution of these characters in other Therevidae and Scenopinidae requires further study. Three characters (2, 11, and 14) provide apomorphies for the Bombyliidae on this cladogram. Before these can be used with more certainty we need information on their presence in Bombyliidae more plesiomorphic than the Bombyliinae. In particular, character 11 concerns an asymmetry of musculature which is probably absent in subfamilies with unrotated male genitalia.

Finally, it is clear that homoplasy is a feature of characters drawn from musculature, as it is of characters of skeletal anatomy. Muscle morphology alone does not provide better data, just more data. However, when integrated with other forms of structural evidence, muscle morphology can clarify homologies.

CLASSIFICATION OF THE BOMBYLIIDAE INTO SUBFAMILIES

Other authors, notably Bezzi (1924), Hull (1973) and Evenhuis (1983) have summarized the work of previous systematists studying the Bombyliidae. They have detailed the chronology of generic descriptions, numbers of species described by previous authors, and such. I wish to take a slightly different perspective and place the characters in the spotlight, specifically those characters used to differentiate the subfamilies of Bombyliidae.

THE INITIAL STAGES

At the very beginning bee flies were classified into two different groups which represent the two largest modern subfamilies. Linnaeus, in the tenth edition of *Systema Naturae* (1758), included three bee fly species in his genus *Bombylius* and three in his genus *Musca*. Latreille (1802) included bee fly species in his families Bombylarii and Rhagionides, and two years later moved species from Rhagionides to his family Anthracii. Meigen (1820) was the first to merge the Anthracii with the Bombylii, producing the family-level grouping in use today.

Schiner (1868) proposed two new subfamilies, the Lomatiinae (as Lomatinae) and Toxophorinae. He distinguished the Lomatiinae from other subfamilies based on the shape of the head, proboscis, and abdomen. Characteristic features of the Toxophorinae included the wings, antennae, humped thorax and long, narrow abdomen. Anthracinae were distinguished from Bombyliinae by the form of the base of wing vein R_{2+3}.

In 1880 Brauer erected the Systropodinae (as Systropinae) with characteristic thin body, thin legs longer than the Toxophorinae, lancetlike flagellum, and long proboscis.

Melander (1902) erected the Mythicomyiinae (within the Empididae) and distinguished them from other empidids because the anal cell reaches the wing margin and the body lacks large bristles. Melander later (1928) realized that *Mythicomyia* Melander itself belonged in the Bombyliidae.

The Platypyginae was proposed by Verall (1909) for genera at that time classified in the Bombyliinae, distinguishable by an almost total lack of vestiture and a humped appearance.

CONFRONTING THE DIVERSITY OF THE FAMILY

Becker (1913) produced the most detailed and synthetic classification of Bombyliidae published up to that time. He increased the number of subfamilies substantially, to a total of 15, describing 11 of these himself. Becker is responsible for setting the traditional breadth or scope of the subfamilies in use today, thus from Becker's day on there have been 13 or more bee fly subfamilies recognized. Today's classification scheme is largely based on Becker's (1913) and Bezzi's (1924) work. Becker, Bezzi, and later Hesse were all concerned to find a single character that would divide the family into two. The differences in their classifications can largely be traced to the different character chosen to make this division. Becker rejected Bezzi's earlier (1908) suggestion that the form of the posterior eye margin may divide the family into two large groups. Instead, he focused on the traditional character used to divide the Bombyliinae from the Anthracinae, the form of the base of the vein R_{2+3}. He hypothesized that bombyliids could be divided into two groups, one containing Anthracinae and Exoprosopinae, with R_{2+3} arising at a right angle and close or opposite to the r-m crossvein, and others with R_{2+3} arising from R_{4+5} at an acute angle and proximal to the r-m crossvein. He also recognized that there were some intermediates between these two forms, such as *Petrorossia* Bezzi, with R_{2+3} arising at or almost a right angle and basal to the r-m crossvein. According to his figure (fig. 3) and text, Becker believed that the Anthracinae were the most primitive Bombyliidae, and the Bombyliinae the "youngest." His belief is not supported by this work or other cladistic analyzes such as that of Mühlenberg (1971b), which place the Anthracinae as one of the most derived subfamilies. Consequently, some of Becker's arguments regarding character evolution are difficult to comprehend. Becker considered that characters subordinate to the form of R_{2+3} such as the "total habitus," form of the head, and the position of bristles on the body could be used to separate the Bombyliidae into major groups. By inference the total habitus referred to the relative widths and shapes of the head, thorax, and abdomen.

Becker (1913) characterized the Exoprosopinae as having a round head; small frons; well-developed occiput; indentation on the hind margin of the eyes; proboscis seldom lengthened; R_{2+3} arising distally at or near the r-m crossvein; abdomen flattened and as wide as thorax; scales on the body and short front legs. He distinguished the Anthracinae from Exoprosopinae primarily on the shape of the flagellum, the Anthracinae having a circlet of hairs at the apex. His Cythereinae were distinguished by widely separated antennae, head wider than thorax, frons broad, and proboscis longer than that of the Exoprosopinae, hind margin of eye without indentation, R_{2+3} branching at an acute angle or at a right angle proximal to the r-m crossvein, and r-m distal to the middle of cell dm. These features are prominent in more recent diagnoses of the subfamily (Hall, 1976). Becker's Tomomyzinae were characterized by having a head wider than the thorax, abdomen narrower than the thorax and tapered apically, face produced anteriorly, proboscis short, hind margin of eye with an indentation, and delicate, narrow legs. He considered the Lomatiinae closely related to the Tomomyzinae, and characterized the former as having a wider body, head narrower than the thorax, face not tumid, eyes very close in male, and posterior margin of the eyes with an indentation.

Becker characterized the Aphoebantinae as smaller than the Lomatiinae, with a barrel-shaped abdomen and the r-m crossvein placed

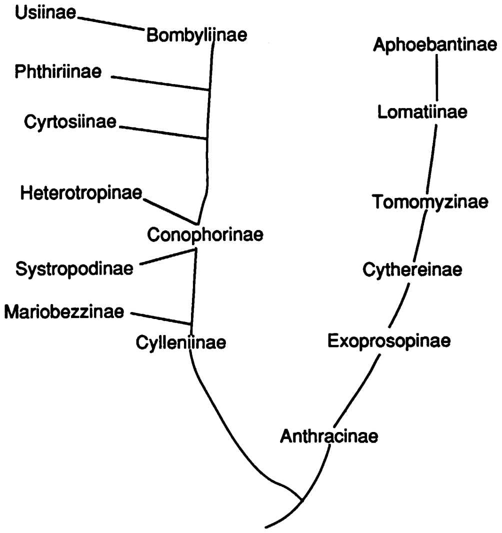

Fig. 3. The phylogenetic tree of the Bombyliidae subfamilies by Becker (1913), redrawn after his figure on p. 502.

midway along the discal medial cell. Becker considered the Mariobezziinae as nearest the Cythereinae, and containing only *Mariobezzia*. The subfamily was characterized by a relatively small compound eye without indentation on the hind margin, the pedicel of the antenna with a small thornlike protuberance apicodorsally, proboscis short, oral cavity small, anal cell closed on the wing margin, abdomen cylindrical and as wide as remainder of the body, legs delicate, and the body lacking bristles.

The Systropodinae remained much as Brauer (1880) had originally defined them, having a very long abdomen and legs, relatively small wings lacking squama and alula, and hind tarsi much longer than foretarsi.

Becker characterized the Cyrtosiinae as follows: small body lacking prominent vestiture; humped thorax with head inserted anteroventrally; eyes lacking an indentation on the hind margin and wing venation reduced with Rs only having two branches. Becker considered the Cylleniinae a difficult group and he was not able to ascertain its closest relative subfamily. Because this subfamily included *Toxophora*, previously placed in the Toxophorinae, he considered it one of the more primitive subfamilies. His phylogenetic tree (fig. 3) indicates that he considered the Cylleniinae to be at the base of the stem leading to the Bombyliinae. The subfamily was characterized by the humpbacked, thin body shape.

The Conophorinae were characterized as having a short broad habitus, short proboscis, thickened and strongly haired scape, and the remainder of the body having a well-developed vestiture. The wing possesses two or three submarginal cells, R_{2+3} arising proximally (except *Aldrichia*). Becker considered the subfamily Heterotropinae, containing only *Heterotropus*, to be transitional between either Empididae or Therevidae in the text, yet they were shown nested above other subfamilies of Bombyliidae in his phylogenetic tree. *Heterotropus* does indeed possess many plesiomorphic features in both larvae and adults (Yeates and Irwin, 1992). Becker removed the genera of the Usiinae from the Bombyliinae because of their sparse body vestiture and small head. The scape, pedicel, and proboscis were short. Becker also removed the Phthiriinae from the Bombyliidae because of their smaller size, sparse vestiture, more humped thorax, cylindrical abdomen, and wing veins R_4 and R_5 entering the wing margin without sinuosity. Later authors were to add the characteristic terminal sulcus to the definition (Hesse, 1938; Hull, 1973; Hall, 1976). The Bombyliinae have a short, broad body with antennae approximated, scape and flagellum usually lengthened, wing with usually only two submarginal cells, and R_4 and R_5 entering the wing margin with varying sinuosity.

Becker did not place some genera, all but one of which is restricted to the New World: *Desmatomyia* Williston, *Paracosmus* Coquillett, *Amphicosmus* Coquillett, *Metacosmus* Coquillett, *Mancia* Coquillett, *Astrophanes* Osten Sacken, *Exepacmus* Coquillett, *Nectaropota* Phillipi, *Parabombylius* Williston and *Peringueyimyia* Bigot.

From a modern cladistic perspective, Becker's classification suffers from two major problems. Firstly, his belief that the wing venation found in the Anthracinae was primitive led him to conclude that this was one of the most plesiomorphic subfamilies. Secondly, the form of his phylogenetic tree (fig. 3) suggests that the Phthiriinae, Usiinae, Mariobezziinae, Heterotropinae, Cyrtosiinae, and Systropodinae were monophyletic, each occupying a separate branch. However, the form of his tree also indicates that he considered the Bombyliinae, Cylleniinae, Conophorinae, Anthracinae, Exoprosopinae, Cythereinae, Tomomyzinae, and Lomatiinae to be paraphyletic. Thus the basis of the current bombyliid classification assumes rampant paraphyly and the incorrect polarization of characters.

Bezzi (1924) was the next author to make a major contribution to the classification of the family, in his "Bombyliidae of the Ethiopian Region." He considered that the subfamilies Anthracinae and Bombyliinae represented the main stems along which the family had evolved. He differed with Becker (1913) on the most suitable character used to divide the Bombyliidae into two, and relied on the form of the eye margin, in combination with the form of the postcranium. He proposed the name **Homeophthalmae** for those subfamilies with a simple hind eye margin and postcranium and **Tomophthalmae** for those subfamilies with an indentation on the hind margin of the eye and a concave postcranium. Bezzi recognized that there were some intermediates; *Cyllenia* Latreille has a simple hind eye margin and concave postcranium and *Heterostylum* Macquart has a indented hind eye margin but simple postcranium. Bezzi concluded that both the Tomophthalmae and Homeophthalmae originated from flies with simple eyes and flat postcraniums, and the Homeophthalmae comprized the most ancient forms such as the Systropodinae and Toxophorinae. He considered the Bombyliinae to be one of the more recent forms of the Homeophthalmae. Bezzi's stress on different characters led him to uproot Becker's tree, placing the Bombyliinae (belonging to the Homeophthalmae) closer to the base than the Anthracinae (belonging to the Tomophthalmae). Bezzi deferred to Becker's scheme of classification but adapted it to conform with his eye character and placed the Conophorinae within the Bombyliinae, and reduced the number of subfamilies to 13. He also reinstated the subfamily Toxophorinae, characterized by an enlarged prothorax with large bristles. Bezzi transferred the genera of the Tomomyzinae to either the Lomatiinae or Cylleniinae. As characterized by Bezzi both these latter subfamilies were paraphyletic. The Cylleniinae were Tomophthalmae that lacked the apomorphic indentation on the hind eye margin of the eyes common to other Tomophthalmae and the Lomatiinae were Tomophthalminae that lacked the apomorphic form of the base of R_{2+3} common to the Anthracinae and Exoprosopinae.

Hesse (1938, 1956a, b) published the largest work on Bombyliidae in his 2000+ page, three-part revision of the fauna of southern Africa. The fact that there are considerably more Bombyliidae known from the Afrotropical region than any other is due to Hesse, and it is chiefly through Hesse's work that the Bombyliidae of South Africa are far better known than the faunas of the other southern continents. Hesse (1938) made a small adjustment to the classification of Bezzi (1924) when dividing the family into two, and placed greatest weight on the shape of the postcranium rather than the shape of the hind eye margin as Bezzi had. Hesse's Division I (corresponding closely with the Homeophthalmae) contained those subfamilies with a flat or slightly depressed postcranium and Division II (corresponding closely with the Tomophthlamae) contained those subfamilies with a deeply concave postcranium. This had the effect of moving the Cylleniinae and Tomomyzinae, with concave postcranium but simple posterior eye margin, from Bezzi's Homeophthalmae to Division II. Hesse described two new subfamilies, one found worldwide and the other restricted to southern Africa. Hesse raised three closely related (and subsequently synonymized) genera in his new subfamily Gerontinae (as Geroninae), characterized by three posterior cells, flagellum tapering to a fine point, male genitalia complex, and female tergite 8 with lateral lobes. Hull (1973) later noted that the Gerontinae differed from the Phthiriinae because the clypeus of the latter reached the bases of the antennae. Hesse (1956b) also proposed the Xenoprosopinae for a single female specimen placed in his new genus *Xenoprosopa*. The Xenoprosopinae have reduced, nonfunctional mouthparts, scape with a large rounded ventral lobe, legs short and feeble, wings short, and bristles absent on the body and legs.

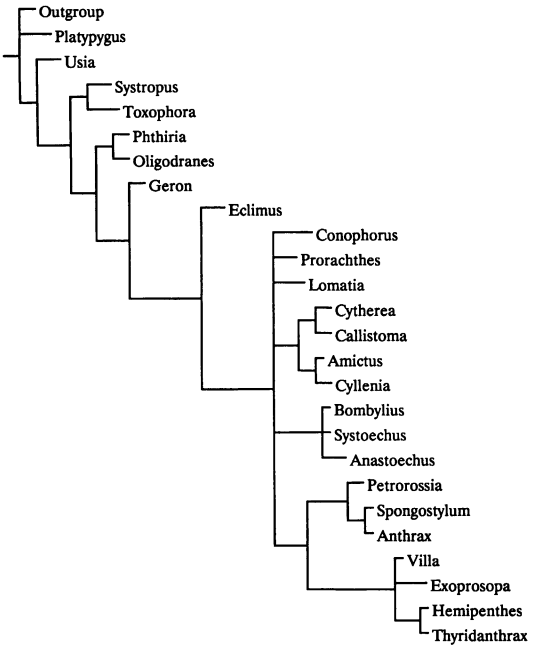

Fig. 4. The strict consensus tree produced after reanalysis of the data (in Appendix 3) of Mühlenberg (1971b). See text for details.

In 1969 Hall reviewed the subfamily Cylleniinae and described two new subfamilies, the Ecliminae and the Enicinae (as Henicinae). The diagnosis of the Cylleniinae was similar but more detailed than it had been Bezzi's time, and the subfamily remained paraphyletic. Hall considered the Ecliminae to be intermediate between the Cylleniinae and the Toxophorinae, being separated from the former by the absence of a concave postcranium and from the latter by the weakly developed prothorax. He considered the Enicinae (including the genera *Neosardus* Roberts, *Enica* Macquart, and *Nomalonia* Rondani) to be intermediate between the Cylleniinae and Lomatiinae.

RECENT CONTRIBUTIONS: EVALUATION AND REANALYSIS

Michael Mühlenberg published a series of papers (1968, 1970, 1971a) containing detailed comparative morphological studies of the female genitalia of Bombyliidae which culminated in the first cladistic analysis of the Bombyliidae (Mühlenberg, 1971b). This study improved our understanding of the relationships of the Bombyliidae more than any other and his hand analysis deserves a detailed reanalysis, described in Appendix 3. Mühlenberg's earlier morphological studies led him to discover 48 characters of the musculature and skeletal anatomy of the female genitalia; to these he added eight characters of the head and wings which had been prominent in the earlier classification schemes of Becker, Bezzi, and Hesse. On reanalysis Mühlenberg's data matrix results in 48 most parsimonious trees; their consensus is shown in figure 4.

The resolution within the Bombyliinae genera *Bombylius*, *Systoechus*, and *Anastoechus* in Mühlenberg's original tree is based on symplesiomorphy and was not recovered under reanalysis. The consensus tree reveals that Mühlenberg's original hand analysis is sound except that the bombyliines, eclimines, cyllenines, cythereines, lomatiines, and (anthracines + exoprosopines) form a large polytomy. Thus Mühlenberg's data does not support the monophyly of the Tomophthalmae, as the Tomophthalmine Lomatiinae, and Cylleniinae form a large polytomy with some subfamilies of the Homeophthalmae.

In discussing Mühlenberg's conclusions, Bowden (1974), criticized the reliance on a small number of exemplars drawn from the Mediterranean region and the sampling of characters biased toward one character system. Bowden considered it likely that the female genitalia of the Bombyliinae and Anthracinae were advanced, however he disagreed with the corollary that the female genitalia of genera (e.g. *Systropus* Wiedemann, *Geron* Meigen) more basal on Mühlenberg's scheme were plesiomorphic.

Mühlenberg deserves credit for exploring and discovering interesting and informative characters and selecting by hand one of the most parsimonious trees dictated by the data. However, it is clear that the characters he chose were unable to resolve the relationship between some subfamilies unambiguously. His study illustrates that female genitalia do possess characters of merit that can resolve some questions of Bombyliidae subfamily relationships alone. His analysis corroborates Bezzi's original contention that the Anthracinae were among the most derived Bombyliidae, and contradicts Becker's (1913) belief that they were among the most plesiomorphic. Of the Homeophthalmae, a genus of the Mythicomyiinae was the most plesiomorphic.

F. M. Hull's "Bee flies of the World" (1973) is by far the most comprehensive taxonomic treatment of the Bombyliidae on a worldwide basis. He tackled the Bombyliidae after similar treatments of the Syrphidae and Asilidae. The work compiles a large portion of the references to the Bombyliidae, host records, and fossils, describes all genera known at that time, and is replete with over 1000 figures. Hull considered that "The taxonomy of the family has been overburdened and today is top heavy with subfamilies" (p. 63). He attempted to rectify this situation by uniting a number of the subfamilies and introducing the tribal level into Bombyliidae classification. His scheme included 14 subfamilies; 12 of these he described as "scarcely disputable"; two others, Heterotropinae and Xenoprosopinae, he thought may possibly be subsumed as tribes within the Bombyliinae. His phylogenetic scheme was not graced with character support, however the cladistic topology extracted from Hull's provisional phylogenetic tree is shown in figure 5. Hull did not refer to Mühlenberg's (1971b) findings, and added little to our understanding of the phylogenetics of the Bombyliidae. Citing Cockerell's (1914) work on fossils, he considered the Homeophthalmae to be the oldest group and of Old World origin. With a similar emphasis as Hesse, Hull stressed the importance of the concave postcranium in delimiting the subfamilies belonging to the Tomophthalmae.

The phylogenetic scheme of Hull (fig. 5) exhibits a broad similarity to that of Becker (fig. 3); both schemes divide the Bombyliidae into two main lineages, corresponding fairly closely to the Homeophthalmae and Tomophthalmae as conceived today. There are two main differences: (1) Hull included the Cylleniinae on the branch leading to the remaining Tomophthalmae, while Becker considered the Cylleniinae to be the most plesiomorphic branch leading to the Homeophthalmae, and (2) Hull considered the Exoprosopinae (now a component of the Anthracinae) one of the most advanced subfamilies of the Tomophthalmae whereas Becker considered the Exoprosopinae to be one of the most primitive in the tomophthalmine lineage.

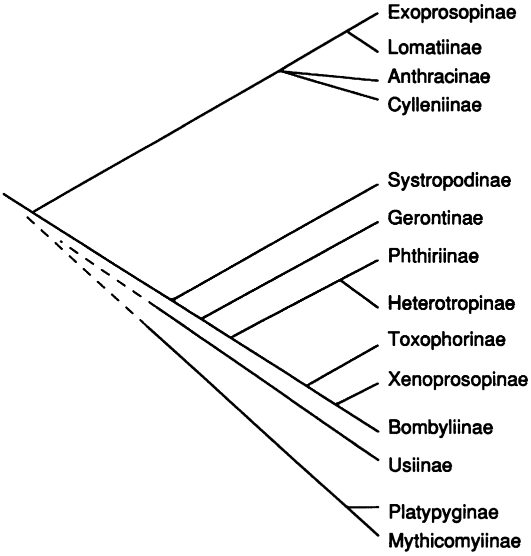

Fig. 5. Phylogenetic tree of the Bombyliidae subfamilies by Hull (1973), redrawn after his text figure 18.

Hull validly proposed a total of 30 tribes in 7 subfamilies as follows: 2 in the Mythicomyiinae, 2 in the Platpyginae, 1 in the Systropodinae, 10 in the Bombyliinae, 7 in the Lomatiinae, 5 in the Cylleniinae, and 3 in the Exoprosopinae. Of the tribes of the Bombyliinae, the Cythereini, Conophorini, Mariobezzini, and Eclimini represented subfamilies of previous authors. This expanded concept of the Bombyliinae has met with a mixed reception from subsequent workers, and led Hull to propose an amorphous characterization of the subfamily, including only plesiomorphic features such as discal medial cell present, two branches of M, and bases of the antennae close together. Only plesiomorphic characters have been used by more recent authors in characterizing the Bombyliinae (e.g. Hall, 1976).

The five tribes Hull included in the Cylleniinae included the Henicini and Tomomyzini, subfamilies of previous authors. Hull characterized the Cylleniinae as having a concave postcranium, simple posterior eye margin and R_{2+3} arising proximally at an acute angle. The last two characters are symplesiomorphies, and the first applies to the

Tomomyzinae, Lomatiinae, Antoniinae, and Anthracinae, thus the Cylleniinae remain paraphyletic. He considered the Cylleniinae and Lomatiinae closely related, and entertained the possibility, which I substantiate later, that *Perigueyimyia* belongs in the Lomatiinae.

Hull's tribes of the Lomatiinae included the Aphoebantini, one of Becker's (1913) subfamilies. Hull concluded that the form of the posterior eye margin and shape of the base of R_{2+3} distinguish the Lomatiinae from the Cylleniinae, however R_{2+3} arises proximally and at an acute angle in both subfamilies. Many tribes which Hull (1973) included in the Lomatiinae have since been removed to either the Antoniinae or Anthracinae, for example the Aphoebantini, and the genera centered around *Plesiocera* and *Petrorossia*.

Greathead (1972) reexamined the Afrotropical Cythereinae, and raised the genus *Oniromyia* to subfamily status. He considered the Oniromyiinae (as Oniromyinae) was closely related to the Cylleniinae, but was different because of its long proboscis clothed in scales, femora and abdomen without strong bristles, and form of the male genitalia.

The cytotaxonomy of Bombyliidae received attention from Boyes and Shewell (1973). They examined the karyotypes of bee flies belonging to the subfamilies Toxophorinae, Usiinae, Bombyliinae, and Anthracinae. They found that chromosome number was generally higher in the Tomophthalmae than in the Homeophthalmae, and proposed that only two subfamilies of Bombyliidae be recognized, the Bombyliinae and Anthracinae, corresponding to the Homeophthalmae and Tomophthalmae, respectively. Their suggestion has not been followed by more recent authors.

Bowden (1980), in the "Catalogue of the Diptera of the Afrotropical Region," classified the Bombyliidae according to a new scheme formulated in collaboration with David Greathead. The chief innovations of this new classification compared to that of Hull were as follows. The Systropodinae and Gerontinae were treated as tribes of an expanded Toxophorinae, the Exoprosopinae were reduced to a tribe within the Anthracinae, the Platypyginae were subsumed within the Mythicomyiinae, the Tomomyzinae and Cythereinae were reinstated, and a new monogeneric subfamily was proposed, the Antoniinae. The Cythereinae was enlarged to include flies that Becker (1913) and Bezzi (1924) included in the Mariobezziinae. Thus the character which distinguished the Cythereinae in these older schemes, the very broadly separated antennae, no longer applied to this subfamily. Many genera of the Lomatiinae were also transferred to the Anthracinae. Unfortunately this new classification, proposed in a catalog format, remains unsubstantiated by evidential support. Future workers should be encouraged not to make major classificatory changes in the absence of supporting evidence.

Theodor (1983) produced a monumental descriptive work on the genitalia of Bombyliidae, including over 750 figures, which is an indispensable reference for bombyliid workers. Theodor divided the family into three groups of subfamilies which he did not formally name, and introduced the number of occipital foramina as a character in Bombyliidae systematics. Group 1 included those sufamilies with a normal postcranium, simple hind eye margin, a single occipital foramen, normal or reduced wing venation, and female genitalia lacking acanthophorite spines and a sand chamber. Group 2 was similar to group 1 except the females possessed acanthophorites and a sand chamber. Group 3, a monophyletic group corresponding closely to the Tomophthalmae of previous authors, included those subfamilies with a concave postcranium, two occipital foramina, and female terminalia like those of group 2. Theodor also suggested that *Prorates* belonged in a separate subfamily, the Proratinae, and may be better placed in the Scenopinidae. This suggestion has been pursued elsewhere (Yeates, 1992a), with the Proratinae formally classified in the Scenopinidae.

Hall and Evenhuis (1987) raised the genera *Desmatomyia* Williston and their new genus *Inyo* to subfamily status in the Desmatomyiinae. They considered that the new subfamily was not closely related to any other and distinguished the Desmatomyiinae because of its wide facial and genal area, peculiar structure of the flagellum, lack of a sclerotized spermathecal bulb, form of the gonostyli, and form of the epiphallus.

Evenhuis (1990) removed *Oligodranes* from the Usiinae to its own subfamily, the Oligodraninae, which he considered phylogenetically close to the Bombyliinae. Characters distinguishing the subfamily include: face present below the antenna, two-segmented palps, form of the flagellum, and the presence of only three posterior cells.

Evenhuis (1991) produced the most recent classification of the Bombyliidae in tabular form. He adopted a revised concept of the Tomophthalmae, equating them with Theodor's group 3, the Homeophthalmae therefore corresponding to Theodor's groups 1 and 2. Thus the concept of the Tomophthalmae has evolved from Bezzi's original proposal. Initially it was to include those bee flies with an indented hind eye margin, although Hesse and Hull modified it to be those with a concave postcranium and most recently Evenhuis included those with two occipital foramina. This gradual change has had the effect of increasing the generality of the Tomophthalmae. Apart from this change, Evenhuis's classification owes much to that of Bowden (1980), in comparison to the classification of Hull (1973). In particular, the Exoprosopinae were reduced to a tribe within the Anthracinae, the Platypyginae were subsumed within the Mythicomyiinae [however the tribes of Mythicomyiinae in Evenhuis (1989) were not used], and the Tomomyzinae and Cythereinae were reinstated. However, unlike Bowden's scheme (1980) the Toxophorinae and Gerontinae were treated as separate subfamilies, because Evenhuis (1990) supposed that the characters used by Bowden to unite the subfamilies were incorrectly polarized. Thus Evenhuis's (1991) system selectively uses major changes first proposed in an earlier classification which was not supported by evidence.

A recent attempt has been made to divide the Bombyliidae into five families (Zaytsev, 1992) and resurrects the idea of dividing the Homeophthalmae into a number of small families first proposed by Rhodendorf (1974). The rearrangement of Zaytsev (1992) increased the classificatory rank and broadened the scope of some of the traditionally recognized subfamilies. Although evidence supporting the topology of Zaytsev's phylogenetic tree (fig. 6) was not supplied, it clearly indicates that the five family-level groupings together form a monophyletic group. This begs the question as to the necessity of such a change in rankings for only some of the included subfamilies. Indeed this approach is internally inconsistent in that all the current subfamilies were not raised to family status. The main characters with which Zaytsev supports his classification are derived from the form of the flagellum, proboscis, postcranium, wing venation, and female genitalia. The work is not cladistic, and the definition of the Phthiriidae contains only plesiomorphic characters.

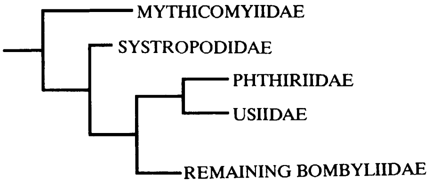

Fig. 6. The phylogenetic tree of the Bombylioidea by Zaytsev (1992), redrawn after his figure 1.

Zaytsev (1992) proposed raising the monophyletic Mythicomyiinae to family status, as had been suggested by Rhodendorf (1974). Within this subfamily, three subfamilies were recognized, equivalent to the divisions in this grouping of flies proposed by Hull (1973). Systropodinae was also raised to family status and included the traditional subfamilies Systropodinae and Toxophorinae. Zaytsev (1992) used an old (Hall, 1969; Hull, 1973) concept of Toxophorinae including a number of eclimine genera, an arrangement criticized effectively by Greathead (1988).

Zaytsev (1992) also raised the Phthiriinae to family status, however he increased the content of this grouping so that it bears little resemblance to the Phthiriinae recently revised by Evenhuis (1990). The additions are the Crocidiinae, traditionally recognized as a plesiomorphic tribe of Bombyliinae; the Mariobezziinae, traditionally recognized as a tribe of the Cythereinae, and the Heterotropinae. The concept of Heterotropinae used by Zaytsev has been abandoned in the recent literature, and Yeates (1992a) removed many genera to the Scenopinidae.

Thus Zaytsev's proposed "Phthiriidae" contains flies currently placed in both Scenopinidae and Bombyliidae, and within the Bombyliidae contains both homeophthalmine (Phthiriinae and Crocidini) and tomophthalmine (Mariobezzini) genera. The recognition of this artificial assemblage as a group can only hinder our attempt to build a phylogenetic classification of the Bombyliidae.

Zaytsev (1992) also raised the Usiinae to family status, and included the traditional subfamilies Oligodraninae and Gerontinae. The inclusion of the Oligodraninae contradicts the findings of Evenhuis (1990), and the inclusion of the Gerontinae apparently ignores the close relationship of this subfamily to the Systropodinae and Toxophorinae (Bowden, 1980; Greathead, 1988).

Zaytsev's revised concept of the Bombyliidae included only those subfamilies plesiomorphically possessing a sand chamber, and is largely equivalent to the Psammophoridae of Mühlenberg, (1971b), and groups 2 and 3 of Theodor (1983). Within the Bombyliidae Zaytsev (1992) was more conservative, deviating from the traditional subfamily boundaries by moving the Neosardini from the Cythereinae to the Cylleniinae, demoting the Antoniinae to a tribe of the Lomatiinae, moving the Aphoebantini from the Anthracinae to the Lomatiinae, and resurrecting the Exoprosopinae from within the Anthracinae.

It is evident from this discussion that there is a diversity of opinion regarding the subfamily-level classification of the Bombyliidae. Many recent changes have been formulated in the absence of adequate data, or in the absence of any data at all in catalogs. It is pertinent at this time to review characters used in previous classifications and make a survey for additional characters before proposing a revised, phylogenetic classification.

METHODS

NAMES FOR HIGHER CATEGORIES OF DIPTERA

The traditional group called the "Orthorrhapha" and comprising the Xylophagomorpha, Stratiomyomorpha, Tabanomorpha, Asiloidea and Empidoidea of recent workers is paraphyletic and is clearly indicated as such here by surrounding the name in quotation marks (Wiley, 1981). The Manual of Nearctic Diptera, Volume 3, (1989) introduced some confusion into the naming of higher categories of the Diptera. The higher Diptera traditionally referred to as the Cyclorrhapha (e.g., Griffiths, 1986) has been termed the Muscoidea by Woodley (1989) and Muscomorpha by McAlpine (1989); I use Woodley's nomenclature here; thus the Muscomorpha includes the Nemestrinidae, Acroceridae, Asiloidea, Empidoidea, and Muscoidea.

MORPHOLOGICAL TERMINOLOGY

The morphological terminology I use is based on McAlpine (1981). Following Wood (1990a), I use the term phallus for the complex intromittent organ found in the taxa examined here which is composed of the aedeagus surrounded by a sclerotized aedeagal sheath. Wood (1990b) prefers "parameral sheath" for this structure. Within the Bombyliidae I have attempted to reconcile the various schemes of terminology used by previous authors. Terminology for vestiture follows Yeates (1988).

DATA ACCUMULATION AND CLADISTIC ANALYSES

Data were gathered and organized using the spreadsheet program Quattro Pro Version 2.0 (Registered Trade Mark of Borland International, Inc.) and exported in a form suitable for phylogenetic packages. Additional taxa and characters can be easily added to the spreadsheet and it will become a database of phylogenetic information on the Bombyliidae to be used in future analyses. Initial trial analyses with 50 terminals were conducted with Hennig86 Version 1.5 (Farris, 1988). The final data matrix with 87 terminals was analyzed with Hennig86 using the mhennig* command followed by bb*, and PAUP Version 3.0s (Swofford, 1991). The PAUP runs were conducted on a workstation by Dr. David Swofford using 100 random addition sequence replicates, to overcome the possibility of finding trees belonging to only one "island" of most parsimonious trees (Maddison, 1991).

Clados Version 1.2 (Nixon, 1992) was used to check character scoring, character change, and optimization, and to parse the output of Hennig86 for those most parsimonious trees with nodes offering potential character support only. Clados also facilitated the printed output of the trees in figures 1, 2, 4, 6, 7, and 509–514.

I have included autapomorphies in the data matrix because they may prove to have a wider distribution when the phylogenetics of individual subfamilies, tribes, or genera are studied by future workers (Yeates, 1992b).

In cases where I refer to exemplars by their generic name I do not cite the author of the name.

TAXON SAMPLING

The species scored in the data matrix are listed in table 1. As discussed above, recent workers have placed the Bombyliidae in either the Asiloidea or in a superfamily with the Nemestrinidae plus Acroceridae. The Nemestrinidae and Acroceridae were placed in the Nemestrinoidea by Woodley (1989), and he considered them the sister group of the Asiloidea. These two superfamilies contain over 11,000 described species and we are just beginning to understand the phylogenetic relationships among and within the families. To root these two clades I used two members of the Tabanomorpha belonging to the Rhagionidae, members of the genera *Rhagio* and *Arthrocerus*.

Among the Nemestrinoidea and Asiloidea I attempted to choose members of plesiomorphic genera according to currently accepted ideas of intrafamilial relationships. As taxon choice is a critical aspect of any cladistic study, I discuss my choices below in detail.

I have not included represenatives of the Eremoneura in this analysis. I have taken as a working hypothesis that the Asiloidea is monophyletic, as set out by Woodley (1989), and any member of the Eremoneura would be less informative about cladistic relationships within the Bombyliidae than any member of the Asiloidea.

NEMESTRINIDAE

This family is found on all continents except Antarctica and comprises about 250 species. The peculiar diagonal vein of the wing provides a convenient synapomorphy for the entire group (Woodley, 1989). Bernardi (1973) last revised nemestrinid classification and partitioned them into one fossil and five extant subfamilies. Bernardi provided a table of 40 characters divided into primitive and specialized states and used 10 of these characters in a comparison of the subfamilies. Four of these characters are autapomorphies of the specialized Atriadopsinae, two are autapomorphies of the Cyclopsideinae, and two are autapomorpies of all extant members of the family. Excluding the fossil Archinemestriinae, the subfamilies Hirmoneurinae and Nemestrininae have the fewest apomorphic features, and Bernardi stated that the Hirmoneurinae are the most primitive. Perusing the subfamily definitions, these two subfamilies are similar except that the Nemestrininae have a longer proboscis than the Hirmoneurinae and the former have a larger hypandrium. Bernardi clearly considered *Trichophthalma* Westwood the most primitive member of the Nemestrininae in his phylogenetic scheme (his fig. 75).

Hirmoneurinae contains a single living genus, *Hirmoneura* Meigen. *H. exotica* has retained a hypandrium, unlike many other members of the genus, and I consider this to be a primitive characteristic. *H. exotica* and a member of the Nemestrininae, *Trichophthalma costalis*, were chosen as exemplars.

ACROCERIDAE

This is a family of approximately 380 described species found on all continents except Antarctica. There is consensus on the monophyly of members of the family, being characterized by a peculiar single antennal flagellomere, enlarged lower calypter, and the parasitism of spiders by their larvae (Woodley, 1989).

The Acroceridae have been divided into three extant subfamilies, Acrocerinae, Panopinae, and Philopotinae (Schlinger, 1957, 1987). Schlinger (1957, 1987) considered the Panopinae to be the most primitive subfam-

TABLE 1

Exemplar Taxa Scored in the Analysis and Included in the Data Matrix of Appendix 4

The classification of the Bombyliidae used below follows the revised classification presented here

Coded species	Provenance
Rhagionidae	
Rhagio mystaceus (Macquart)	Minnesota, USA
Arthroceras fulvicorne Nagatomi	Utah, USA
Acroceridae	
Lasia colei Aldrich	Costa Rica
Eulonchus smaragdinus Gerstäcker	California
Nemestrinidae	
Hirmoneura exotica Wiedemann	Uruguay, South America
Trichophthalma costalis (Westwood)	New South Wales, Aust.
Asilidae	
Dioctria atricapilla Meigen	Sweden
Stenopogon inquinatus Loew	Washington, USA
Leptarthrus brevirostris (Meigen)	USA
Leptogaster flavipes Loew	New Jersey and New York, USA
Scenopinidae	
Caenotus hospes Melander	Arizona, USA
Prorates frommeri Hall	California, USA
Scenopinus fenestralis (Linnaeus)	Mass. and Utah, USA
Propebrevitrichia sp.	Botswana, Africa
Therevidae	
Thereva fucata Loew	California, USA
Phycus rufofemoratus (Kröber)	Chad, Africa,
Bonjeania sp. 1	New South Wales, Australia
Apsilocephalidae	
Apsilocephala sp.	Arizona, USA
Apioceridae	
Apiocera aldrichi Painter	California, USA
Neorhaphiomidas hardyi Norris	Western Australia, Australia
Mydidae	
Apiophora paulseni Phillipi	Valparaiso, Chile
Mydas clavatus (Drury)	Indiana, USA
Hilarimorphidae	
Apystomyia elinguis Melander	California, USA
Hilarimorpha mentata Webb	Saskatchewan, Canada
Bombyliidae	
Mythicomyiinae	
Glabellula rotundipennis Melander	California, USA
Mythicomyia illustris Melander	Arizona, USA
Acridophagus sp.	Western Australia
Paraconsors scutellaris (Melander)	Arizona, USA
Cephalodromia fusca Sequy	Kenya, Africa
Oligodraninae	
Oligodranes sp.	Israel
Usiinae	
Usiini	

TABLE 1—(*Continued*)

Coded species	Provenance
Usia atrata (Fabricius)	France,
Apolysis cinctura (Coquillett)	California, USA
Phthiriini	
Phthiria gaedei Wiedemann	Yugoslavia
Poeciognathus sculphurea Loew	Massachusetts, USA
Toxophorinae	
Toxophorini	
Toxophora virgata Osten Sacken	Arizona, USA
Toxophora compta Roberts	Queensland, Australia
Gerontini	
Geron albaria Painter	Colorado and Wyoming, USA
Geron grandis Painter	Arizona, USA
Systropodini	
Systropus macer Loew	New York and New Jersey, USA
Dolichomyia gracilis Williston	Arizona and Utah, USA
Zaclava clavifemorata Hardy	NSW and Qld, Australia
Heterotropinae	
Heterotropus gilvicornis Yeates	South Africa
Lordotinae	
Lordotus pulchrissimus Williston	California, USA
Bombyliinae	
Conophorini	
Conophorus fenestratus (O.S.)	California, USA
Aldrichia ehrmanii Coquillett	Ohio, USA
Acrophthalmydini	
Acrophthalmyda paulseni (Philippi)	Chile
Bombyliini	
Bombylius major Linneaus	New Jersey, USA
Bombylius androgynus Loew	Egypt
Eurycarenus laticeps Loew	Mozambique, Africa
"Dischistini"	
Dischistus mystax Wiedemann	South Africa
Eusurbus crassilabris Macquart	New South Wales, Australia
Heterostylum robustum (Osten Sacken)	Arizona, USA
Eclimini	
Paratoxophora cuthbertsoni Engel	Zimbabwe, Africa
Marmasoma sumptuosum White	Australian Capital Terr.
Lepidophora lutea Painter	New Jersey, USA
Thevenetimyia californicus Bigot	California, USA
Eclimus gracilis Loew	Turkey
Cyrtomyia chilensis Paramonov	Chile
Crocidiinae	
Crocidium karooanum Hesse	South Africa
Desmatomyia anomala Williston	New Mexico, USA
Incertae sedis	
Sericosoma furva Edwards	Chile

TABLE 1—(*Continued*)

Coded species	Provenance
Mariobezziinae	
Corsomyza brevicornis Hesse	South Africa
Mariobezzia lichtwardti Becker	Egypt
Megapalpus capensis Wiedemann	South Africa
Oniromyiinae	
Oniromyia pachycerata Bigot	South Africa
Cythereinae	
Cytherea obscura Fabricius	Turkey
Pantarbes capito Osten Sacken	California, USA
Neosardus sp.	Queensland, Australia
Enica longirostris Wiedemann	South Africa
Amictus validus Loew	Egypt and Greece
Cyllenia maculata Latreille	Spain and Italy
Tomomyzinae	
Docidomyia sp.	Western Australia
Amphicosmus cincturus Williston	Mexico
Tomomyza philoxera Hesse	South Africa
Antoniinae	
Antonia suavissima Loew	Saudi Arabia and Somalia
Myonema humile Roberts	Queensland, Australia
Lomatiinae	
Peringueyimyia capensis Bigot	South Africa
Comptosia fascipennis Macquart	Queensland, Australia
Ylasoia pegasus (Wiedemann)	Uruguay
Lomatia belzebul (Fabricius)	France
Ogcodocera analis Williston	Mexico
Anthracinae	
Prorostomatini	
Plesiocera psammophila Hesse	South Africa
Aphoebantini	
Aphoebantus cervinus Loew	Mexico
Xeramoebini	
Petrorossia gratiosa Bezzi	Liberia
Anthracini	
Anthrax analis Say	New York, USA
Uxoprosopini	
Exoprosopa caliptera (Say)	Arizona and Colorado, USA
Villini	
Villa alternata (Say)	New York, USA

ily, and (1957) placed the genera *Lasia* Wiedemann and *Eulonchus* Gerstäcker on the common stem leading to the remaining subfamilies. All known hosts of Panopinae are primitive mygalomorph spiders whereas hosts of the other subfamilies are the more recently derived araneomorphs. Representatives of two different genera of Panopinae, *Lasia* and *Eulonchus*, were used in this study.

ASILIDAE

One of the largest families of Asiloidea, with about 5000 described species found worldwide. The robber flies are characterized by a number of apomorphies and their monophyly has not been seriously questioned. Characters that unite the family concern the specialized predatory nature of the adults (Woodley, 1989): (1) labellae reduced and fused with prementum; (2) hypopharynx strongly sclerotized and modified into a needlelike structure; and (3) face with mystax. Woodley (1989) disagreed with Martin's (1968) attempt to recognize the Leptogastrinae as a separate family, however I have included a species of *Leptogaster* in this analysis.

Few studies have addressed the phylogenetic system within the Asilidae. Hull (1962) considered the Dasypogoninae as the most generalized members of the family because of their two-segmented palps and open marginal cell. Within the Dasypogoninae, Hull considered five tribes (Dioctrini, Phellini, Chrysopogoninae, Damalini, and Laphystini) primitive because the females lacked acanthophorites, and thereby also lacked acanthophorite spines.

Adisoemarto and Wood (1975), in a revision of the Nearctic Dioctrini, disagreed with Hull (1962) and considered acanthophorites and their spines to be a groundplan feature of Asiloidea, and that the Dasypogoninae possessing them are more primitive than those without. I concur.

Papavero (1973a) discussed the phylogeny of the Asilidae and considered that the most primitive asilids should have the following plesiomorphic features: (1) two-segmented palpus; (2) two-segmented antennal style; (3) prosternum fused to pronotum; (4) foretibiae lacking an apical spur; (5) wings with three submarginal cells and all cells widely open; (6) tergal bristles present on all tergites; (7) meso- and metapleura with several strong bristles; (8) female terminalia with spines on acanthophorites; and (9) male genitalia with free hypandrium, free epandrial halves, and gonostyli placed apically on the gonocoxites.

Papavero's ideas on the evolutionary development of the asilids from this ancestor and his branching diagram do not directly indicate the extant group retaining most plesiomorphic features. The Stenopogoninae (Stenopogonini of Hull, 1962) appear to have acquired fewer derived characters than the remaining subfamilies.

I chose a Nearctic stenopogonine, *Stenopogon inquinatus* Loew, and Nearctic and Palearctic dasypogonines, *Leptarthrus brevirostris* (Meigen) and *Dioctria atricapilla* Meigen, as exemplars of the Asilidae, in addition to the genus *Leptogaster*. *Stenopogon inquinatus* retains the following features that Papavero considered primitive: 1,2,4,8,9. The marginal cell is open, however there are only two submarginal cells. The male epandrium is divided longitudinally. *Leptogaster brevirostris* retains only 1, 2, and 9, however the male terminalia have an undivided epandrium. *Dioctria atricapilla* has only primitive features 2 and 9, with the epandrium undivided.

APIOCERIDAE

Containing only about 150 species in five genera, the family has a widely disjunct distribution in North America, Chile, South Africa, Australia, and Borneo. Woodley (1989) considered that their closest relatives were the Mydidae, as did Cazier (1941). Woodley considered that the supernumary rectal papillae unite the mydids and apiocerids apomorphically. However, without a firm apomorphy for the Apioceridae, they may be no more than plesiomorphic mydids (Cazier, 1941; Woodley, 1989).

Little has been published on the phylogeny of the apiocerid genera. Cazier (1941) revised the genera and divided the family into two subfamilies, the Apiocerinae (as Apioceratinae) and Megascelinae, based on differences in wing venation, male terminalia, and palps. The Megascelinae share with the Apiocerinae a derived reduction to a single antennal flagellomere whereas Mydidae have the more plesiomorphic two flagellomeres. Cazier (1941) considered that *Apiocera* was the generalized stock of the family.

A review of the relationship between the Apioceridae and Mydidae is urgently required. Because of the confused phylogeny within the family it was difficult to select exemplars for this study, however the North American member of the Apiocerinae, *Apiocera aldrichi* Painter and an Australian member of the Megascelinae, *Neorhaphiomydas hardyi* Norris, were chosen.

MYDIDAE

This family of large, striking flies contains about 340 species described from all zoogeographic regions (Wilcox, 1981). They are easily recognized and monophyletic, the adults having a characteristic swollen second flagellomere and stout spines on the underside of the hind femur (Woodley, 1989).

Papavero and Wilcox (1974) revised the world classification of the family, dividing it into nine subfamilies, of which the Ectyphinae possess an array of primitive character states. The hypandrium is only partially fused to the gonocoxites (fused in other subfamilies) and the females have spines on the acanthophorites. Papavero and Wilcox indicated that this subfamily also possesses gonostyli (which are absent in the other subfamilies) but Wood (personal commun. 1991) considered the loss of gonostyli an autapomorphy for the family. A member of the Apiophorinae, *Apiophora paulseni*, and a member of the Mydinae, *Mydas clavatus*, were chosen to code in this analysis. Both lack gonostyli, supporting Wood's interpretation.

THEREVIDAE

This family contains about 830 described species found worldwide except the poles. Recent systematic work has concentrated on the Nearctic, Palaearctic, and Afrotropical faunas (Irwin and Lyneborg, 1981a,b; Lyneborg, 1976, 1983). The family is as yet rather poorly characterized, the only apomorphy suggested to date being the spatulate metacephalic rod of the larvae (Malloch, 1917; Woodley, 1989). Irwin and Lyneborg (1981b, 1989) suggested that the Nearctic *Apsilocephala longistyla* Kröber and Australian *Clesthentia abberans* White belong elsewhere, and Nagatomi et al. (1991a) place these genera in a new family, the Apsilocephalidae. I have included a species of *Apsilocephala* in this study.

The family has been divided into two subfamilies, Therevinae and Phycinae (Irwin and Lyneborg, 1981a), largely on the basis of genitalic characters. The Therevinae have: (1) a strong sclerotized bridge between the phallus and gonocoxite (paramere in Irwin and Lyneborg's terminology) usually lacking; (2) anterior apodeme of aedeagal sheath (ventral apodeme of aedeagus in Irwin and Lyneborg's terminology) well developed and simple; (3) females with spines present on the acanthophorites; (4) membrane of the female between the furca and sternite 8 sclerotized; (5) pregenital spiracles in the pleural membrane; and (6) vein R_1 not setose. Phycinae, on the other hand have: (1) a strongly sclerotized bridge between the phallus and gonocoxite usually present; (2) anterior apodeme of aedeagal sheath poorly developed or forked; (3) females without a group of distict large spines on the acanthophorites; (4) membrane of the female between the furca and sternite 8 not sclerotized; (5) pregenital spiracles in the tergal sclerites; and (6) vein R_1 sometimes setose.

Some genera that are therevines on the basis of characters 2–6 above (e.g., *Ozodiceromyia* Bigot) have a well-developed bridge between gonocoxites and aedeagal sheath and some phycines (*Henicomyia* Coquillett) lack the bridge.

One member from each of the subfamilies was chosen as an exemplar: *Thereva fucata* and *Phycus rufofemoralis*. I have also included a member of the Australian genus *Bonjeania*, which appears closest to the Therevinae but has highly derived male genitalia which are outside the range of variation found in genera from the Northern Hemisphere.

Woodley (1989) expressed the opinion that the Therevidae may not be monophyletic, the Scenopinidae perhaps being a derived clade arising from within the former. This point could be settled if a series of convincing apomorphies of the Therevidae excluding the Scenopinidae could be found. Woodley (1989) united the Therevidae by the following: possession of a posteriorly spatulate metacephalic rod in the larva. Other apomorphies may be found when the comparative morphology of asiloid larvae is known in greater detail.

SCENOPINIDAE

A family of diminutive flies found in all biogeographic regions and containing about 400 described species (Kelsey, 1989). Woodley considered them the sister group of the Therevidae because of a similarity in the larvae of the two families; however he noted the possibility that they were an apomorphic offshoot from the Therevidae, making the latter paraphyletic. This possibility exists because apomorphies of the Therevidae are poorly documented.

Yeates (1992a) transferred the genera of the bombyliid subfamily Proratinae (excluding *Apystomyia*) to the Scenopinidae, following a suggestion made by Theodor (1983). As currently constituted the family shares the following apomorphies: male eyes divided into larger dorsal facets and smaller ventral facets; wing cell bm with apex blunt; scutum without setae; abdominal tergite 2 with an area of modified setae; two spermathecae; epandrium divided in the midline and phallus divided into one or two apical tubes (Yeates, 1992a).

Kelsey (1969) revised the world fauna but did not divide the family into subfamilies or discuss their phylogeny. Yeates (1992a) found the Caenotinae to be the most plesiomorphic subfamily and sister group to the Proratinae plus Scenopininae. As exemplars for this study I have chosen *Caenotus hospes* from the subfamily Caenotinae, *Prorates frommeri* from the subfamily Proratinae, and *Scenopinus fenestralis* and *Propebrevitrichia* sp. from the subfamily Scenopininae. *Scenopinus fenestralis* is a large common species found worldwide, and *Propebrevitrichia* sp. was chosen because females have spines on the acanthophorites, as some other species in the family do (e.g., *Heteromphrale* Kröber).

A member of the Hilarimorphidae and the proratine genus *Apystomyia* were also included to complete the sampling of asiloids other than Bombyliidae.

BOMBYLIIDAE

My taxon sampling in the Bombyliidae was informed on the basis of my main aim, to examine the relationships between the subfamilies. Where possible I included at least two members of each subfamily in order to test its monophyly.

I have not chosen to sample bee fly taxa in proportion to their numbers of described species, and my sampling has been deliberately biased away from this simplistic approach in various ways. In particular, I have included a disproportionate number of the more plesiomorphic members of the family. The advanced, putatively monophyletic subfamily Anthracinae is represented by only six species, even though this group accounts for almost half (42%) of the described species. By contrast, the subfamily Bombyliinae is represented by 12 species even though it accounts for a little over 20% of the described species.

I have endeavored to score a member of the type genus of each tribe of each subfamily and have used Evenhuis (1991) as a guide to the traditional classification of the family. Where possible I have chosen the type species. Tribes within the Mythicomyiinae have not yet been consistently proposed, and in this case I relied on the advice of Neal Evenhuis, who is currently revising the subfamily, in order to include a broad sampling of its morphological diversity.

Of the subfamilies currently recognized, the only one not present in my data matrix is the Xenoprosopinae. This subfamily is represented in collections to date by a single female specimen which I was unable to study.

PREPARATION OF MATERIAL

For each exemplar examined, I dissected the whole body of the female and the male genitalia or the whole body of both sexes. Usually only a single specimen of each sex was examined, although I examined multiple male and female *Bombylius major* and *Exoprosopa calyptera*. Specimens were soaked in 5% cold KOH overnight and examined under a Wild M3 and Zeiss SV8 stereomicroscope and a Zeiss compound microscope. The three-dimensional structure of the male and female genitalia was retained by mounting them in glycerine gel without a coverslip for microscopic examination.

Some external structures, notably the antennae and body vestiture, were examined under a scanning electron microscope. I examined the internal sclerotized parts of the occiput, scutum, and spermathecae under the scanning microscope using the following technique. Macerated specimens were carefully dissected in water and transferred through ascending concentrations of alcohol before being critical-point dried, mounted on a SEM stub, and coated in the usual way.

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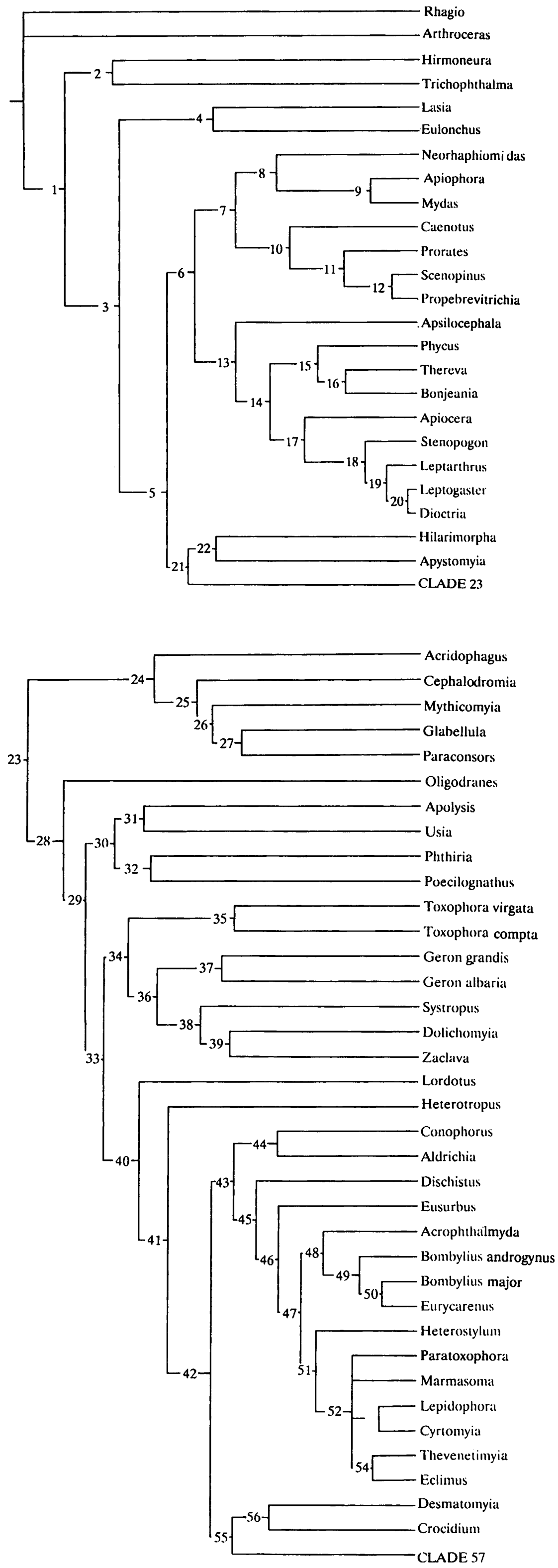

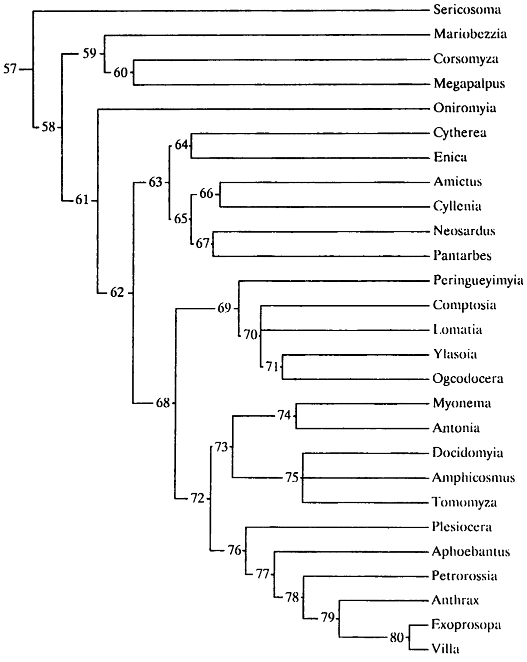

Fig. 7. Results of Hennig86 analysis of 174 characters for 87 species. A total of eight most parsimonious trees were found (length = 716, consistency index = 0.25, retention index = 0.71). The strict consensus is shown here. Node numbers are referred to in the text.

the assistance of Nic Monzu, who supported my leave of absence from the Western Australian Department of Agriculture while this work was underway.

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CLADISTIC RESULTS

Analysis with Hennig86 and PAUP produced eight most parsimonious trees with a length of 716 steps, consistency index (Kluge and Farris, 1969) of 0.25, and a retention index (Farris, 1989) of 0.71. The consensus of these trees is shown in figure 7, and clade numbers in figure 7 correspond to clade numbers in figures 509 and 510. The eight most parsimonious trees differ in their resolution of the Eclimini (clade 52) and Tomomyzinae (clade 75), as can be seen by the polytomies in these clades. A polytomy also exists in the Lomatiinae in the consensus tree (clade 70), however this was found in each most parsimonious tree and is the result of a lack of characters to support resolution, rather than conflict among characters. The polychotomies occur among branch tips, and the main stem of the cladogram is resolved. The two alternative resolutions of clade 52 are shown in figures 511–512, with characters mapped onto the cladogram under ACCTRAN optimization (Farris, 1970; Swofford and Maddison, 1987). The two alternative resolutions of clade 75 are shown in figures 513–514, with characters mapped onto the cladogram under ACCTRAN optimization.

Complete node diagnoses output from Clados and individual character fits output from Hennig86 can be found in Appendices 5 and 6.

The consistency index is a measure of homoplasy in cladistic data, and its value is reduced as the number of homoplastic, or extra, steps increases. It is negatively correlated with the number of taxa in an analysis

(Sanderson and Donoghue, 1989). As taxa are added to a phylogenetic data matrix, it is likely that the number of homoplastic character state changes required to explain that additional data on a cladogram will increase (Farris, 1990). The number of taxa used in this analysis (87) is high in comparison to other cladistic analyses (see Sanderson and Donoghue, 1989, for a survey), and it is not surprising that the consistency index should be relatively low in comparison to other cladistic analyses using fewer taxa. Klassen et al. (1991) calculated a mean consistency index of just 0.072 for 30 randomly generated data matrices of 49 taxa and 124 characters. Thus the mean consistency index for randomly generated matrices of 87 taxa and 154 characters is likely to be much lower than 0.25. The retention index for this matrix of 0.71 is relatively high, indicating that a large proportion of similarity present in the data matrix is retained as homologies on the cladogram.

CHARACTER ANALYSIS

Here I include a list of all characters scored for the cladistic analysis. This study is based largely on adult characters (characters 1–147), and the remaining characters 148–154 are from larvae. The larval characters are included so that all evidence relevant to this cladistic problem is used in finding a solution (Kluge, 1989). Larval characters are taken from the literature and comprise those used by Woodley (1989) and additional data on the larvae of *Heterotropus* from Yeates and Irwin (1992). A useful goal for future studies is to examine the larvae of asiloids in more detail in order to furnish additional characters. For each character system, I discuss previous authors' interpretations and use of the character states where appropriate. For each character, I discuss the plesiomorphic state and the definition and distribution of the apomorphic state(s) I have recognized. The data matrix derived from this character analysis is given in Appendix 4.

The larval characters are scored as they occur in each genus coded here; if the larvae of an included genus are not known the character is scored as such (?). Inappropriate character states are scored with a dash (-).

Character distributions are reported here in relation to the cladogram in figure 7, and these may be described in terms of clade numbers on that cladogram, or in terms of the tribes and subfamilies recognized in the classification derived here.

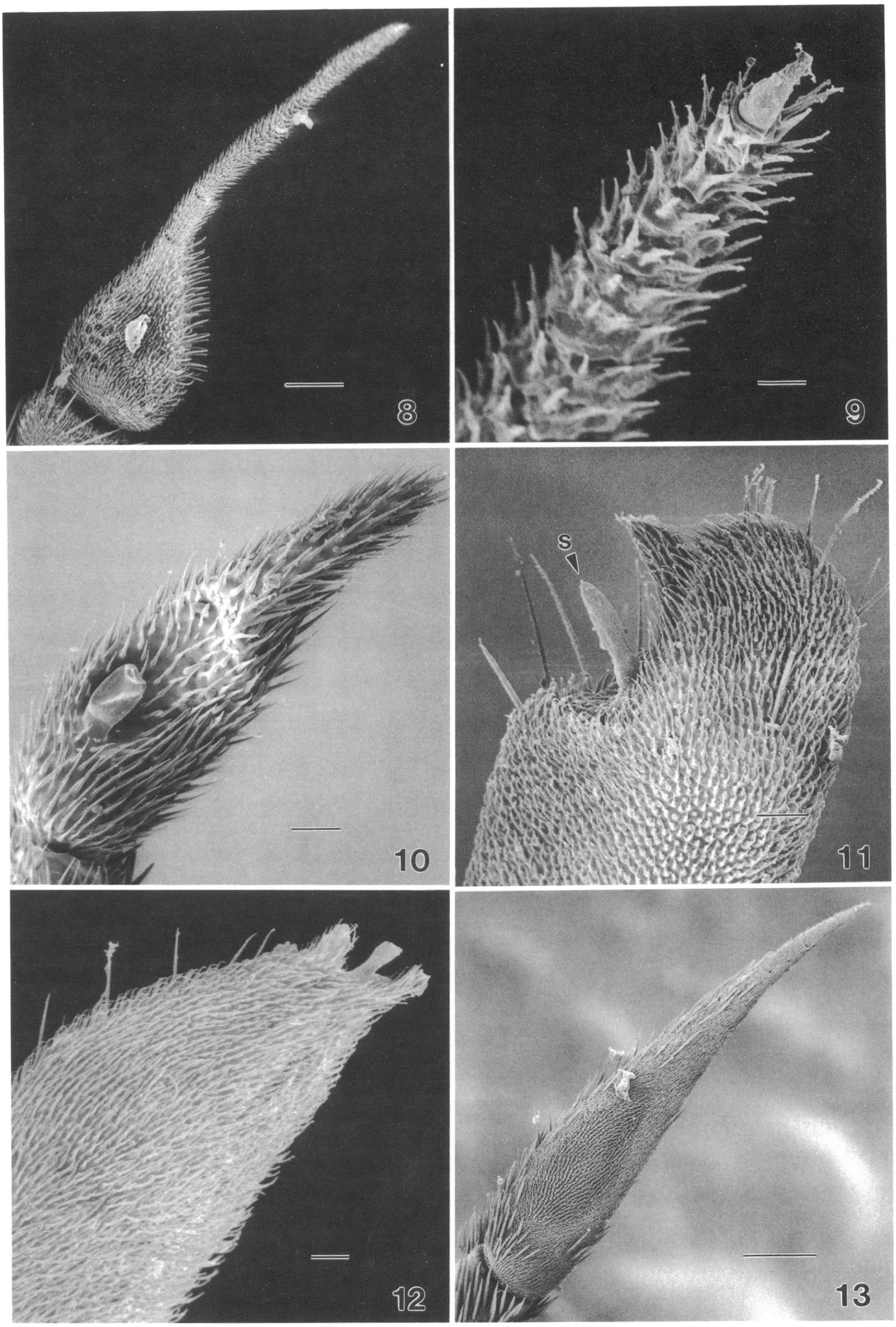
HEAD

1. Dimensions of the scape. The scape of most asiloids is approximately cylindrical and 1–2 times as long as wide (figs. 30, 71, 120, 127, 137, 139, 141). The apomorphic state of this character occurs in a few Bombyliidae such as *Toxophora*, *Systropus*, and a number of genera of the Eclimini where the scape becomes very elongate and greater than six times longer than wide (figs. 24, 36).

2. Shape of the scape. *Conophorus* and *Aldrichia* have an exceptionally broad and fat scape (figs. 25, 163) which was coded as the apomorphic state. This feature was used by Becker (1913) in his diagnosis of the Conophorinae. *Oniromyia* (fig. 183) and *Xenoprosopa* Hesse have a bulge on the ventral surface of the scape which was not considered homologous because of its different shape. This ventral bulge may indicate a relationship between *Oniromyia* and *Xenoprosopa* (Evenhuis personal commun., 1991).

3. Dimensions of the pedicel. The pedicel of most asiloids is shaped similarly to the scape: cylindrical and 1–2 times as long as wide (figs. 23, 30, 71, 120, 127, 129). In three genera of Bombyliidae (*Lepidophora*, *Systropus* and *Toxophora*) the pedicel is extremely elongate—often more than five times longer than wide, and this was considered apomorphic. While most *Systropus* species have very elongate pedicels, that of *S. bicoloripennis* Hesse is only twice as long as wide.

4. Shape of the pedicel. Most asiloids have a pedicel with a simple rounded apical margin (e.g., fig. 171). Becker (1913) first used the presence of a small dorsal, apical spine on the pedicel to characterize the Mariobezziinae and it was coded as the advanced state for *Mariobezzia*, *Corsomyza* and *Megapalpus* (figs. 173, 175, 177). Bowden (1975) considered that the Mariobezzini (as Corsomyzini) usually have the advanced state,



Figs. 8–13. Scanning electron micrographs of asiloid antennae: **8**, Apsilocephalidae, *Apsilocephala* sp., entire flagellum, scale 50 μm; **9**, *Apsilocephala* sp., tip of flagellum, scale 5 μm; **10**, Bombyliidae, *Mythicomyia illustris*, scale 10 μm; **11**, Bombyliidae, *Apolysis mus*, s = style, scale 20 μm; **12**, Bombyliidae, *Poecilognathus sulphurea*, scale 20 μm; **13**, Bombyliidae, *Toxophora virgata*, scale 100 μm.

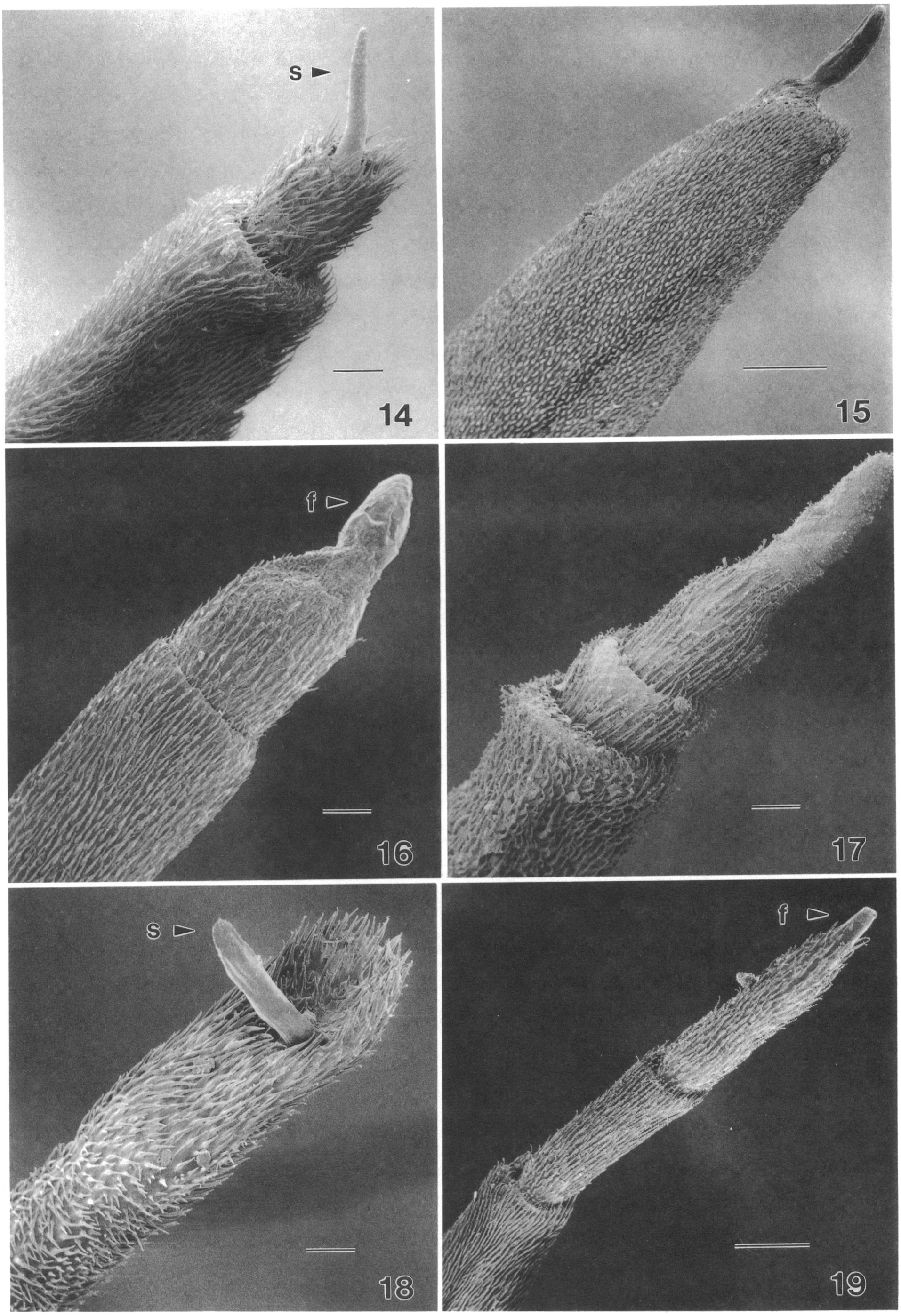
however it is absent in *Hyperusia* Bezzi and variable in *Zyxmyia* Bowden. *Dischistus*, *Acrophthalmyda*, and *Ylasoia* have a similar feature (fig. 165), gained independently.

My conception of the subdivisions of the antennal flagellum differs slightly from that of previous authors. The flagellum of many asiloids has a distinct, terminal or subterminal, small, smooth, hyaline, apically acute spine which is here termed the style (figs. 10–12, 14, 18, see char. 7). This is a more restrictive definition of the term than that of McAlpine (1981), who refers to the antennal stylus as a reduced, rigid, terminal or subterminal division. Examination of McAlpine's figures (e.g., 2.23, 2.30, 2.33), shows that his conception of the stylus was simply the reduced terminal flagellomere(s) that may bear vestiture. The style, as here defined, is not considered a flagellomere of the flagellum but an appendage of it, and its presence/absence is treated as a separate character. For example, the flagella of *Apsilocephala, Mythicomyia, Apolysis*, *Poecilognathus*, *Eusurbus*, *Enica*, and *Desmatomyia,* (figs. 9–12, 15, 18, 22) have apical or subapical styli, but the flagella of *Toxophora* and *Geron* lack them (fig. 13). Subapical flagellar styli are simple to distinguish; however, in some cases the distinction between style and terminal flagellomere is difficult to make because the terminal flagellomere is slender and vestiture is absent at the very tip (for example *Heterostylum, Bombylius*, and *Marmasoma*, figs. 16, 17, 19). In these cases I consider the style present only if the smooth apical portion is clearly articulated with the more proximal portion.

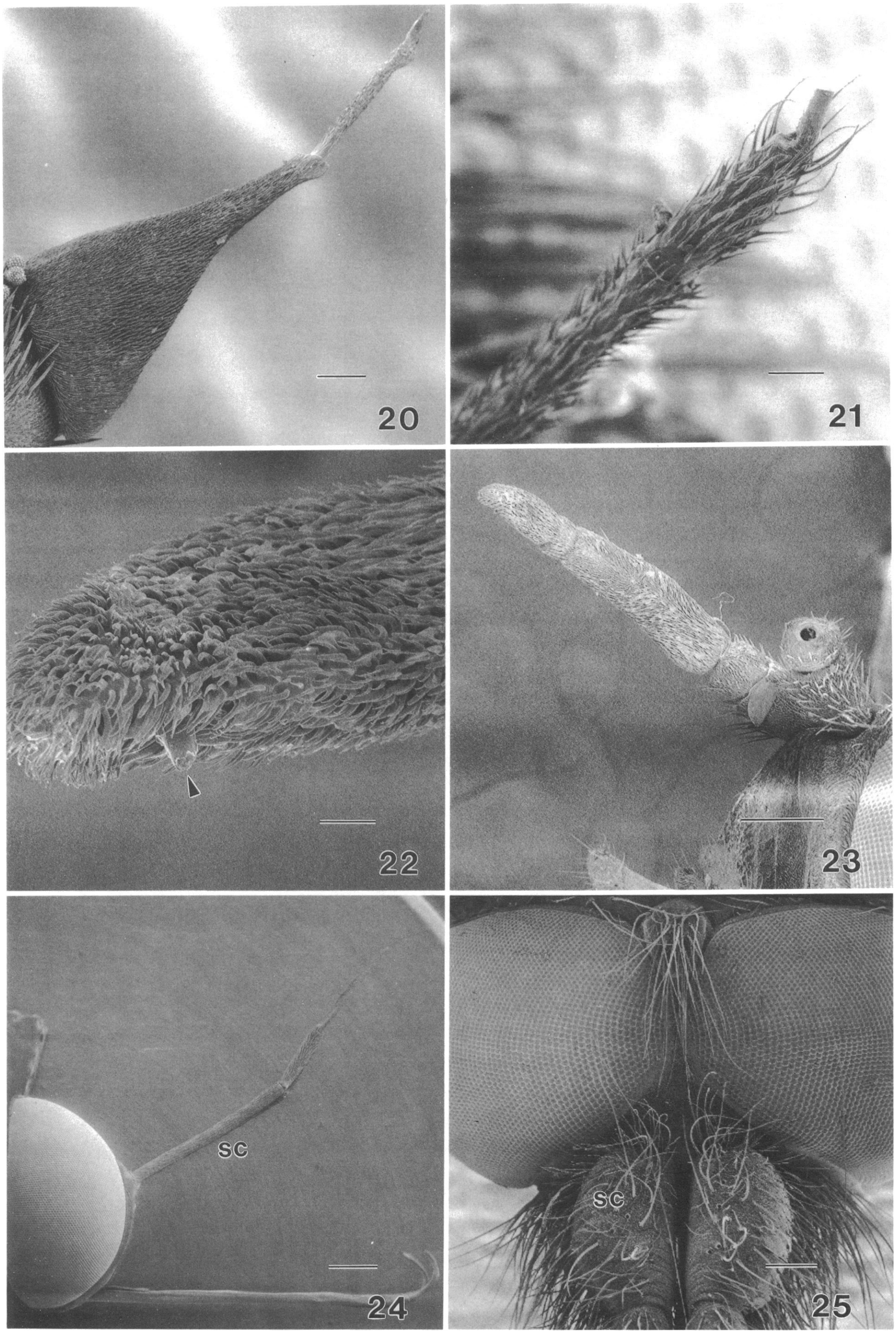
5. Number of flagellomeres comprising the antennal flagellum. A reduction in the number of flagellomeres comprising the antennal flagellum is a trend throughout the Diptera. The presence of four or fewer flagellomeres on the antennal flagellum is considered an apomorphy of the Muscomorpha (Woodley, 1989), and this state was considered primitive here. The only Muscomorpha examined in this study with 4 antennal flagellomeres were the Nemestrinidae. All asiloids have three or fewer flagellomeres on the antennal flagellum, and it appears that reduction to two flagellomeres has occurred in several families independently. Scenopinids and acrocerids have one antennal flagellomere. The presence of 3 antennal flagellomeres was coded 1, 2 flagellomeres coded 2 and a one flagellomere coded 3. This character goes through many convergent changes in the Asiloidea and was analyzed in nonadditive form. Within the Bombyliidae there are many examples with three flagellomeres such as species of *Desmatomyia*, *Bombylius*, *Marmasoma*, *Eurycarenus*, *Antonia*, and *Aphoebantus*. A reduction to two flagellomeres was found in many others; for example the Mythicomyiinae, *Apolysis*, *Conophorus*, *Cyllenia*, *Anthrax*. A single flagellomere was found in the Lomatiinae, Tomomyzinae, *Mariobezzia*, *Paratoxophora*, *Lordotus*, *Toxophora*, *Geron*, and *Systropus*, among others.

6. Shape of the antennal flagellum. The flagellum of asiloids is usually rounded in cross-section and is either an elongate-oval shape or tapers toward the apex. Occasionally the flagellum is very narrow and aristate at the apex, e.g., in *Apsilocephala* (figs. 8–9). *Systropus* has a laterally compressed flagellum (fig. 24). The Usiinae have distinct sulci on the flagellum (Evenhuis, 1990); Phthiriini have a terminal sulcus (fig. 12) (coded 1) and and Usiini have a subterminal sulcus (fig. 11) (coded 2). The terminal sulcus of the Phthiriini is formed by dorsal and ventral lobes of the flagellum. The ventral prong is often largest (e.g., in *Acreotrichus*), however, sometimes the dorsal prong is largest (in most *Phthiria*). The sulci of Usiinae most often contain a style (sensillum or arista of Evenhuis, 1990, see character 7). In *Apolysis* a style and the second flagellomere arise from the sulcus. Because the antennal style is primitively apical (character 7), I coded the apical sulcus as plesiomorphic relative to the subapical fulcus.

7. Style of antennal flagellum. The flagellar style was defined above as a small, smooth, hyaline, apically acute spine (see char. 5), being an appendage of the flagellum rather than the reduced terminal flagellomere. In the rhagionids, nemestrinids, and acrocerids a style is absent, and this was considered the primitive condition. A style is present in many asiloids, and its occurrence has undergone much homoplasy. In some asiloids such as the Scenopinidae the style is terminal and was coded 1; in others, such as the mythicomyiines *Mythicomyia* and *Paraconsors*, Usiini, and *Desmatomyia* it is subterminal



Figs. 14–19. Scanning electron micrographs of bombyliid antennae: **14**, *Conophorus fenestratus*, s = style, scale = 20 μm; **15**, *Eusurbus crassilabris*, scale 50 μm; **16**, *Heterostylum robustum*, f = terminal flagellomere, scale 20 μm; **17**, *Bombylius major*, scale 20 μm; **18**, *Enica longirostris*, s = style, scale 20 μm; **19**, *Marmasoma sumptuosum*, f = terminal flagellomere, scale 50 μm.



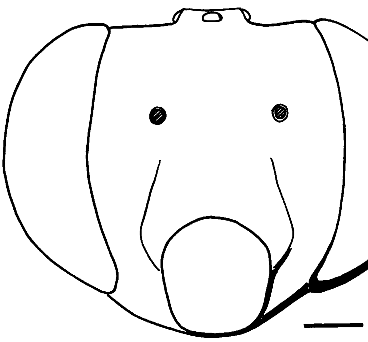
Figs. 20–25. Scanning electron micrographs of bombyliid antennae and heads: **20**, *Exoprosopa caliptera*, scale 50 μm; **21**, *Anthrax analis*, scale 20 μm; **22**, *Desmatomyia anomala*, tip of flagellum, arrow = style, scale 20 μm; **23**, *Desmatomyia anomala*, entire antenna, scale 200 μm; **24**, *Systropus macer*, entire head, sc = scape, scale 500 μm; **25**, *Conophorus fenestratus*, sc = scape, scale 200 μm.

and coded 2. The character was analyzed additively with a transformation from an apical to subapical antennal style.

8. Vestiture at tip of flagellum. In the plesiomorphic state the flagellum is clothed entirely in microtrichia. Some Phthiriini (e.g., *Acreotrichus*) have long hairs on the dorsal margin of the flagellum (Hull, 1973; Evenhuis, 1990). A conspicuous apomorphy of the tribe Anthracini (except *Walkeromyia* Paramonov) is the presence of an apical circlet of hairs on the flagellum (Becker, 1913) (fig. 21).

9. Position of the antennal bases. Most asiloids have the antennal sockets close together, within one or two diameters of each other (figs. 25, 27, 30, 31). *Cytherea*, *Sericosoma*, and *Pantarbes* coded here have antennal bases widely separated, greater than four times the diameter of the antennal socket apart (fig. 26) and were coded 1. Becker (1913) first used this feature in his characterization of the Cythereinae, which corresponds to the Cythereini of more recent authors such as Hull (1973) and Bowden (1980). Hull (1973) noted that *Pantarbes willistoni* Osten Sacken had antennae but little separated. It is unknown whether this feature is apomorphic or plesiomorphic in *P. willistoni*. According to the topology of the cladogram (fig. 7) the wide antennal bases have evolved independently in these three genera.

10. Size and distribution of the eye facets in the male. The compound eyes of many male Diptera have been modified so that the facets on the dorsal region of the eye are much larger than those on the ventral part. Often there is a distinct line of division between eye facets of different size (fig. 32). Although divided facets are found in some Nematocera and Tabanomorpha, simple male eyes were considered the plesiomorphic state here. The division of facets is often associated with the holoptic condition. Downes (1969) hypothesized that the enlarged upper facets were modified for female capture in flight before mating. I found the line of division between the facets to be of variable distinction. In the Scenopinidae, *Heterotropus, Hilarimorpha*, and *Apystomyia* it was most distinct; however, among other Bombyliidae the division was less obvious, especially toward the anterior region of the eye.



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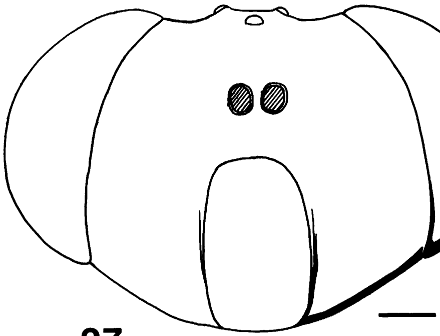

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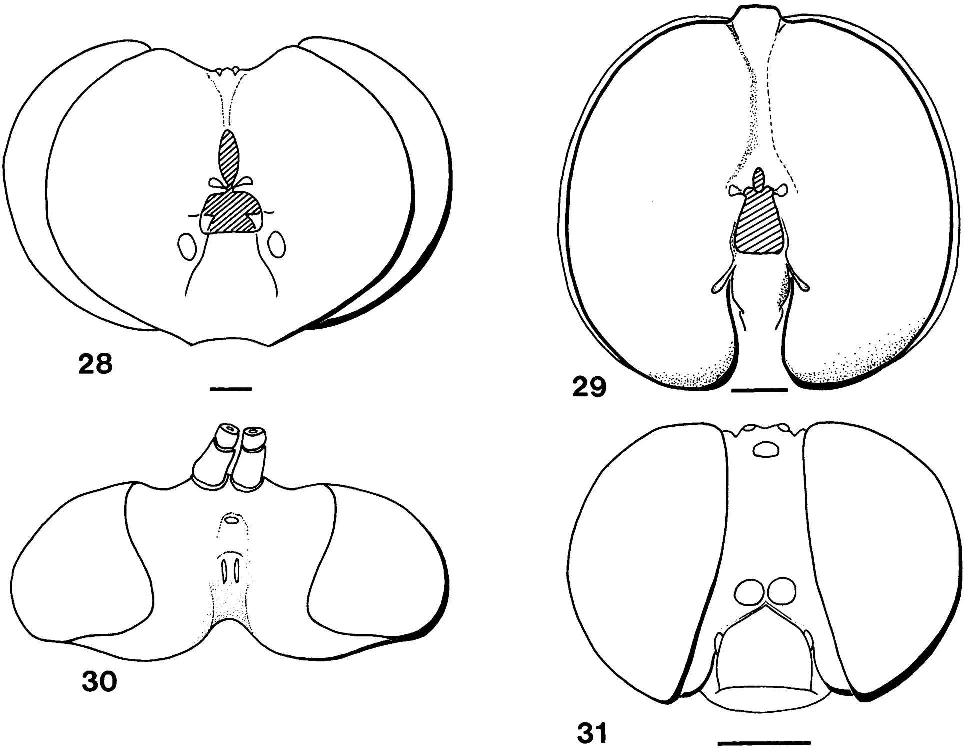
Figs. 26–27. Anterior views of Bombyliidae heads with vestiture not shown and appendages removed. Hatched areas are antennal insertions. **26**, *Cytherea obscura*, **27**, *Corsomyza brevicornis*. Scales 0.5 mm.

The eye facets closest to the frons are often enlarged in comparison to those on the posterior margin of the eye (e.g. *Leptogaster, Systropus*, *Toxophora*, fig. 35). This condition was not considered homologous with the advanced state coded here.

None of the species with indented hind eye margins (character 45) have the eyes divided into large and small facets.

11. Male eye separation. Most Diptera are sexually dimorphic in frons width, males having eyes closer together than females. In some cases the male eyes are so very closely approximated (or merge) that they are termed holoptic. The plesimorphic condition for asiloids was found to be male eyes very close (less than the width of the ocellar tubercle), with the dorsal part of the frons being correspondingly narrow (figs. 38–39). The com-



Figs. 28–31. Heads with vestiture not shown. Hatched areas are the occipital foramen. **28**, Mydidae, *Mydas clavatus*, posterior view, scale 0.5 mm; **29**, Nemestrinidae, *Hirmoneura exotica*, posterior view, scale 1.0 mm; **30**, Mydidae, *Mydas clavatus*, dorsal view, scale as for figure 28; **31**, Apioceridae, *Apiocera aldrichi*, scale 1.0 mm.

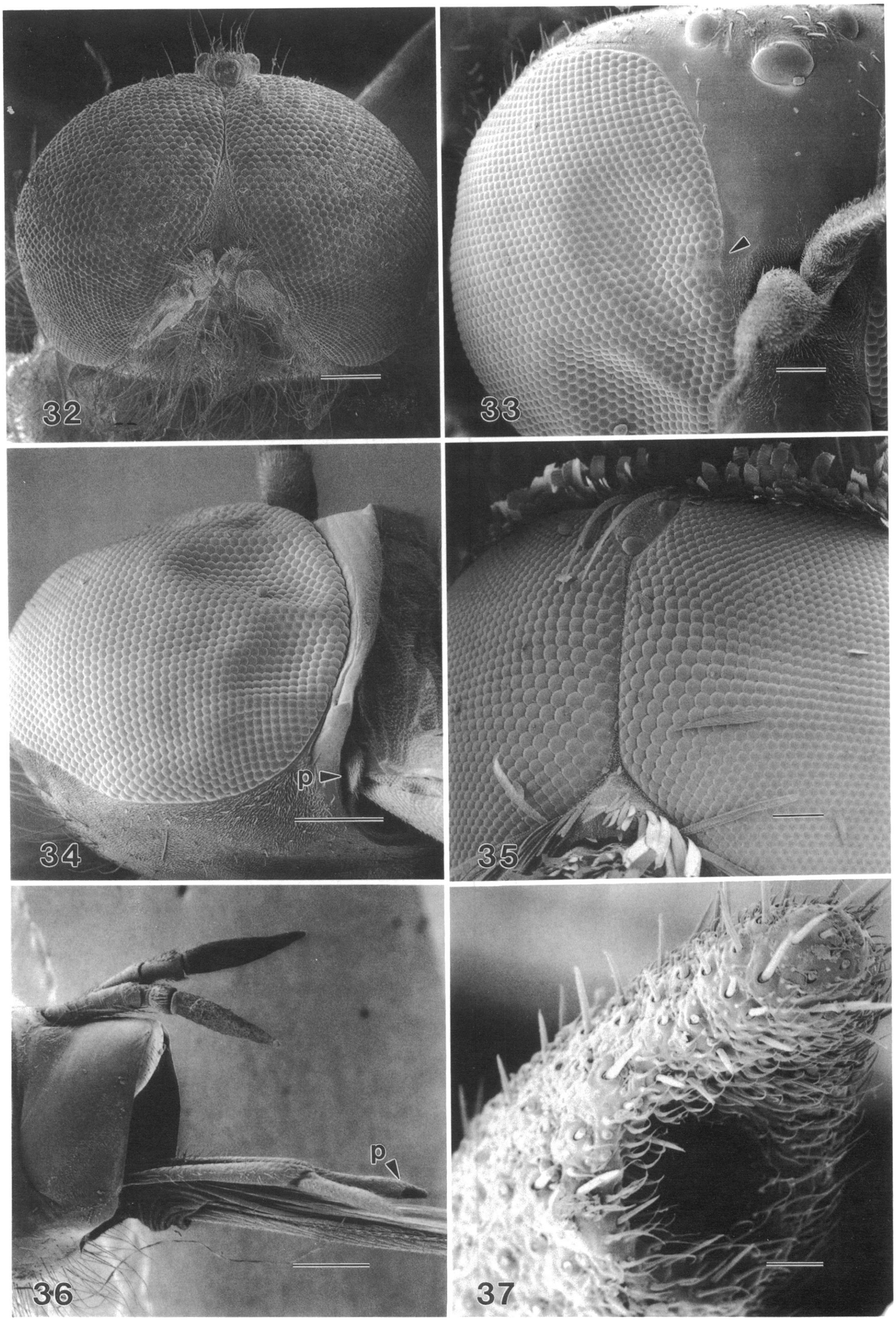
pound eyes of Bombyliidae are always separated by at least a thin strip of cuticle. In some groups, such as the Mydidae (fig. 30), Apioceridae (fig. 31), Asilidae, Mythicomyiinae (except *Mythicomyia*), *Usia*, *Oniromyia*, and many Cythereinae, Tomomyzinae, and Anthracinae the eyes of the male are relatively wide apart and this was coded as the advanced state. Becker (1913) considered that well-separated eyes characterized the Cythereinae and Tomomyzinae.

12. Position of the ocellar tubercle. In the plesiomorphic state the ocellar tubercle is situated posterior to the compound eyes or level with their posterior margin, when viewed from above. In the advanced state the ocellar tubercle is in a more anterior position between the compound eyes, at least the width of the ocellar triangle anterior to the posterior margin of the compound eyes (fig. 30). This state was only found in the Mydidae, *Leptogaster*, *Exoprosopa*, the Tomomyzinae, and Antoniinae. This character in *Docidomyia* was discussed by Yeates (1989) .

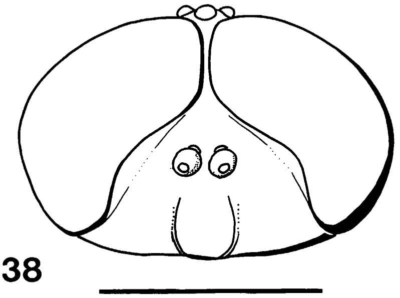
13. Shape of the lateral ocelli. All three ocelli are normally rounded in outline, however in the Mydidae the lateral ocelli become elongated along the anterior-posterior axis of the body (fig. 30).

Bezzi (1921) considered there was no ocelli in *Oniromyia pachyceratus* and Hull (1973) reported that *O. pachyceratus* lacked anterior ocelli. Hesse (1938) reported that the lateral ocelli were present in *O. pachyceratus* but the anterior ocelli were reduced and variable, sometimes being absent. Greathead (1972) illustrated the anterior ocellus of *O. caffrariae* Hesse, and the *O. pachyceratus* examined here had lateral ocelli present and the anterior ocelli present but reduced.

14. Shape of the inner margin of the eye. The inner margin of the eye is usually shaped in a smooth curve, and this was considered the plesiomorphic state. In some ingroup taxa



Figs. 32–37. Scanning electron micrographs of asiloid heads: **32**, Scenopinidae, *Caenotus hospes* male head, scale 200 μm; **33**, Bombyliidae, *Mythicomyia illustris*, anterior view of head, arrow = eye indentation, scale 50 μm; **34**, *Mythicomyia illustris*, ventral view of head, p = palp, scale 100 μm; **35**, Bombyliidae, *Toxophora virgata*, dorsal view of eyes, scale 100 μm; **36**, Bombyliidae, *Thevenetimyia californica*, anterior region of head, p = palp, scale 500 μm; **37**, Bombyliidae, *Thevenetimyia californica*, tip of palp showing entrance to palp pit, scale 20 μm.



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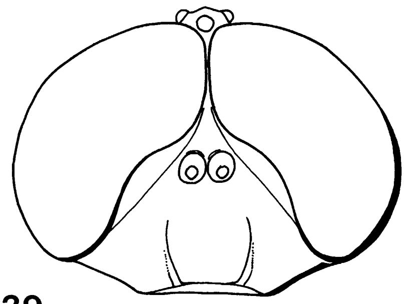

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Figs. 38–39. Anterior view of male heads with vestiture not shown: **38**, *Apystomyia elinguis*; **39**, Hilarimorphidae, *Hilarimorpha mentata*. Scale 0.5 mm.

(*Eulonchus*, *Prorates*, and the Mythicomyiinae except *Acridophagus*) there was a sharp indentation at or about the level of the antennae (figs. 33, 121) and this was coded 1. Female *Desmatomyia*, but not males, have a shallow indentation at the level of the antennae, however this was not considered apomorphic. The occurrence of this indentation is not dependent on the holoptic condition of the male eyes because it occurs in Mythicomyiinae with well-separated eyes.

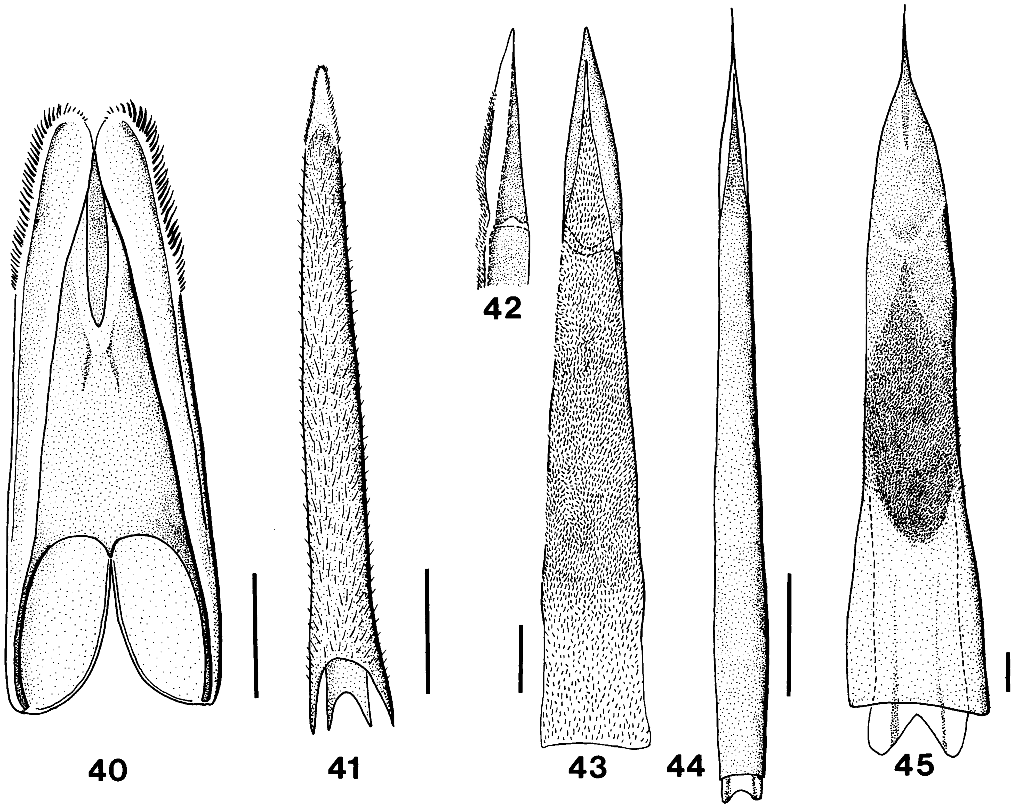
15. Shape of the inner margin of the eye. *Apystomyia* and *Hilarimorpha* have a broader indentation than is found in the apomorphic state of character 14, which extends well below the level of the antennae (figs. 38–39); this was coded as a separate apomorphy.

16. Shape of anterior surface of head. The outgroup, and many asiloids except Bombyliidae, when examined in lateral view had the face flat, not bulging beyond the level of the eyes (figs. 30, 71, 123, 125, 127, 129, 143, 151), and were coded 0. Many Bombyliidae have a tumid face, and I divided this condition into two advanced states, analyzed nonadditively. In the Usiinae, coded 1, the face and frons are tumid and extend beyond the level of the eye margins. The bases of the antennae, forming the dividing line between face and frons are at the apex of the tumidity (figs. 139, 141, 195, 197). In most Bombyliinae and Tomophthalmae the face is also tumid, but the greatest extension is below the level of the antennae, entirely on the face (figs. 155, 161, 163, 165, 167, 169, 171, 173, 175, 177, 179, 181, 185, 187, 189, 191, 193), and these were coded 2. In many Bombyliinae the facial tumidity is smoothly rounded, whereas in many Anthracinae and the Tomomyzinae the face is conically produced in lateral view (figs. 199, 201, 203, 205, 219–220). *Docidomyia*, the Lomatiinae, and *Oniromyia* are conspicuous among Tomophthalmae in having the plesiomorphic condition of this character (figs. 183, 195, 197).

17. Vestiture of face. Most asiloids have rather simple facial vestiture, with decumbent or erect hairs and scales (figs. 23, 32, 219–221). The Asilidae are well known for a group of erect hairs and bristles on the face known as the mystax. This character was found to be apomorphic for the Asilidae by Woodley (1989).

18. Dorsal margin of the clypeus. In most Tabanomorpha and almost all Asiloidea the frontoclypeal suture is situated well below the level of the antennal bases, leaving room for a portion of the face above the clypeus. This was considered the plesiomorphic state notwithstanding that in bloodsucking forms such as Tabanidae the clypeus is bulbous and enlarged, almost obliterating the face. Occasionally in the Asiloidea the frontoclypeal suture extends dorsally to the bases of the antennae, thus the face is divided into two narrow strips on each side of the clypeus. This advanced state was found in *Neorhaphiomidas*, *Apiocera* (fig. 31), and among the Bombyliidae in the Usiinae, *Oniromyia*, *Myonema*, *Docidomyia*, and the Lomatiinae. Yeates (1989) discussed the presence of this character in the Lomatiinae, *Myonema* and *Docidomyia*, and Evenhuis (1990) noted its presence in the Usiinae.

19. Sclerotization of the base of the labrum. The labrum, forming the dorsal wall of the proboscis, is usually well sclerotized dorsally



Figs. 40–45. Dorsal and a lateral view of bombyliid labrums: **40**, *Mythicomyia illustris*; **41**, *Cephalodromia fusca*; **42**, *Oligodranes* sp., tip of labrum, lateral view; **43**, *Oligodranes* sp.; **44**, *Geron grandis*; **45**, *Lomatia belzebul*. Scales 0.1 mm.

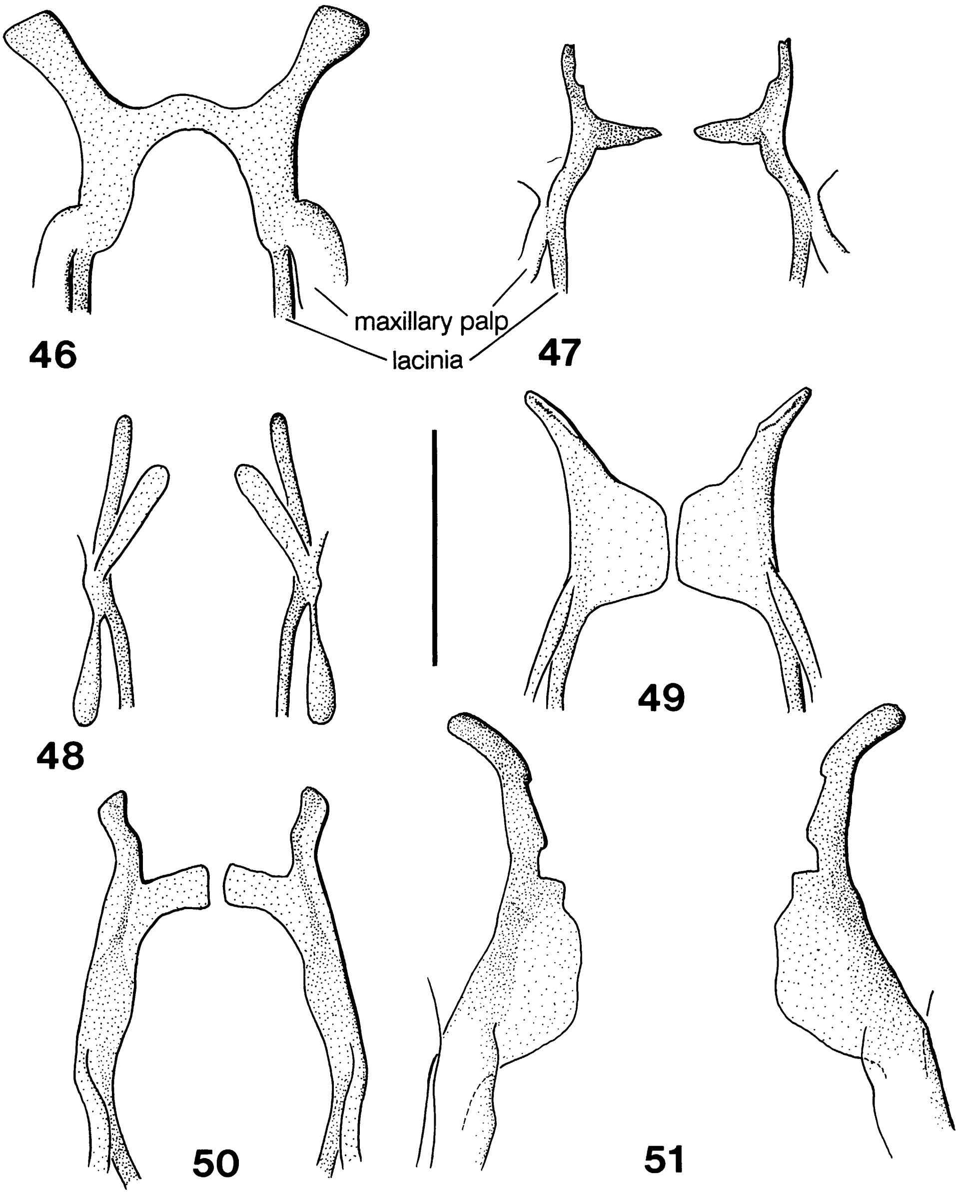
and ventrally (the epipharynx) from its apex to the clypeolabral suture. In the Mythicomyiinae and occasionally in other asiloids (*Apiocera*, *Hirmoneura*, and *Desmatomyia*) the dorsal surface of the labrum has a convex, semicircular, membranous area at its base (figs. 40, 71) which was coded 1.

20. Sclerotization of the base of the labrum. In many Bombyliidae the basal third of the labrum is membranous (figs. 43, 45). In contrast to the apomorphic state of character 18, the line delimiting sclerotized and membranous areas is poorly differentiated. This feature was found in the Cythereinae except *Amictus*, *Mariobezzia*, the Tomomyzinae, the Anthracinae, and the Lomatiinae except *Ylasoia*, and *Ogcodocera*. *Ylasoia* has a very short labrum, and although the base is membranous, the membranous area does not quite cover the basal third. The desclerotization of the labrum may be a modification to assist the retraction of the proboscis into the oral cavity. The hyoid sclerite could be distinguished in any representatives examined here.

21. Form of the apex of the labrum. The apex of the labrum is usually smooth and lanceolate (fig. 44), however in the Mythicomyiinae small microtrichia are present on each side of the apex of the labium (figs. 40, 41). These microtrichia are presumably involved in sensory input during feeding.

22. Vestiture of the labrum. The dorsal surface of the labium most often has small hairs, however on its basal half the vestiture is modified into scales in *Oniromyia*. This feature of *Oniromyia* was noted by Hesse (1938) and Greathead (1972).

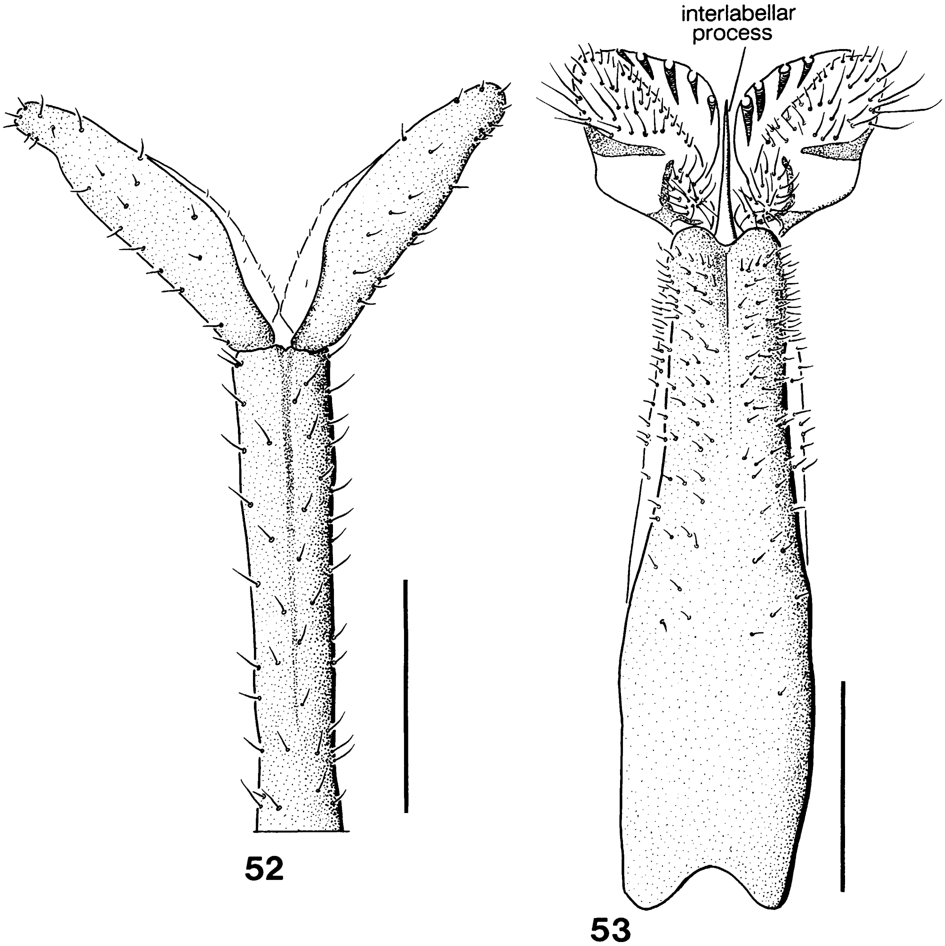
23. Length of the hypopharynx. Primitively the hypopharynx is slightly shorter than the labrum immediately above it. In Asilidae



Figs. 46–51. Base of bombyliid maxilla, ventral view with vestiture not shown; **46**, *Dischistus mystax*; **47**, *Toxophora virgata*; **48**, *Usia atrata*; **49**, *Crocidium karooanum*; **50**, *Amphicosmus cincturus*; **51**, *Exoprosopa caliptera*. Scale 0.5 mm.

the labrum is reduced and the hypopharynx is modified into a prey-stabbing apparatus approximately twice as long as the labrum. This state was coded 1. State 2 was only found in the Acroceridae examined which had short hypopharynxes, being less than one quarter of length of the labrum. A transformation series could not be constructed between the advanced states and this character was analyzed in nonadditive form.

I could not find the two-jointed hypopharynx in *Bombylius major* reported by Na-



Figs. 52–53. Labia of Bombyliidae; **52**, *Cephalodromia fusca*, scale 0.1 mm; **53**, *Conophorus fenestratus*, scale 0.5 mm.

gatomi and Soroida (1985). However, in this species the hypopharynx is noticeably constricted at the apex of the salivary duct.

24. Cardo of maxilla. The maxilla of asiloids consists of a small, basal cardo and a distal stipes represented by the maxillary palps and laciniae. The cardo is reduced to a small sclerotized area at the base of the laciniae and palps. Plesiomorphically the small sclerotized areas are well separated (figs. 48, 51) but in a few Bombyliidae they are united in the midline (fig. 46). This advanced state was found in *Geron*, *Dischistus*, *Bombylius*, *Lordotus, Eurycarenus*, and scattered representatives of the Tomophthalmae. Some Bombyliidae, such as *Toxophora*, *Crocidium*, and *Amphicosmus*, have broad sclerotized plates extending toward the midline but not meeting (figs. 47, 49, 50).

The prementum of the labium is an elongate sclerite, "u"-shaped in cross section, which forms the ventral wall of the proboscis. At its apex the prementum bears paired labella. The prementum of the rhagionids, nemestrinoids, and asiloids (except some Bombyliidae, discussed below) examined here is most often short with fleshy labella containing 10–20 pseudotracheae each. This was considered plesiomorphic. The Acroceridae examined have very long proboscides with elongate labella containing up to five pseudotracheae each.

25. Form of labella. The labella of asilids are reduced and functionally fused to the pre-

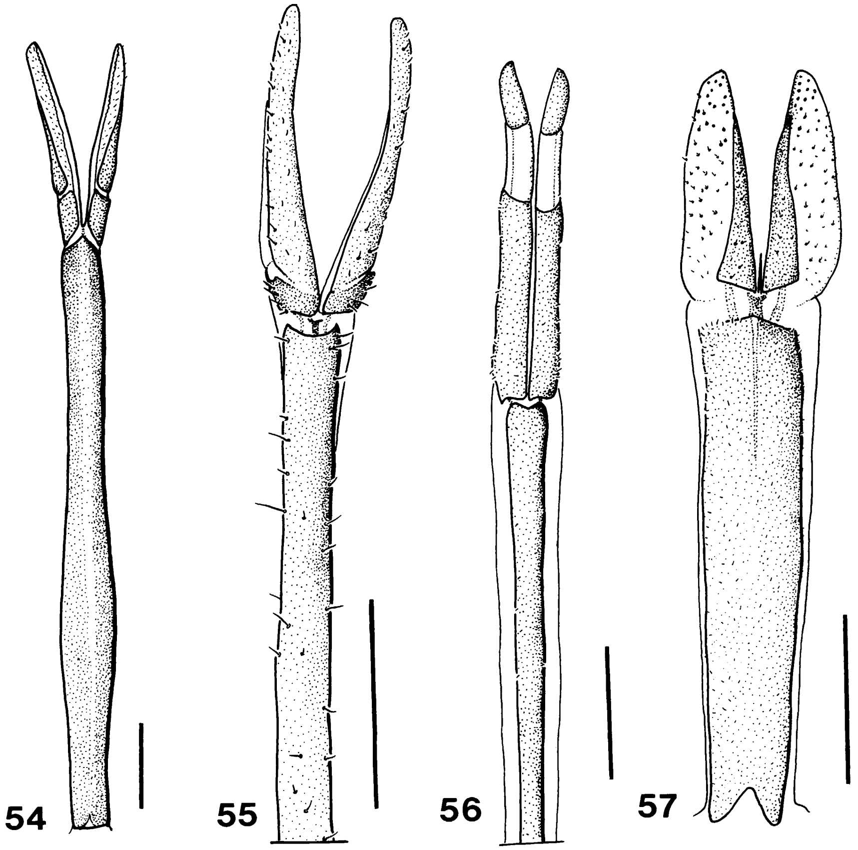
mentum, however a line of desclerotization is still evident in all the species examined here. Woodley (1989) used this advanced state as a synapomorphy for the Asilidae.

Among Bombyliidae the length of the proboscis varies enormously. The proboscides (including the labella) have become elongate in the majority of the Geronini, Systropodini, Bombyliinae, Usiinae, and Eclimini. This is presumably an adaptation to feeding at flowers while hovering (Zaytsev, 1982). Among the subfamilies of Anthracinae, Tomomyzinae (fig. 57), and Lomatiinae, the majority of species have short proboscides, which fit inside the oral cavity when at rest, and fleshy labella.

There are many exceptions to these generalizations, such as the lomatiine *Comptosia wilkinsi* Edwards species group (Yeates, 1991) and the anthracine genus *Stonyx* Osten Sacken which have very long proboscides and elongate labella, and *Conophorus* of the Bombyliinae which have short proboscides and fleshy labella (fig. 53). However, these general tendencies have formed evidence used in the classifications of previous authors such as Becker (1913) and Hull (1973). A few Bombyliidae not coded here have the mouthparts reduced and nonfunctional (e.g., *Xenoprosopa* Hesse and the Villoestrini).

Zaytsev (1982, 1984) examined the microstructure of the labellae of Diptera, concentrating his taxon sampling in the Bombyliidae and focusing on the morphology of the margins of the pseudotracheae, which he called the "closing apparatus." After detailed examination with an electron microscope, Zaytsev (1982) divided the closing apparatus of the Bombyliidae into two categories, the plesiomorphic dentate and apomorphic spinose forms. He found that the spinose type was more common in the Bombyliidae overall, and was particularly prevalent in those species with long proboscides (length 2.4–4.8 times head length). Zaytsev (1982) also found the spinose form of closing apparatus in Tabanidae and Syrphidae. He considered the spinose closing apparatus an adaptation for flower feeding, the interdigitating spines providing a more efficient food filter. Zaytsev (1984) also made a detailed examination of the labellae, concentrating on the arc-shaped sclerotized ridges which make up the pseudotracheal framework. He divided the ridges into plesiomorphic "serrate" and apomorphic "mortise and tenon" forms. Although not made explicit (or lost in translation), it appears that the serrate form corresponds to the dentate type of Zaytsev (1982) and the mortise and tenon form to the spinose type of Zaytsev (1982). I did not include the form of the pseudotracheal closing apparatus in the data analyzed here because I could not adequately score the states under a light microscope and was not able to examine all taxa under the electron microscope. However, I will discuss the distribution of the character states as listed in the table of Zaytsev (1982). Perusal of this list shows that the apomorphic spinose closing apparatus is distributed widely throughout the family. Zaytsev only observed the spinose closing apparatus in the Mythicomyiinae, Toxophorinae, Oligodraninae, Tomomyzinae, and Antoniinae. The other subfamilies contained a mixture of apomorphic and plesiomorphic states, except the Cythereinae and Lomatiinae which only have the plesiomorphic dentate closing apparatus. Thus the apomorphic spinose closing apparatus is found in the most plesiomorphic subfamilies, the only exception being the Phthiriini. Among more advanced subfamilies the spinose closing apparatus is distributed widely, and is probably a more useful cladistic character at genus rather than subfamily level.

I did not use the length of the proboscis or form of the labella as characters here because the states were difficult to define clearly and variability at the genus and tribal level was high. However, the labella of some Bombyliidae with functional mouthparts are highly modified and do deserve comment. The outer surface of fleshy labella usually have a small basal sclerotization well separated from an apical one (fig. 53); these may correspond to the two sclerites noted on the elongate labella of *Acridophagus*, *Cytherea* (fig. 54), and *Megapalpus* (fig. 55). I assume that these segments are secondary developments and not homologous with the two-segmented labella of primitive Nematocera. Those species with fleshy labella usually have 5–30 pseudotracheae on each, however the number of pseudotracheae is reduced in forms with elongate proboscides and elongate labellae. *Bombylius*

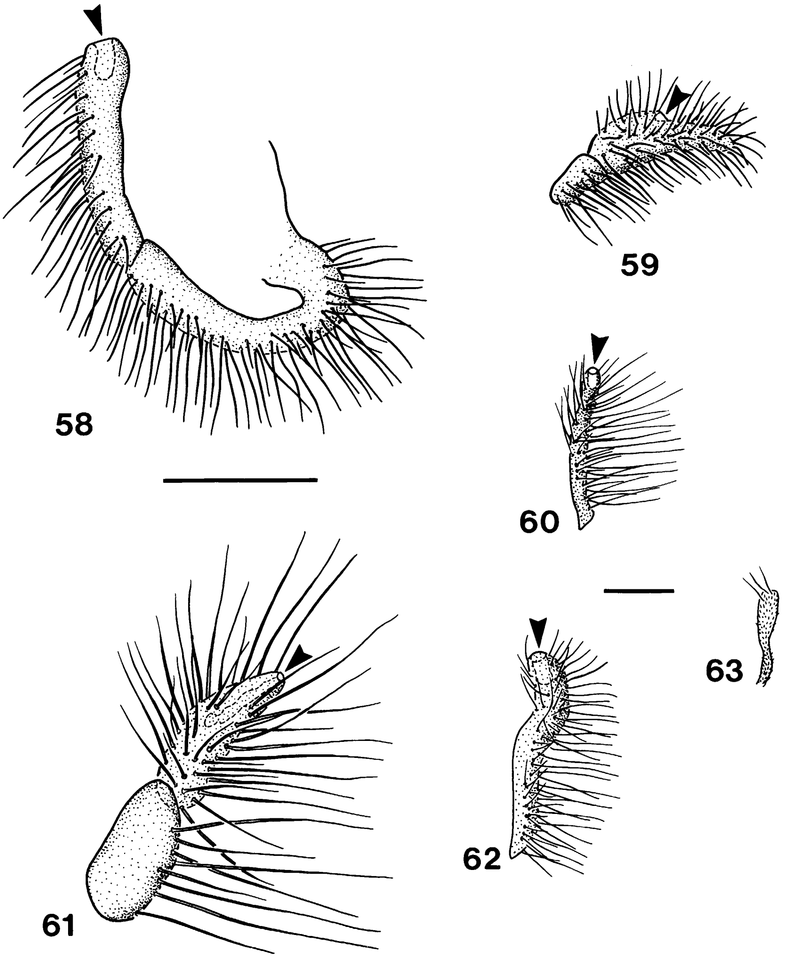


Figs. 54–57. Labia of Bombyliidae; **54**, *Cytherea obscura*; **55**, *Megapalpus capensis*; **56**, *Oniromyia pachycerata*; **57**, *Amphicosmus cincturus*. Scale lines 0.5 mm.

major has only three pseudotracheae on each labellum; *Cytherea* has two and *Geron, Heterostylum, Sericosoma,* and *Corsomyza* have only one. *Oniromyia* also has only one pseudotrachea, and the outer surface of each labellum has a sclerotized area at its base, followed by a median membranous area and a small sclerotized apex (fig. 56).

At the apex of the food canal an elongate spine extends into the region between the bases of the labellae. Nagatomi and Soroida (1985, p. 306) referred to this as the "mid-distal interlabellar process." I found the interlabellar process to be present in most Bombyliidae (fig. 53), however lost in all Mythicomyiinae (fig. 52) except *Acridophagus*. I found a variety of intermediate states in the reduction of this feature and was unable to use it as an apomorphy. The lomatiine *Bryodemina* Hull has a particularly large interlabellar process, variation of which may prove useful at generic or tribal level.

26. Number of palpal segments. Two palpal segments were found in the rhagionids and nemestrinids and in various asiloids (figs. 58, 59, 61). Thus it appears that the plesiomorphic number of palpal segments in the Asiloidea is two, with reduction to one (scored 1) occurring independently in a number of families. Among the Bombyliidae most had one segment (figs. 68, 70) but I found two-segmented palps in *Oligodranes* and *Desmatomyia*; in the bombyliines *Crocidium, Dischistus, Eusurbus,* and *Heterostylum*; and all the eclimines (figs. 64–66, 67, 69). Among the Tomophthalmae I found two segmented palps in *Cytherea, Cyllenia, Neosardus, Myonema,* and the anthracine *Aphoebantus. Lasia* (Acroceridae) and the Mythicomyiines (figs. 34, 71) have the palps reduced to small nubs

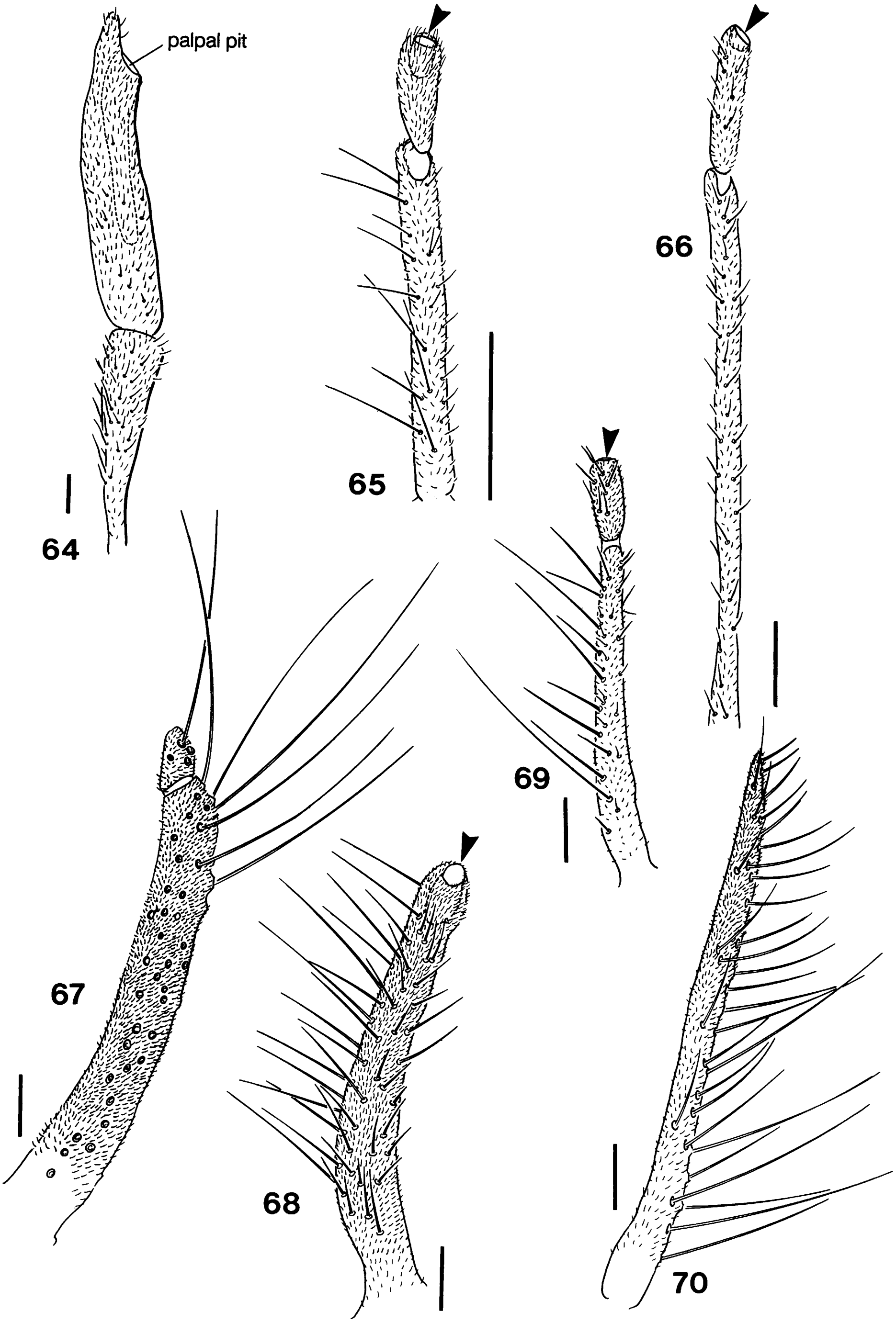


Figs. 58–63. Palps of various asiloids, arrows indicate opening of palpal pit; **58**, Nemestrinidae, *Hirmoneura exotica*, scale 0.5 mm; **59**, Rhagionidae, *Rhagio mystaceus*, scale same as figure 58; **60**, Therevidae, *Thereva fucata*, scale same as figure 58; **61**, Asilidae, *Stenopogon inquinatus*, scale same as figure 58; **62**, Scenopinidae, *Caenotus hospes*, scale 0.1 mm; **63**, *Apystomyia elinguis*, scale same as figure 62.

independently and were scored 2. Because it seems reasonable to assume a transformation series from two-segmented palps through one-segmented palps to palps absent, I analyzed this character in additive form.

27. Apex of terminal palpal segment. A small, deep pit (figs. 36–37, 58) was found in *Rhagio* (Rhagionidae), the nemestrinids, and many asiloids, and was considered plesiomorphic. In most species examined it occurred on segment 2 of the palp, and the subterminal entrance is especially prominent in the Eclimini (figs. 37, 64). In *Thereva, Caenotus, Prorates,* and many bombyliids such as *Amictus* and *Lomatia* however, it occurs at the apex of the single palpal segment (figs. 60, 62). I considered the loss of the palpal pit apomorphic, and this state occurred throughout the Bombyliidae, for example the palpal pit was lost from the Mythicomyiinae, Systropodini, *Mariobezzia, Comptosia, Myonema, Plesiocera,* and *Anthrax.*

A similar, presumably homologous, sensory pit is found in many Nematocera on palpal segment 3, and on the single palpal segment of some muscoid flies. Rowley and Cornford (1972), examining the sensory pit on the maxillary palp of *Culicoides*, found



Figs. 64–70. Palps of various Bombyliidae; arrows indicate opening of palpal pit: **64**, *Eclimus gracilis*; **65**, *Oligodranes* sp.; **66**, *Crocidium karooanum*; **67**, *Dischistus mystax*; **68**, *Lomatia belzebul*; **69**, *Paratoxophora cuthbertsoni*; **70**, *Megapalpus capensis*. Scales 0.1 mm.

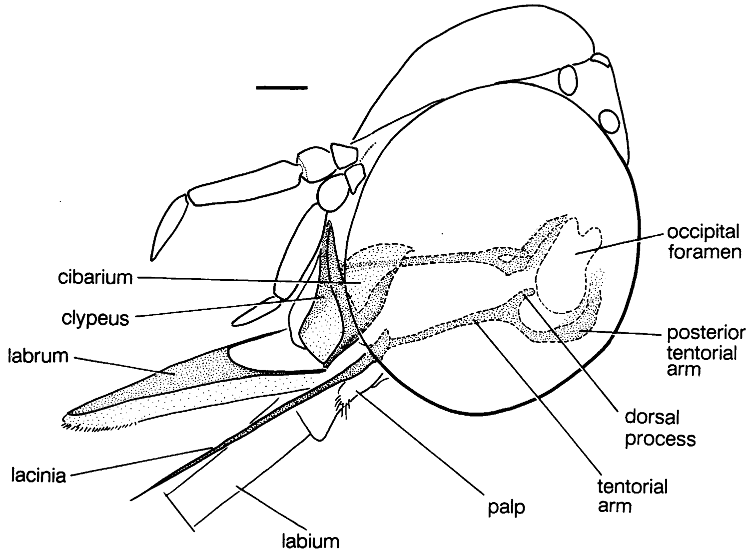


Fig. 71. Head of male bombyliid *Mythicomyia illustris* showing internal structures, hypopharynx hidden. Scale 0.1 mm.

that it contains olfactory and/or carbon dioxide receptors. The position of the pit varies in some nematocerous families, e.g., in Anisopodidae it is found on the first (in species with three-segmented palps) or second (in species with four-segmented palps) segment (Peterson, 1981a) and in Psychodidae it is always found on the penultimate segment, although there may be three to five palpal segments (Quate and Vockeroth, 1981).

If this sensory pit is homologous in the families of Diptera where it occurs, it provides a landmark to determine the homologies of the palpal segments. In most asiloid representatives examined here, it occurs on the second palpal segment. This probably corresponds to the third palpal segment of Nematocera because of the presence of the sensory pit. By inference, the first palpal segment of asiloids probably represents the second (or fused first and second) palpal segment(s) of Nematocera.

28. Apical segment of maxillary palp. When it is present, the terminal segment of the maxillary palp is small (figs. 65, 66–67, 69). In one of the rhagionids examined and all the eclimini (fig. 64) except *Paratoxophora* the apical palp segment is wide and elongate, and was coded the apomorphic state.

At the point where the food canal enters the head capsule there is a complicated sclerotized structure termed the fulcrum by McAlpine (1981) which is associated with the cibarial pump (fig. 71) and includes the clypeus. The fulcrum has two anterior dorsal arms which form the lateral margins of the clypeus and two dorsal posterior arms which surround the anterior portion of the pharynx. These anterior arms show some variation in the taxa examined here. They are reduced and form only the lateral margins of the clypeus and in others such as the Mythicomyiinae (fig. 71) the anterior arms are well developed and form thickened internal ridges which join dorsally. This variation was not coded here because I could not define and score discrete states.

The internal sclerotized parts of the fulcrum, excluding the anterior arms and clypeus, are termed the cibarium (McAlpine, 1981, his fig. 2.51). There are sensilla grouped in the anterior and posterior regions of the cibarium (figs. 72–75, 78, see Grimaldi, 1990, for their distribution in Drosophilidae). The sensilla in the anterior region of the cibarium are arranged in two lateral regions, and the group of two to six posterior sensillae are arranged into one median group (figs. 76, 89, 97), two groups on either side of the midline (figs. 73, 75), or in a row (fig. 72). Because of the presence of intermediate conditions (fig. 83) and the asymmetrical position of some of the posterior sensilla (figs. 91, 103) their distribution was not used as a character. They may well provide useful cladistic information at lower taxonomic levels, however.

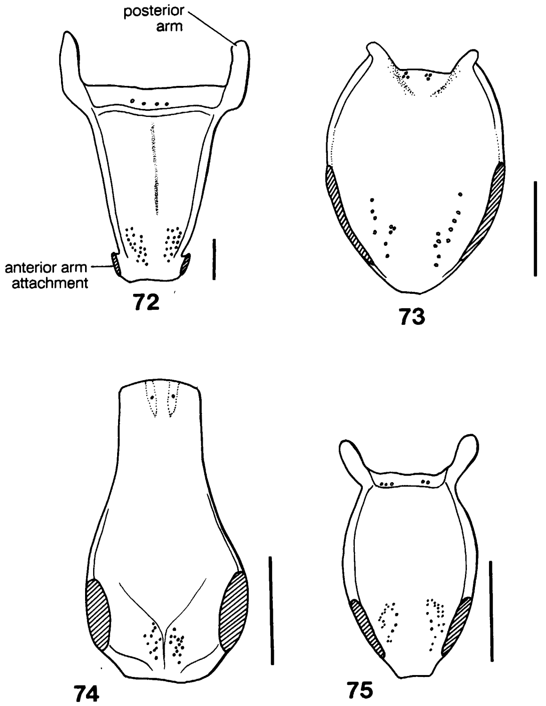
Ventrally the cibarium is boat- or stirrup-shaped, and variation in its form provided a number of useful characters.

29. Length of posterior arms of the cibarium. Plesiomorphically the posterior cibarial arms are rounded in cross section, elongate, and parallel to each other (figs. 76, 81, 85, 87, 89, 91, 93, 95, 99). Apomorphically the posterior cibarial arms have become shortened or lost entirely. The apomorphic state was found in *Hilarimorpha*, *Leptogaster*, the Mydidae (fig. 74), Scenopinidae (fig. 73), and the Mythicomyiinae (fig. 79) except in *Acridophagus* (fig. 76). The Apioceridae have slightly reduced posterior arms which were coded as plesiomorphic (fig. 75).

30. Shape of the posterior arms of cibarium. Plesiomorphically the posterior cibarial arms are long and separate from each other (figs. 89, 91, 93). Among members of the Tomophthalmae median projections develop midway along the length of the cibarial arms (figs. 101, 103, 115, 117) which were scored 1 and found in many cythereines and anthracines. These projections join in *Pantarbes*, the Lomatiinae, Tomomyzinae, and many Anthracinae (figs. 105, 107, 109, 111, 113) and were scored 2. I hypothesize a transformation series from separate median projections to united ones, and this character was treated additively. In comparison to others, the posterior arms unite further towards the apex in *Pantarbes*, and it was independently derived on the cladogram.

31. Posterior arms of the cibarium. In lateral view the posterior arms of the cibarium are usually straight (figs. 100, 102, 104, 106). In the Antoniinae, the Lomatiinae excluding *Perigueyimyia* and *Plesiocera*, and *Exoprosopa* of the Anthracinae the arms angle ventrally midway along their length (figs. 110, 113, 115, 118), at approximately the position where the arms join medially (character 30).

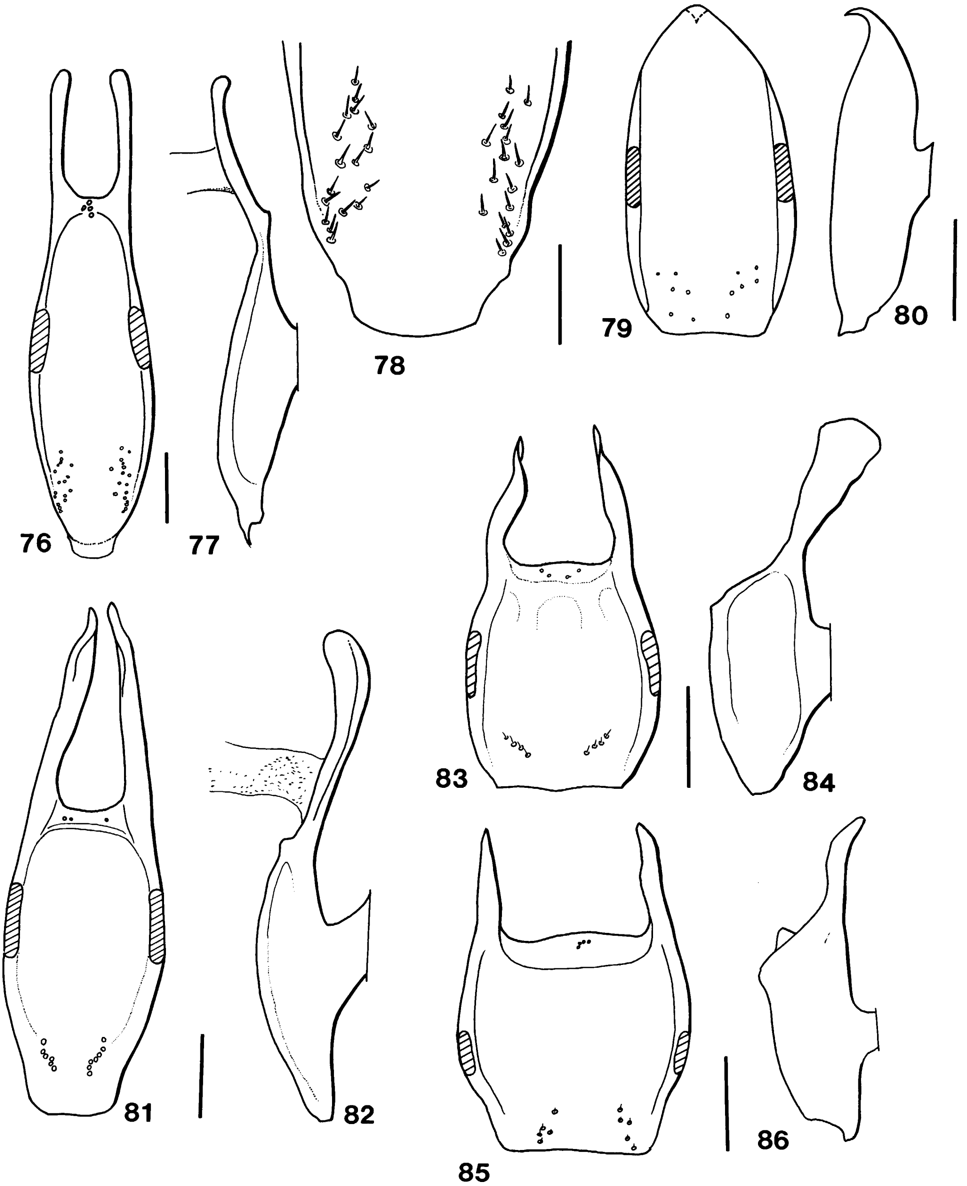
32. Ventral wall of the cibarium. The ventral wall of the cibarium is smooth in most cases (figs. 73–75, 85, 93, 101). In the Asilidae, the bombyliids *Cephalodromia*, *Mariobezzia*, *Cyllenia*, *Antonia*, and all the Anthracinae except *Plesiocera* a median ridge is developed (figs. 72, 99, 103, 113, 117) which was considered apomorphic. It has been independently derived in the Asilidae and in each bombyliid subfamily where it occurs.



Figs. 72–75. Fulcrums of various asiloids: **72**, Asilidae, *Leptarthrus brevirostris*, scale 0.1 mm; **73**, Scenopinidae, *Scenopinus fenestralis*, scale 0.1 mm; **74**, Mydidae, *Mydas clavatus*, scale 0.5 mm; **75**, Apioceridae, *Apiocera aldrichi*, scale 0.5 mm.

33. Shape of the ventral wall of the cibarium. When viewed from above, the cibarium is most often rounded or oval in shape (figs. 93, 101, 103) which I considered to be the plesiomorphic condition. The apomorphic state is a very elongate cibarium, its length (excluding the posterior arms) being at least twice its greatest width (figs. 113, 115, 117). The apomorphic state occurred in the Acroceridae, *Acridophagus* (fig. 76), and appears apomorphic for the Tomomyzinae except *Docidomyia* (fig. 111) and the Anthracinae.

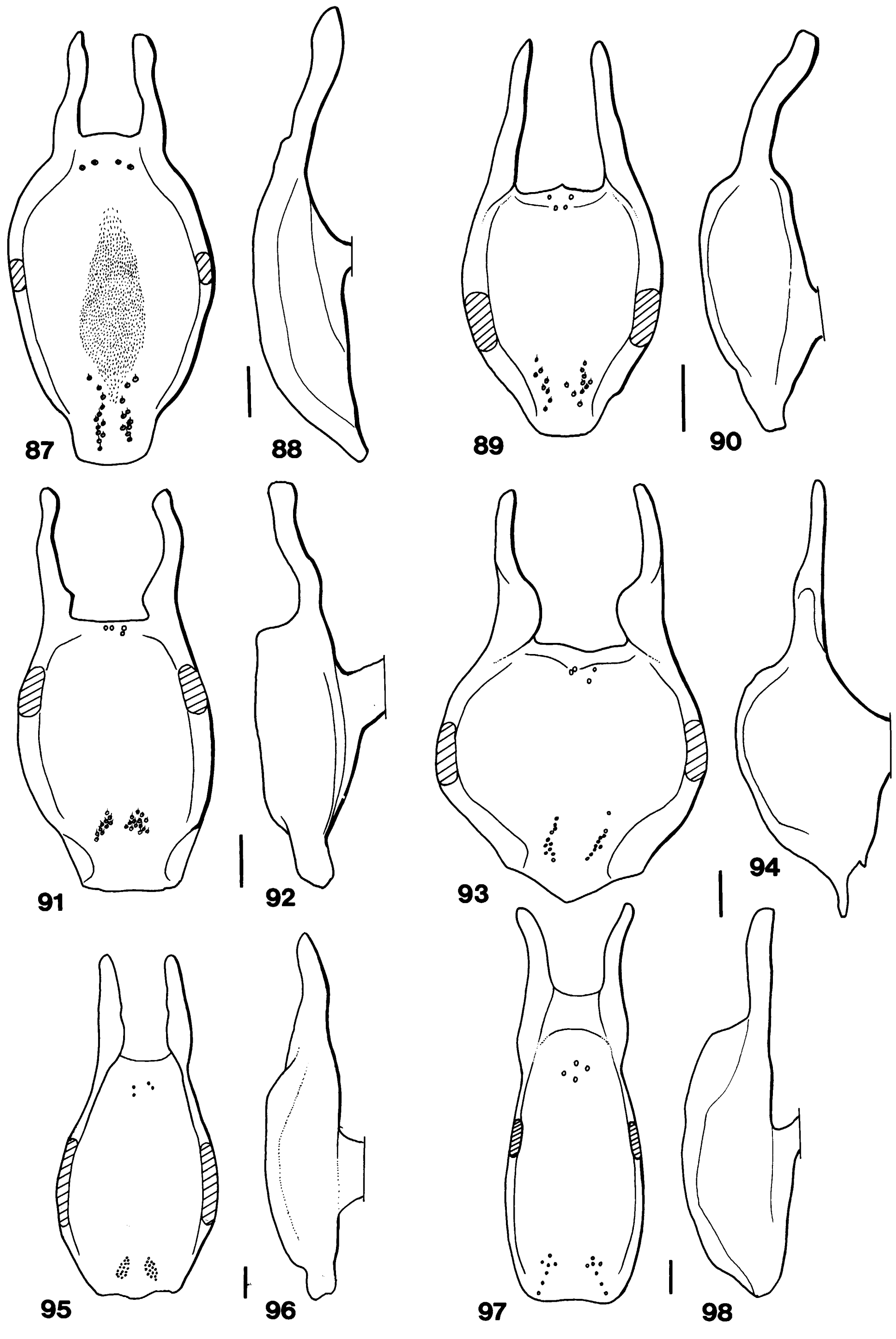
34. Shape of the ventral wall of the cibarium. Asilidae have a characteristically shaped



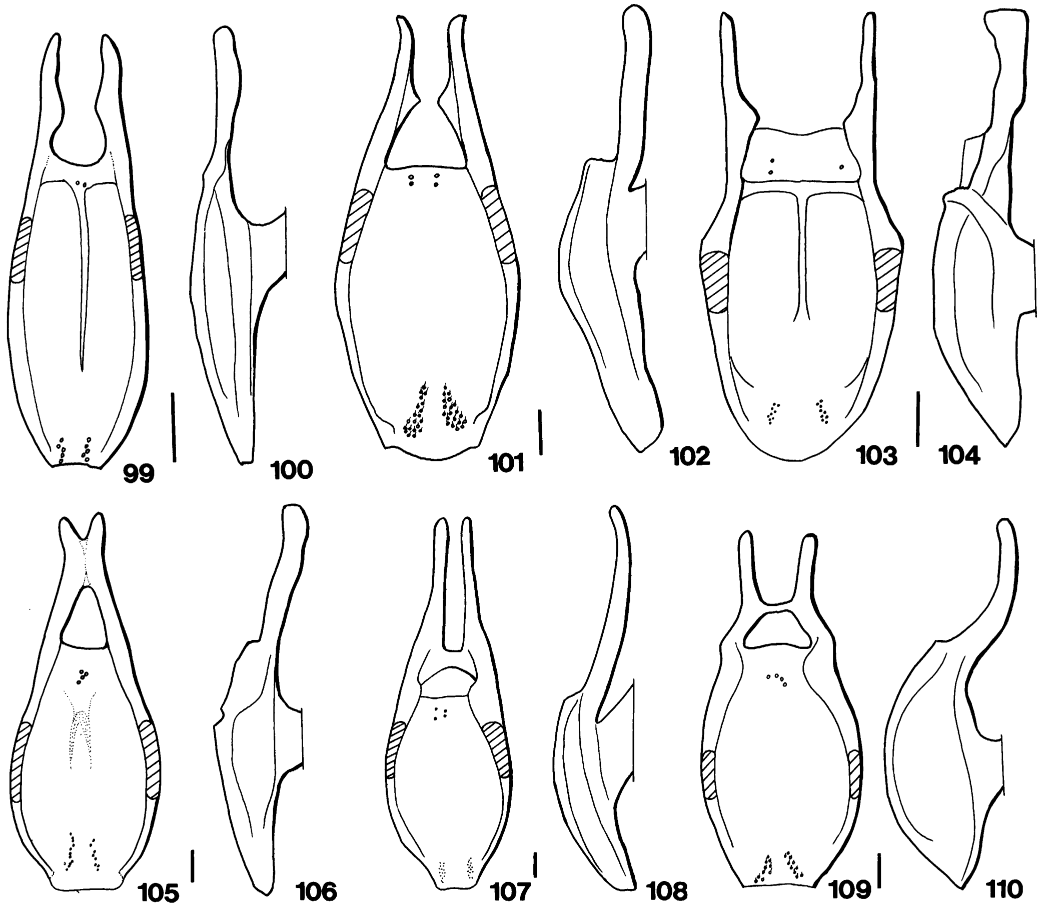
Figs. 76–86. Fulcrums of Bombyliidae: **76**, *Acridophagus* sp. dorsal; **77**, *Acridophagus* sp. lateral; **78**, *Acridophagus* sp. detail of sensillae on dorsal wall of fulcrum; **79**, *Mythicomyia illustris* dorsal; **80**, *M. illustris* lateral; **81**, *Heterotropus gilvicornis* dorsal; **82**, *H. gilvicornis* lateral; **83**, *Oligodranes* sp. dorsal; **84**, *Oligodranes* sp. lateral; **85**, *Desmatomyia anomala* dorsal; **86**, *Desmatomyia anomala* lateral. Scales 0.1 mm except figure 78 0.05 mm.

cibarium, which is trapezoidal in dorsal view (fig. 72), rather than smoothly rounded as in other asiloids. The posterior end of the cibarium is wider than the anterior, and the posterior arms become laterally compressed in *Stenopogon* and *Dioctria*.

The tentorium of the Asiloidea consists of a sclerotized, tubular or laterally compressed rod which runs from the anterior to posterior tentorial pits (figs. 71, 120, 123, 125, 127, 129), and comprises the fused anterior and posterior tentorial arms.



Figs. 87–98. Fulcrums of Bombyliidae: **87**, *Toxophora virgata* dorsal; **88**, *T. virgata* lateral; **89**, *Eclimus gracilis* dorsal; **90**, *E. gracilis* lateral; **91**, *Megapalpus capensis* dorsal; **92**, *M. capensis* lateral; **93**, *Oniromyia pachycerata* dorsal; **94**, *O. pachycerata* lateral; **95**, *Corsomyza brevicornis*, dorsal; **96**, *C. brevicornis* lateral; **97**, *Cytherea obscura* dorsal; **98**, *C. obscura* lateral. Scales 0.1 mm.

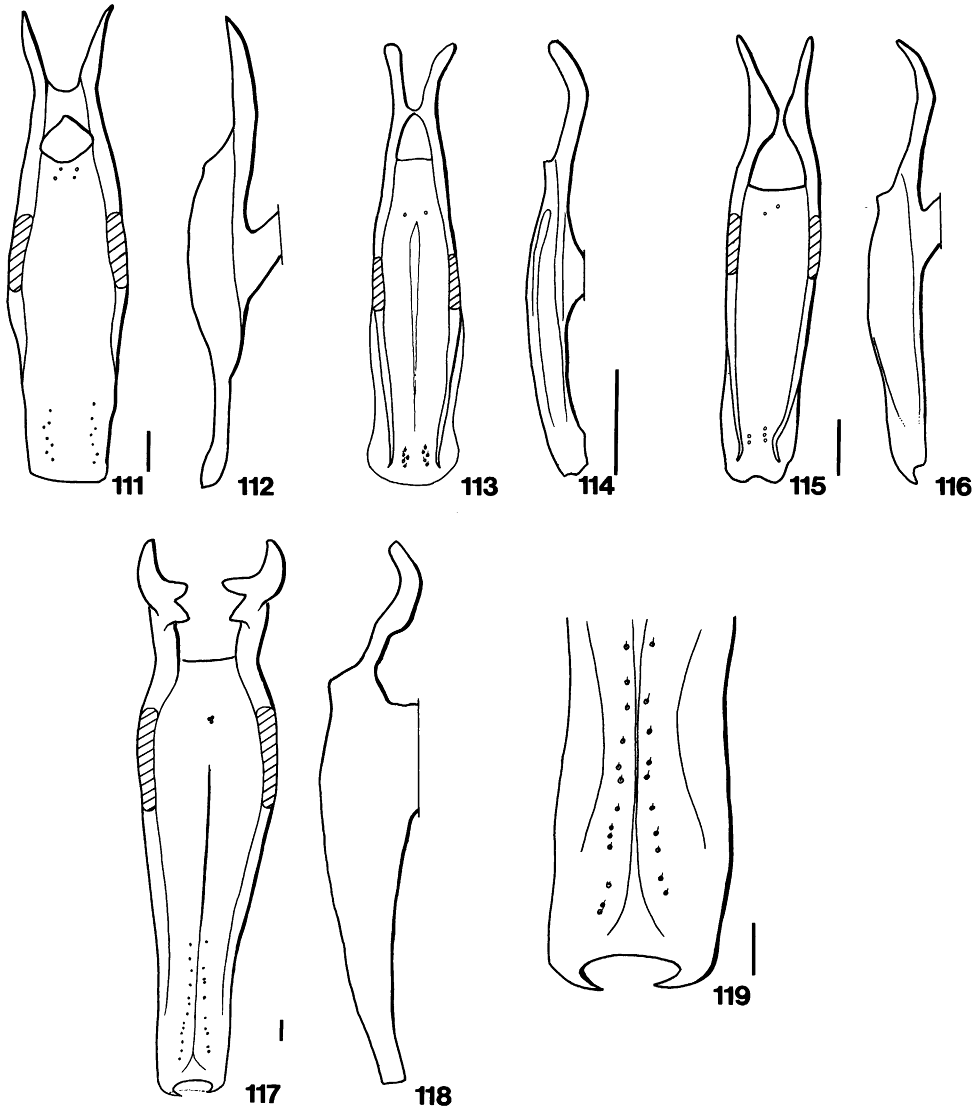


Figs. 99–110. Fulcrums of Bombyliidae: **99**, *Mariobezzia lichtwardti* dorsal; **100**, *M. lichtwardti* lateral; **101**, *Enica longirostris* dorsal; **102**, *E. longirostris* lateral; **103**, *Cyllenia maculata* dorsal; **104**, *C. maculata*; **105**, *Pantarbes capito* dorsal; **106**, *P. capito* lateral; **107**, *Peringueyimyia capensis* dorsal; **108**, *P. capensis* lateral; **109**, *Lomatia belzebul* dorsal; **110**, *L. belzebul* lateral. Scales 0.1 mm.

35. Width of tentorial arm. The tentorial arm is usually relatively thick (figs. 143, 149, 155, 159, 161, 165) but in the apomorphic state of this character it is very slender. A very narrow tentorial arm is found in *Prorates* (fig. 129), *Lepidophora* and *Eclimus* (fig. 181), the Mythicomyiinae except *Acridophagus* (figs. 151, 153), the Usiinae (figs. 139, 141), *Geron* (fig. 148), and the Systropodini except *Systropus*.

36. Shape of posterior tentorial pits. The posterior tentorial pits are primitively rounded (figs. 122, 124, 126, 128, 130), but in *Hirmoneura* (fig. 29) and the Lomatiinae, Tomomyzinae, and Anthracinae of the Bombyliidae they become elongate (figs. 196, 198, 200, 202, 204, 206). This character is an apomorphy for the clade consisting of the latter subfamilies (clade 72).

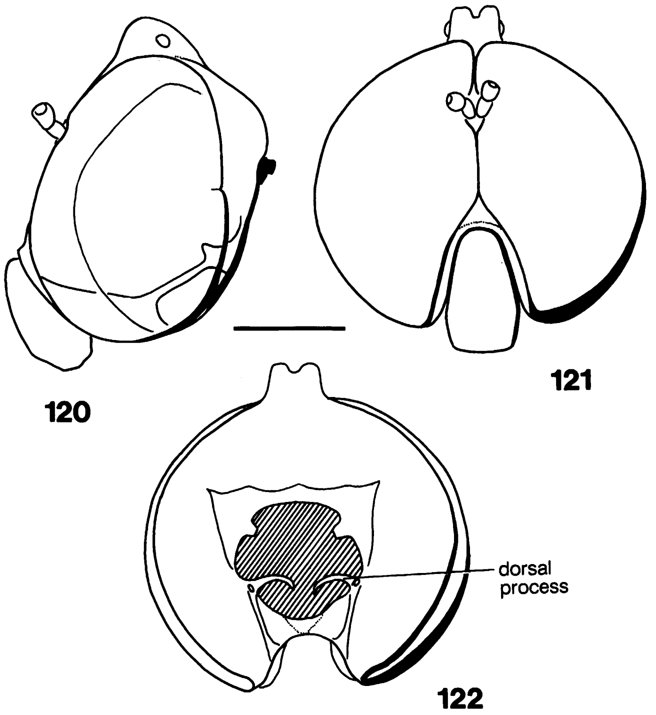
37. Shape of the postcranium (occiput plus postgenae). The plesiomorphic state for this character is found in all the outgroups examined and many Bombyliidae where the postcranium is flattened or slightly tumid and the occipital foramen lies in approximately the same plane as the remainder of the postcranium (figs. 28, 29, 122, 124, 126, 128, 130–131, 138, 140, 142, 207). In *Sericosoma*, the Mariobezziinae, *Oniromyia*, and Cythereinae advanced state 1 was found where the postcranium is moderately produced posteriorly (figs. 132, 186, 188, 190, 192, 194, 208–



Figs. 111–119. Fulcrums of Bombyliidae: **111**, *Tomomyza anthracoides* dorsal; **112**, *T. anthracoides* lateral; **113**, *Exoprosopa caliptera* dorsal; **114**, *E. caliptera* lateral; **115**, *Plesiocera psammophila* dorsal; **116**, *P. psammophila* lateral; **117**, *Antonia suavissima* dorsal; **118**, *A. suavissima* lateral; **119**, *A. suavissima*, detail of sensillae on dorsal wall of fulcrum. Scales 0.1 mm.

211) forming a slight hollow in which the occipital foramen is found. The Lomatiinae, Tomomyzinae, Antoniinae, and Exoprosopinae (clade 68) have advanced state 2 with well-developed, posteriorly directed lobes of the postcranium (figs. 133, 196, 198, 200, 202, 204, 206, 212) surrounding the occipital foramen and causing it to be set in a deep, cup-shaped depression. I hypothesize a transformation series from state 0 through state 1 to state 2 and this character was analyzed in additive form.

The form of the postcranium has been an important character in Bombyliidae higher classification since it was introduced by Bezzi (1924). I discuss the relative emphasis placed



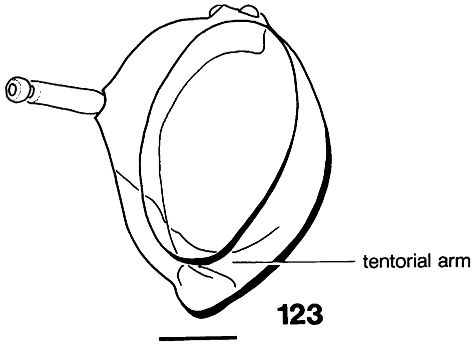
Figs. 120–122. Head of the acrocerid *Eulonchus smaragdinus* female, vestiture not shown, hatched area is occipital foramen: **120**, lateral view showing internal sclerotized structures; **121**, anterior; **122**, posterior. Scale 1.0 mm.

on this character by subsequent authors in the section Classification of the Bombyliidae into Subfamilies.

38. Shape of occipital lobes. The occipital lobes are produced posteriorly in those Bombyliidae with a moderately deep or very deeply set occipital foramen (states 1 and 2 of character 37). The occipital lobes form a complete ring including the postgenae below the occipital foramen except dorsally where they are interrupted by the ocellar tubercle. In the apomorphic state of this character, found in *Cyllenia*, and clade 68 comprising the Lomatiinae, Tomomyzinae, Anthracinae and Antoniinae except *Myonema*, the occipital lobes are very closely approximated behind the ocellar tubercle (figs. 133, 196, 198, 200, 202, 204, 206, 217). Bezzi (1924) noted that this character occurs only in those Bombyliidae with a deeply cup-shaped postcranium.

39. Form of the occipital foramen. The primitive single occipital foramen was found in the outgroups and is present in most Diptera (figs. 122, 124, 126, 128, 138, 140, 142, 144, 146, 148). Theodor (1983) first drew attention to the apomorphic dorsal and ventral occipital foramina in tomophthalmine bombyliids (figs. 133, 134, 174, 176, 178, 184, 186, 188, 190, 192, 194, 196, 198, 200, 202, 204, 206, 217), and it is an apomorphy for clade 57 in this study. The advanced state has been independently acquired in *Hirmoneura* and the mydids (figs. 28, 29) examined. Zaitlin and Larsen (1984) also found two occipital foramina in *Mydas clavatus*.

The single occipital foramen appears to have become divided in the advanced state by the approximation of the occipital condyles (fig. 174). These condyles become very closely associated and almost meet, leading to the constriction of the original foramen into one dorsal and one ventral occipital foramen. Dissections made during this study confirm that no internal organ systems pass through the dorsal foramen; in fact, the dorsal foramen may be blind and not connected to the thorax.



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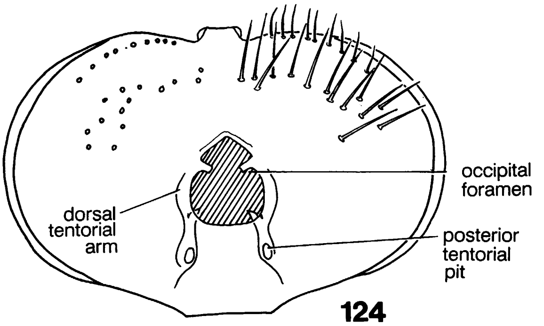

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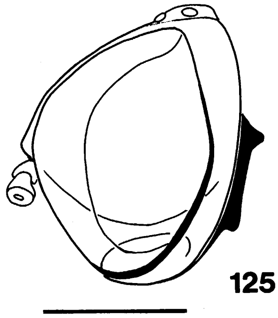

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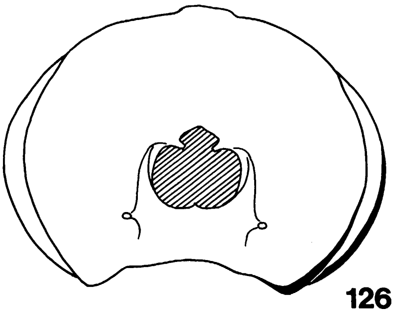

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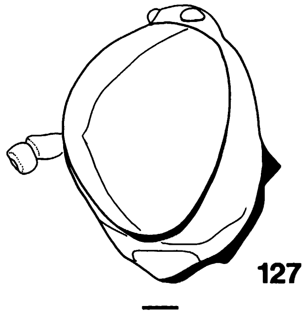

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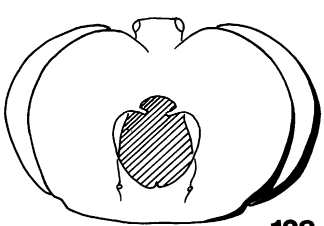

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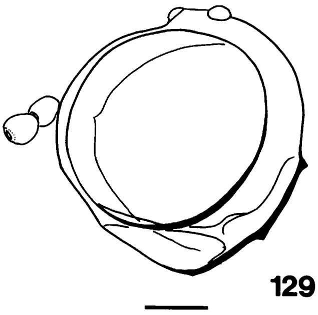

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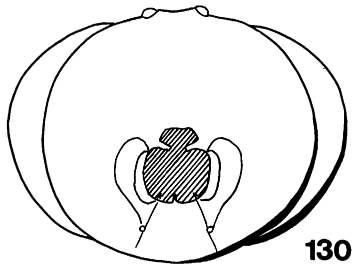

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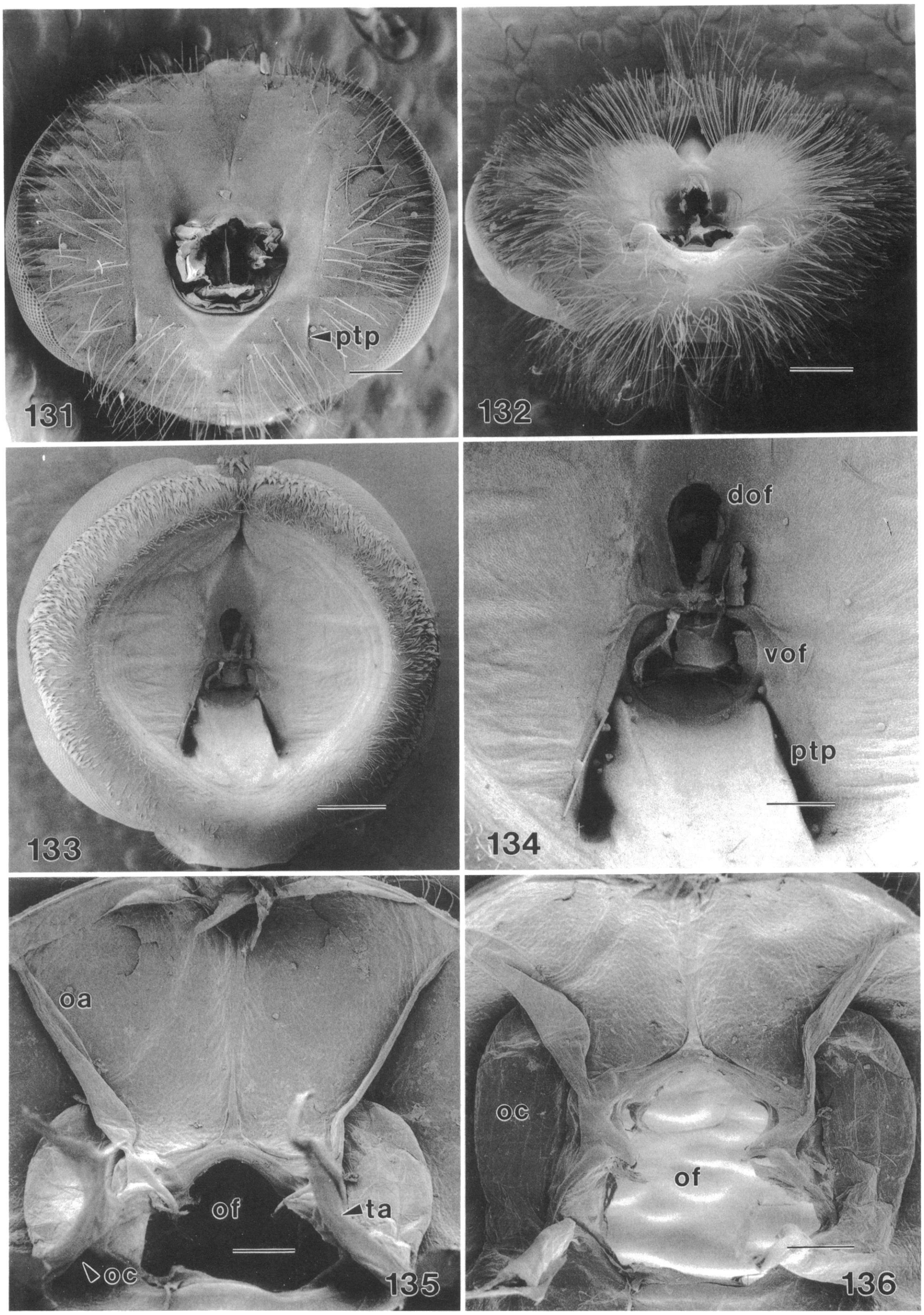
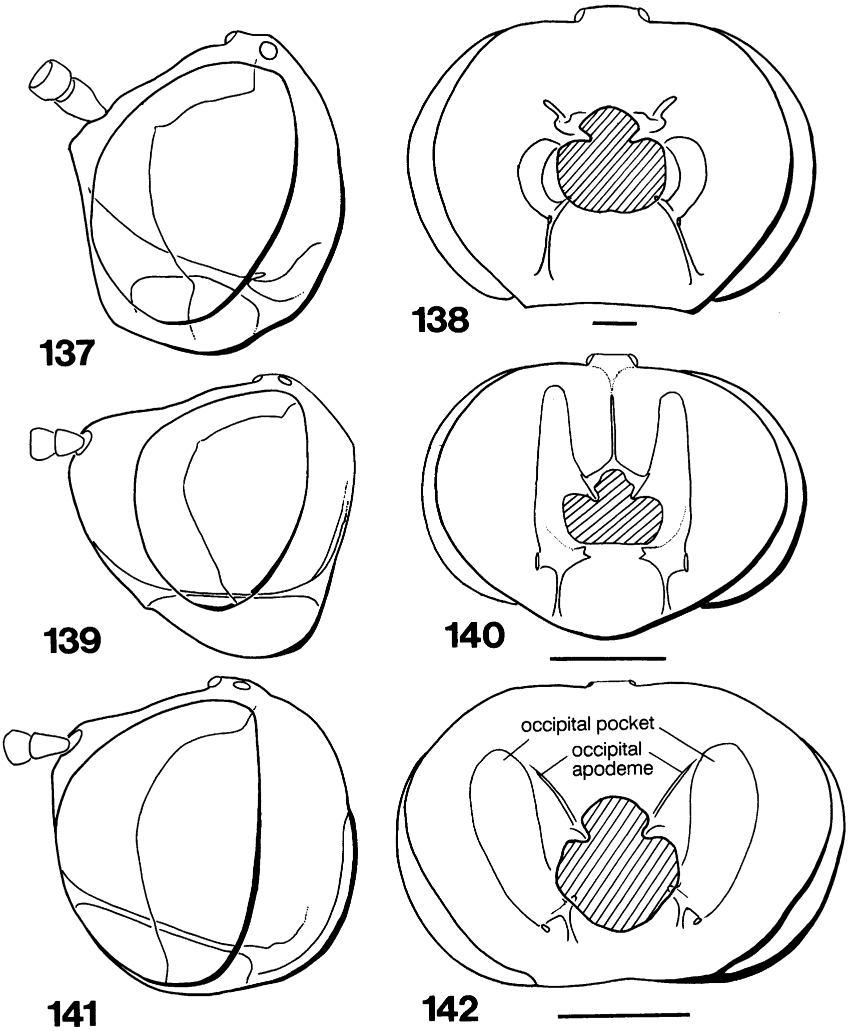
Figs. 123–130. Heads of therevids and scenopinids, lateral views showing internal sclerotized structures, vestiture not shown except setae on figure **124**: **123**, *Thereva fucata* lateral, scale 0.5 mm; **124**, *T. fucata* posterior, scale 0.5 mm; **125**, *Scenopinus fenestralis* lateral, scale 0.5 mm; **126**, *S. fenestralis* posterior, scale 0.5 mm; **127**, *Cenotus hospes* lateral, scale 0.1 mm; **128**, *C. hospes* posterior, scale 0.1 mm; **129**, *Prorates frommeri* lateral, scale 0.1 mm; **130**, *P. frommeri* posterior, scale 0.1 mm.



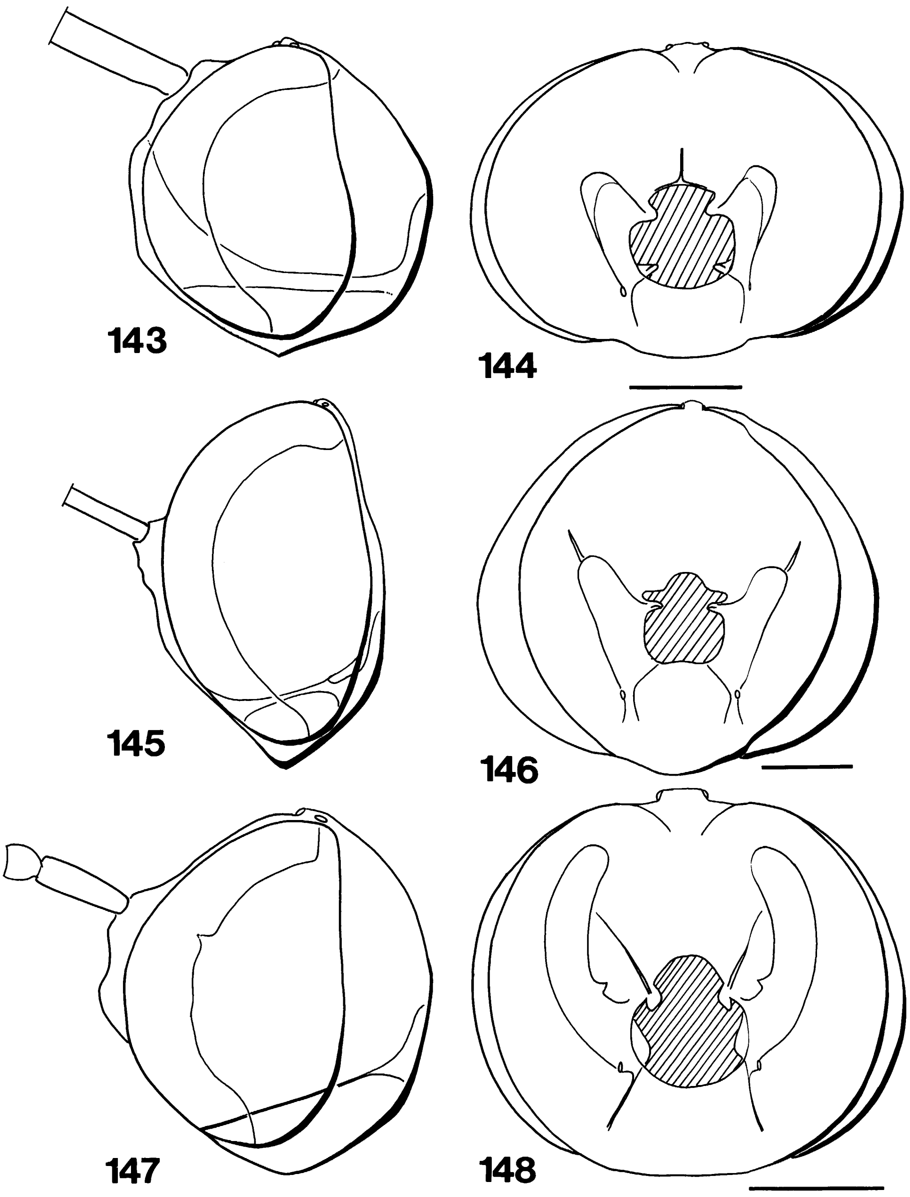
Figs. 131–136. Scanning electron micrographs of the postcranial region of Bombyliidae: **131**, *Poecilognathus sulphurea*, ptp = posterior tentorial pit, scale 200 μm; **132**, *Pantarbes capito*, scale 500 μm; **133**, *Exoprosopa caliptera*, scale 500 μm; **134**, *E. caliptera*, dof = dorsal occipital foramen, vof = ventral occipital foramen, ptp = posterior tentorial pits; **135**, *Bombylius major*, internal view of postcranium, oa = occipital apodeme, of = occipital foramen, op = opening of occipital chamber, ta = tentorial arm, scale = 200 μm; **136**, same as figure 135, oc = occipital chamber.



Figs. 137–142. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **137**, *Oligodranes* sp. lateral; **138**, *Oligodranes* sp. posterior; **139**, *Phthiria gaedei* lateral; **140**, *P. gaedei* posterior; **141**, *Usia atrata* lateral; **142**, *U. atrata* posterior. Scales 0.5 mm except *Oligodranes* 0.1 mm.

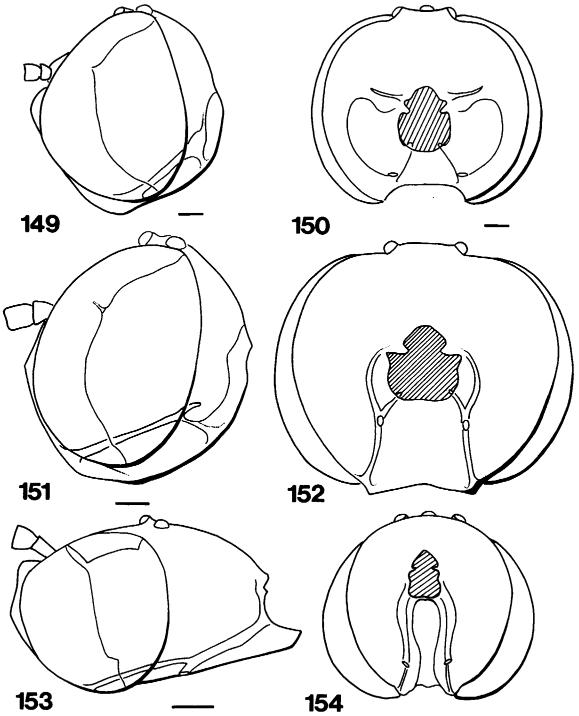
40. Occipital windows. The occipital windows are small areas of reduced sclerotization lateral to the occipital condyles, between the dorsal and ventral occipital foramina (figs. 184, 188, 190, 192, 194, 196). These windows were apomorphically present and found in the tomophthalmine bombyliids except the Mariobezzinae. They have been independently acquired in *Hirmoneura* and the Mydidae (figs. 28, 29).

41. Form of posterior tentorial arm. Variation in the form of the posterior tentorial arm was divided into a three-state additive character. As each tentorial arm approaches the posterior tentorial pit it passes just ventral to the occiput and the laterally compressed posterior tentorial arm extends upward to the occipital rim. In the plesiomorphic state the posterior tentorial arm fuses with the head capsule and in many cases extends as an internal strengthening ridge dorsally and parallel with the lateral margins of the occipital foramen (figs. 124, 126, 160) forming the postoccipital suture externally. The posterior



Figs. 143–148. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **143**, *Toxophora virgata* lateral; **144**, *T. virgata* posterior; **145**, *Systropus macer* lateral; **146**, *S. macer* posterior; **147**, *Geron grandis* lateral; **148**, *G. grandis* posterior. Scales 0.5 mm.

tentorial ridge then turns medially to join the laterodorsal corner of the occipital rim. In state 1, found in *Bonjeania,* the Mydidae except *Neorhaphiomidas, Apiocera, Prorates, Hilarimorpha,* and many Bombyliidae, the posterior tentorial ridge is narrow, high, and often folded mesally back onto the occipital rim on the lateral margins of the occipital foramen (figs. 71, 130, 138, 152). In addition, the posterior tentorial ridge turns laterally before it joins with the occipital rim. In state 2, found only in plesiomorphic Bombyliidae,



Figs. 149–154. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **149**, *Acridophagus* sp. lateral; **150**, *Acridophagus* sp. posterior; **151**, *Mythicomyia illustris* lateral; **152**, *M. illustris* posterior; **153**, *Cephalodromia fusca* lateral; **154**, *C. fusca* posterior. Scales 0.1 mm.

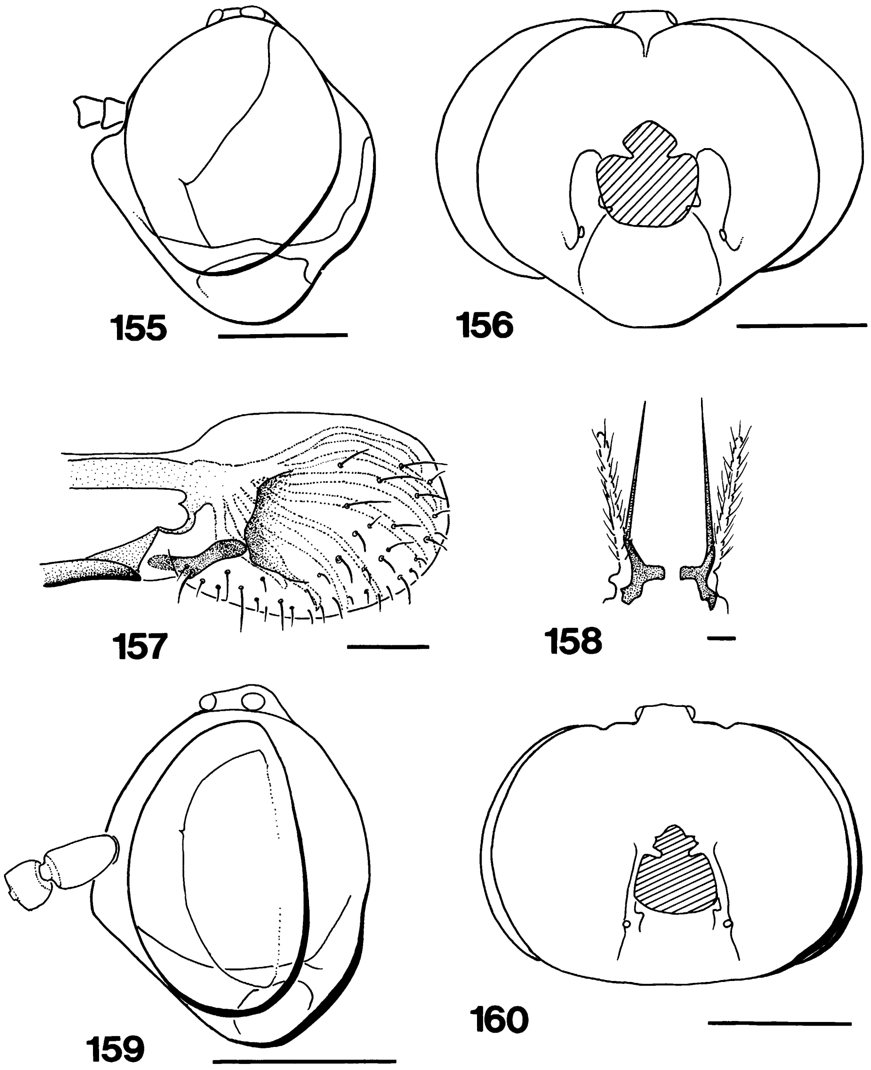
the narrow folded portion of the posterior tentorial ridge fuses with the rim of the occipital foramen and causes a sclerotized chamber to develop with its mouth at the level of the posterior tentorial pits (figs. 135–136, 140, 142, 144, 146, 148, 150), termed by Zaytsev (1986, 1992) the occipital chamber. The chamber extends dorsally as far as the posterior tentorial ridge does, sometimes well above the occipital foramen itself, and is very well developed in the Usiinae and Toxophorinae. The occipital chamber is absent in all Tomophthalmae except *Corsomyza* (fig. 178) and *Megapalpus* (fig. 176) with state 2 and *Pantarbes* with state 1.

A small dorsal process emerges at the point where the anterior and posterior tentorial arms meet (figs. 122, 144, 156, 164, 182), and is probably homologous with a similar process found by Bonhag (1951) in Tabanidae to which neck muscles are attached.

42. Occipital apodemes. A pair of internal cuticular ridges, termed here the occipital apodemes, extend dorsolaterally from the occipital foramen in many Bombyliidae. They are found in the Bombyliidae *Oligodranes*, *Acridophagus* and the Usiini, Gerontini, *Systropus*, the Bombyliinae except *Marmasoma*, *Crocidium*, *Sericosoma*, the Mariobezzinae and Lomatiinae, *Neosardus*, and *Pantarbes* (figs. 135–136, 142, 148, 150, 162, 164, 166, 168, 172, 174, 176, 178, 180, 186, 196). They are separate from the ridge formed by the posterior tentorial arm discussed in character 41.

43. Occipital vestiture. Plesiomorphically the occiput is bare or has a vestiture of soft hairs. Among the Asiloidea, *Apsilocephala*, therevids, asilids, *Apiocera*, and the bombyliids, *Acrophthalmyda* and the Eclimini have a row or group of thick, stiff setae on the occiput (Greathead, 1988). Therevids in particular have distinct rows of heavy setae (fig. 124).

Plesiomorphically the postgena is simple, however the next three characters describe three separate modifications.



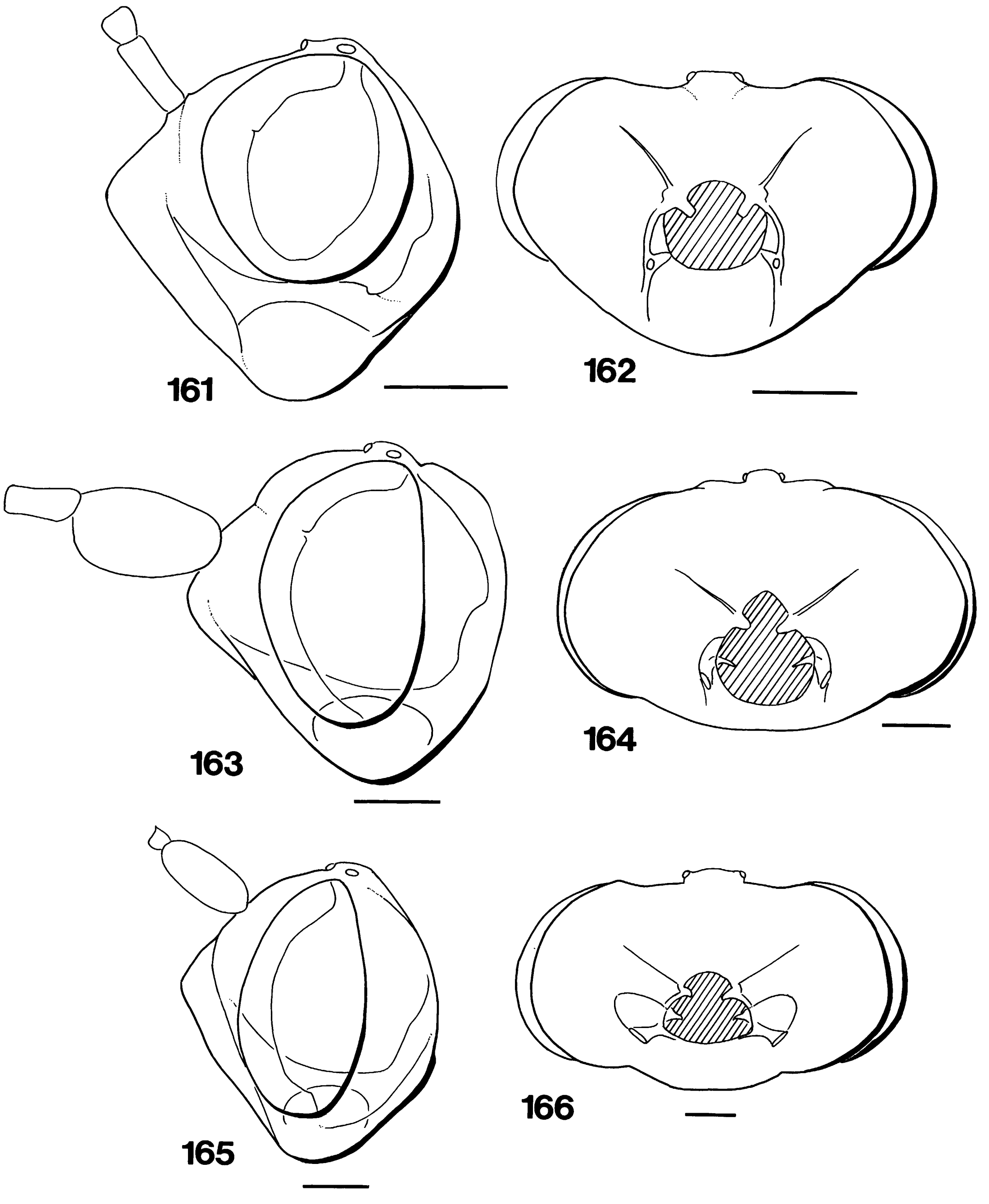
Figs. 155–160. Heads and mouthparts of Bombyliidae, hatched area is occipital foramen: **155**, *Heterotropus gilvicornis* lateral view showing internal sclerotized structures; **156**, *H. gilvicornis* posterior; **157**, *H. gilvicornis* lateral view of labellum; **158**, *H. gilvicornis* ventral view of maxilla showing palps and laciniae; **159**, *Desmatomyia anomala*, lateral view showing internal sclerotized structures; **160**, *Desmatomyia anomala* posterior. Scales 0.5 mm except figures 158 and 159 0.1 mm.

44. *Thevenetimyia*, *Eclimus*, and *Dischistus* have a median, internal sclerotized ridge (figs. 213, 215).

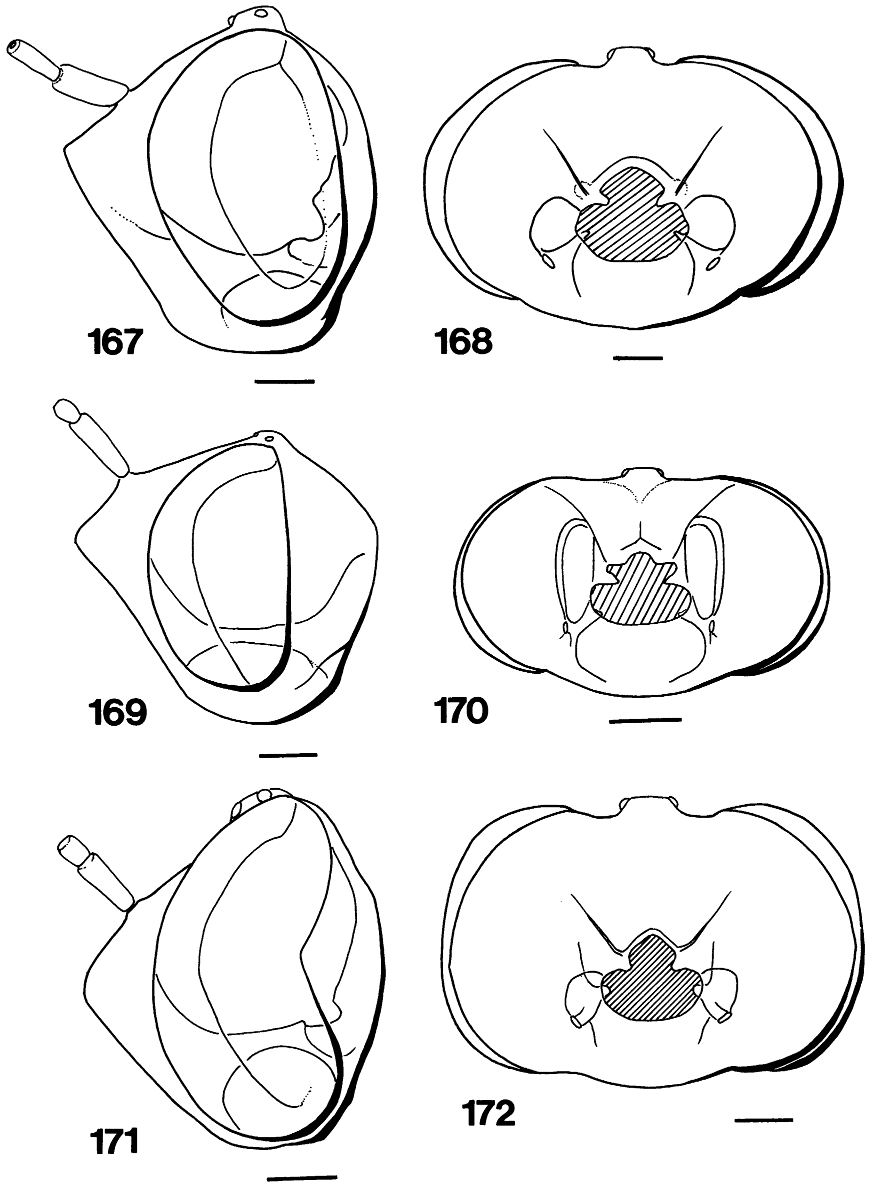
45. *Bonjeania*, *Dolicomyia*, and *Zaclava* have two parallel, internal sclerotized ridges on the postgena (figs. 214, 216).

46. *Villa* and *Exoprosopa* have two poorly sclerotized troughs running from the posterior tentorial pits and joining on the rim of the postcranial cup (fig. 217).

47. Form of the posterior margin of the eye. In the plesiomorphic state the posterior eye margin is straight (figs. 123, 127, 137, 139, 141, 143, 149, 159, 163, 165). In advanced state 1, found in *Eurycarenus*, *Heterostylum*, and the Lomatiinae except *Peringueyimyia*, there is a simple indentation at the level of the antennae (figs. 171, 197, 218). In advanced state 2, found in *Antonia* and the Anthracinae except *Plesiocera*, the in-



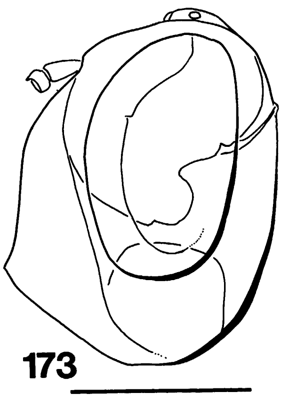
Figs. 161–166. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen; **161**, *Crocidium karooanum* lateral; **162**, *C. karooanum* posterior; **163**, *Conophorus fenestratus* lateral; **164**, *C. fenestratus* posterior; **165**, *Dischistus mystax* lateral; **166**, *D. mystax* posterior. Scales 0.5 mm.



Figs. 167–172. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **167**, *Acrophthalmyda paulseni* lateral; **168**, *A. paulseni* posterior; **169**, *Bombylius major* lateral; **170**, *B. major* posterior; **171**, *Heterostylum robustum* lateral; **172**, *H. robustum* posterior. Scales 0.5 mm.

dentation becomes more complex and includes a short dividing line extending anteriorly between the eye facets (figs. 201, 205, 220). Bezzi (1908, 1924) first drew attention to this character, using the indentation on the posterior margin of the eye to distinguish the Tomophthalmae. State 1 was achieved independently in the Bombyliinae and Lomatiinae, and state 2 was independently derived in *Antonia* and the Anthracinae.

48. Vestiture on the ocellar tubercle. Plesiomorphically the ocellar tubercle is clothed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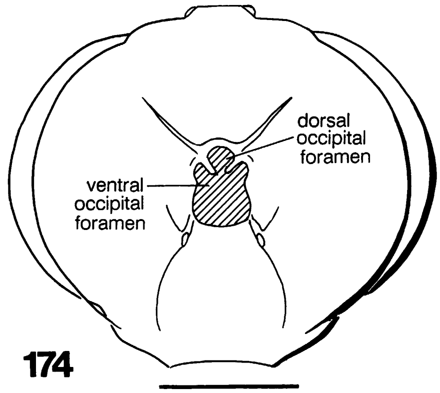
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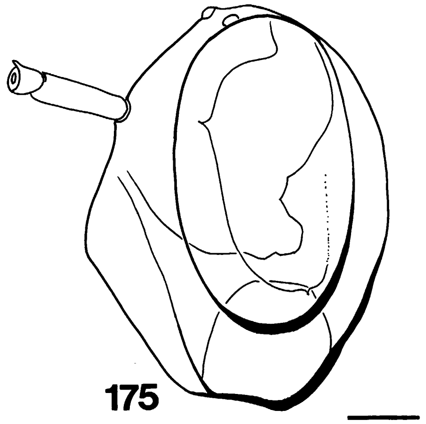
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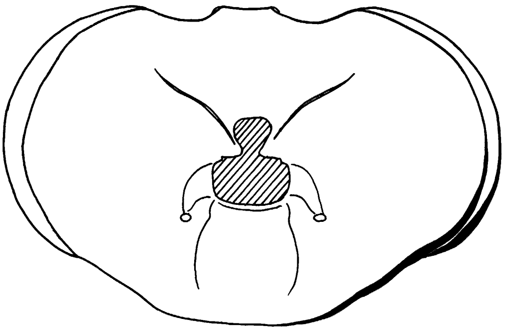
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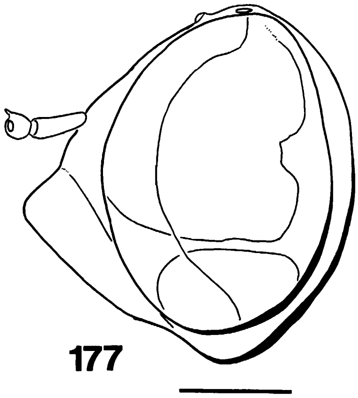
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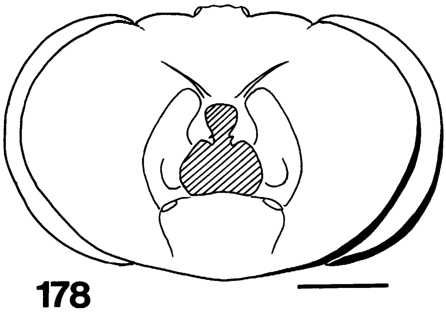
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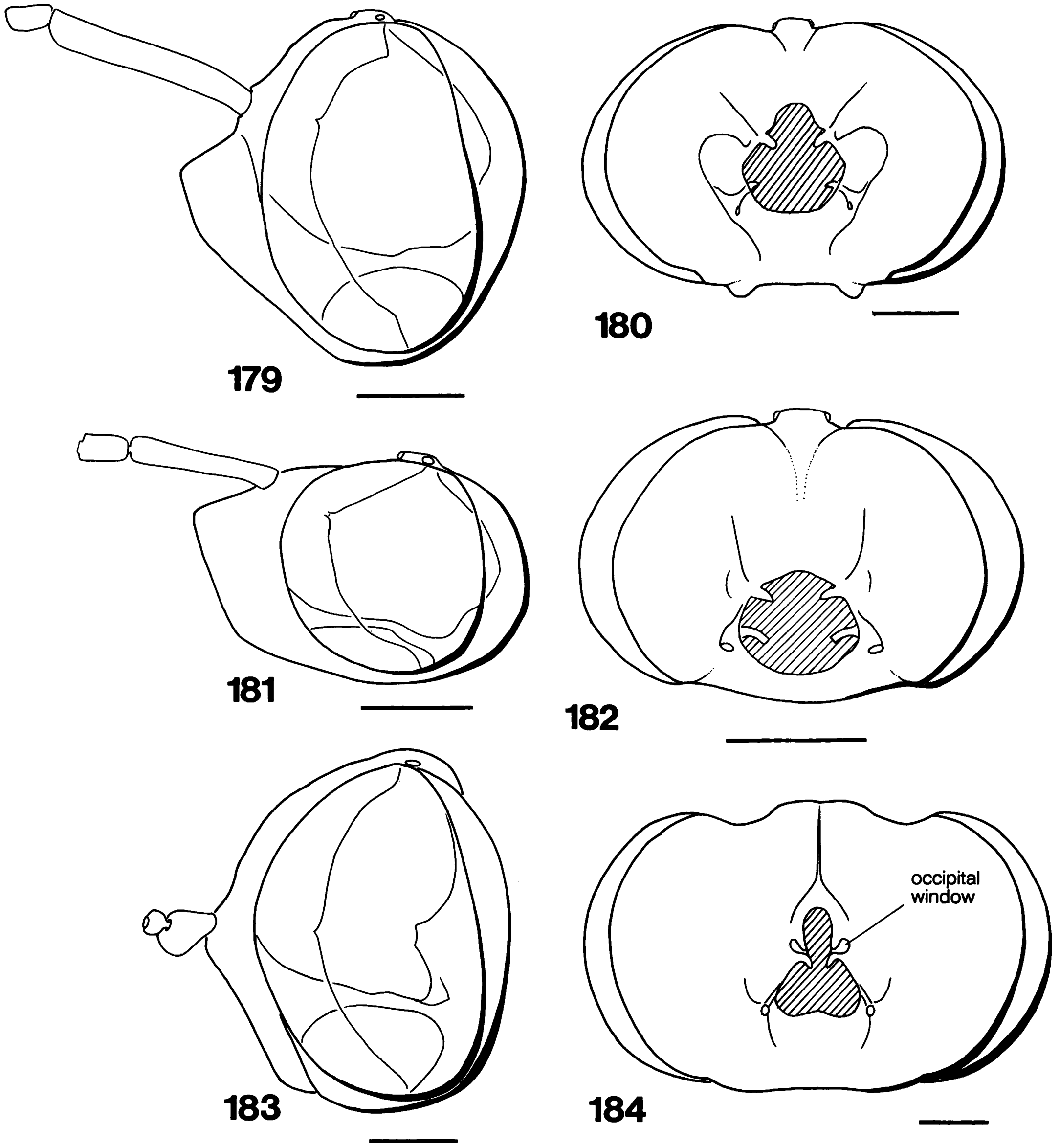
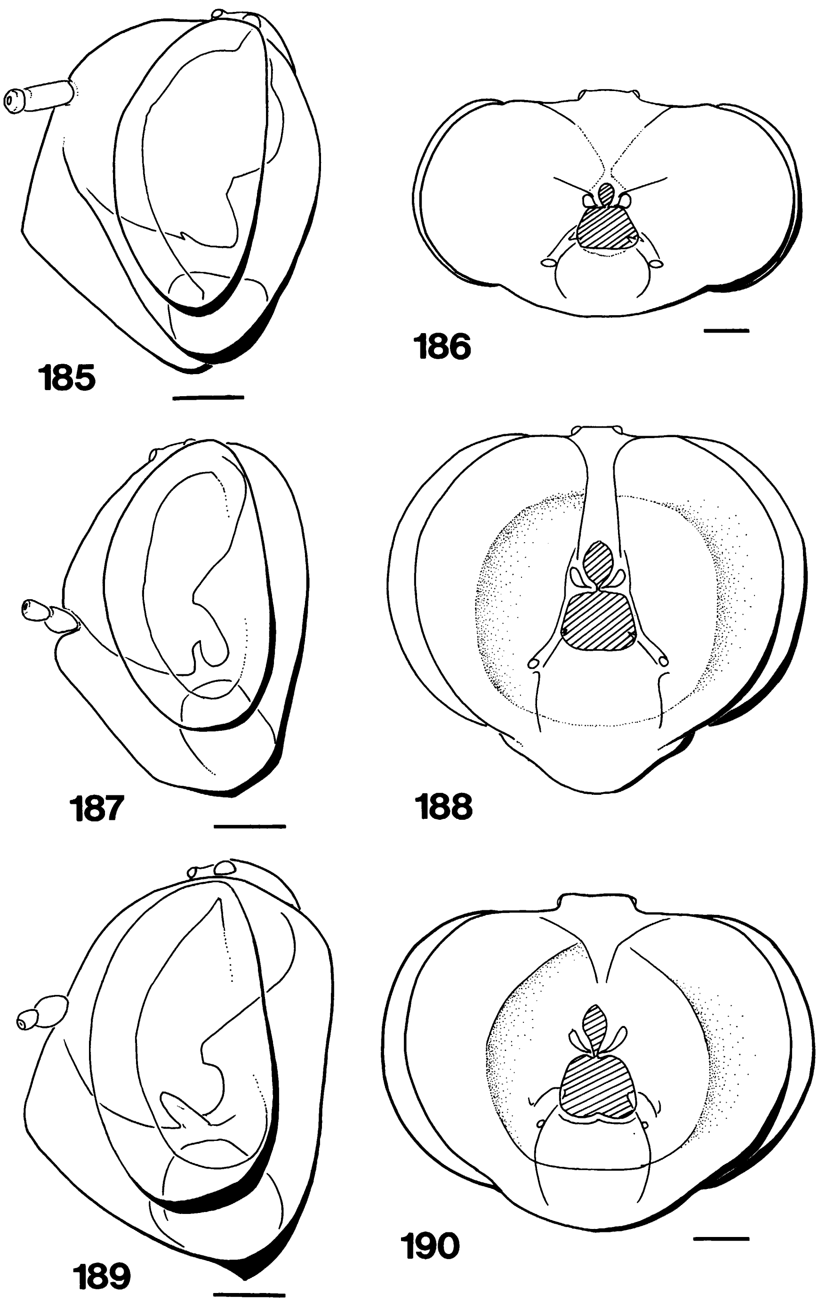
Figs. 173–178. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **173**, *Mariobezzia lichtwardti* lateral; **174**, *M. lichtwardti* posterior; **175**, *Megapalpus capensis* lateral; **176**, *M. capensis* posterior; **177**, *Corsomyza brevicornis* lateral; **178**, *C. brevicornis* posterior. Scales 0.5 mm.



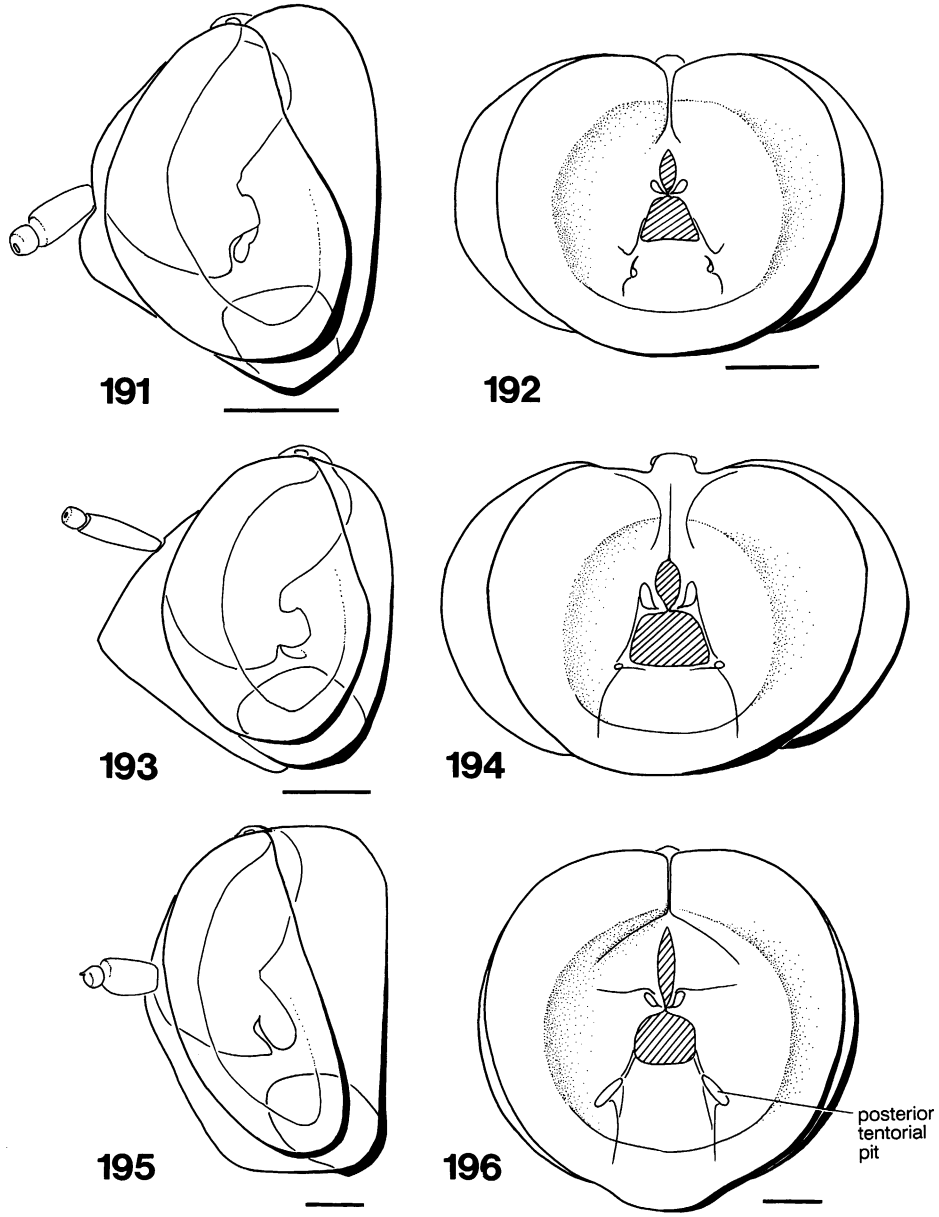
Figs. 179–184. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **179**, *Paratoxophora cuthbertsoni* lateral; **180**, *P. cuthbertsoni* posterior; **181**, *Eclimus gracilis* lateral; **182**, *E. gracilis* posterior; **183**, *Oniromyia pachycerata* lateral; **184**, *O. pachycerata* posterior. Scales 0.5 mm.

in scattered hairs or scales. The advanced state was found in *Toxophora*, which has two large, anteriorly directed setae based on the ocellar tubercle (fig. 35). *Apystomyia* has two pairs of setae on the ocellar tubercle and one pair of post ocellar setae (fig. 280). Wiegmann et al. (1993) considered this reduction in setae number a convergent feature within the Asiloidea and Eremoneura.

49. Head dimensions. Plesiomorphically the heads of asiloids are slightly wider than high (figs. 26, 27, 138, 140, 142, 156, 160,

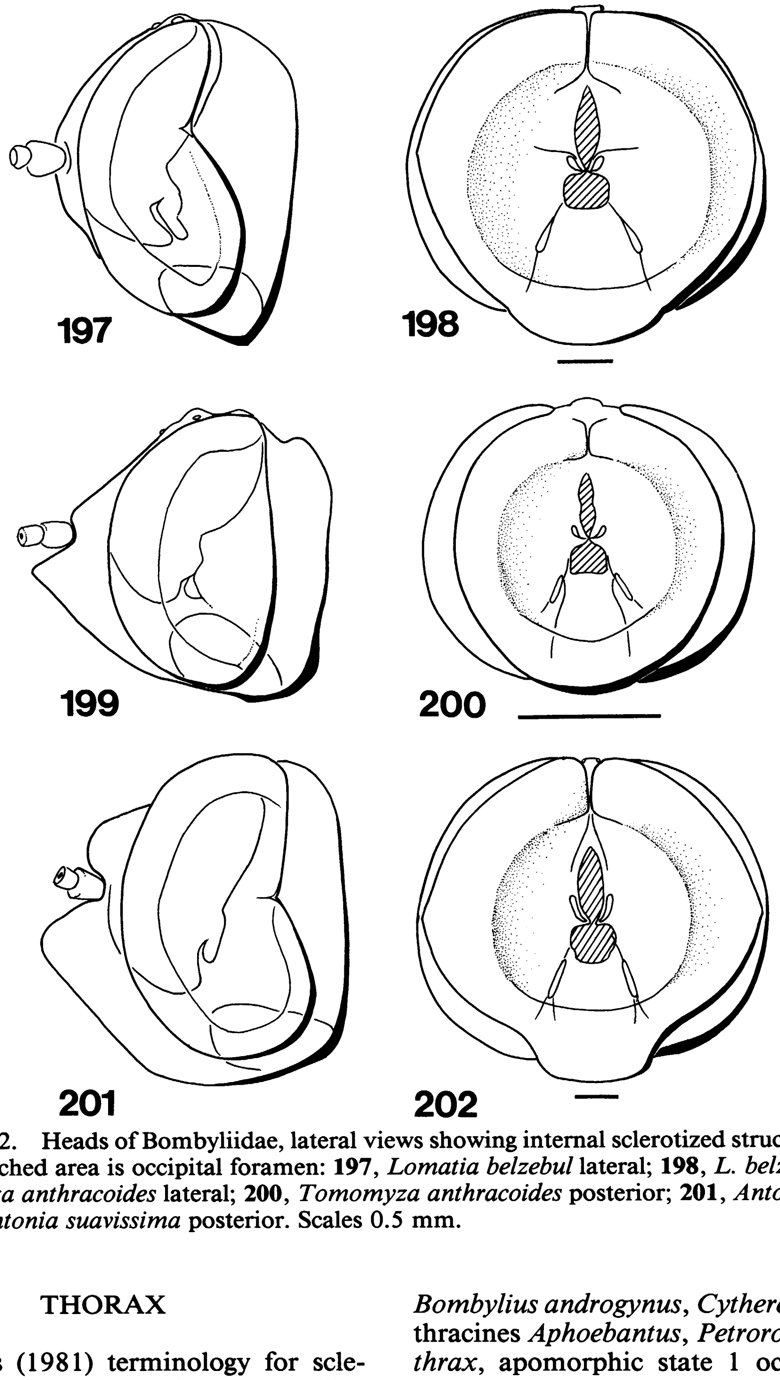


Figs. 185–190. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **185**, *Pantarbes capito* lateral; **186**, *P. capito* posterior; **187**, *Enica longirostris* lateral; **188**, *E. longirostris* posterior; **189**, *Cytherea obscura* lateral; **190**, *C. obscura* posterior. Scales 0.5 mm.



Figs. 191–196. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **191**, *Cyllenia maculata* lateral; **192**, *C. maculata* posterior; **193**, *Amictus validus* lateral; **194**, *A. validus* posterior; **195**, *Peringueyimyia capensis* lateral; **196**, *P. capensis* posterior. Scales 0.5 mm.

162, 164, 166, 168, 170, 172, 176, 178, 186). In a number of Bombyliidae including the Gerontini (fig. 148), Systropodini (fig. 146); and the clade comprising the Lomatiinae, Tomomyzinae, Antoniinae, and Anthracinae the head is rounded, as wide as high (figs. 198, 200, 202, 204, 206). Among the Tomophthalmae the rounded head is associated with a deep postcranial cup (state 2 of character 37).

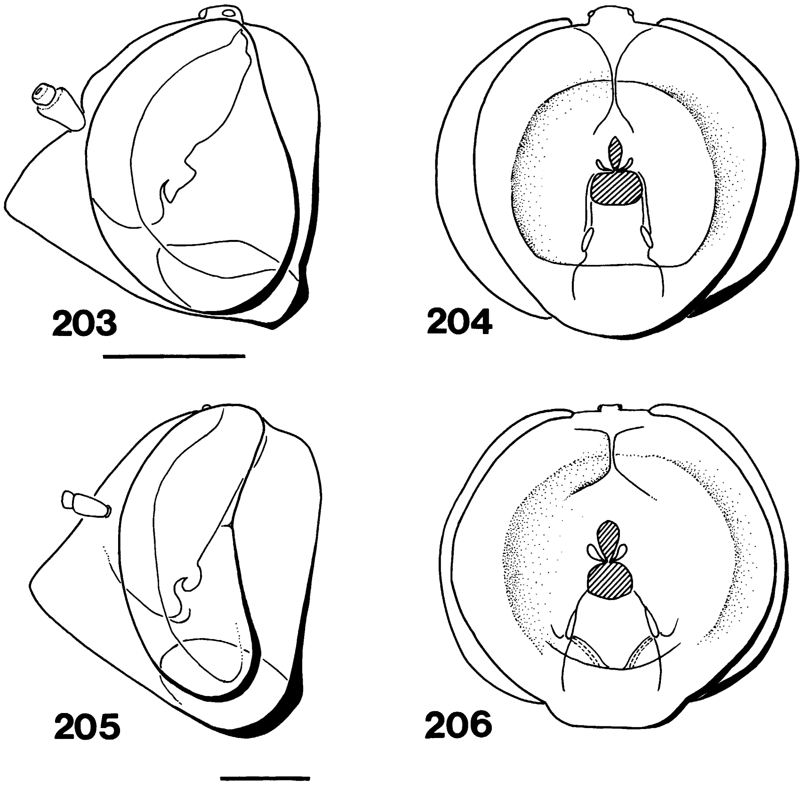


Figs. 197–202. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **197**, *Lomatia belzebul* lateral; **198**, *L. belzebul* posterior; **199**, *Tomomyza anthracoides* lateral; **200**, *Tomomyza anthracoides* posterior; **201**, *Antonia suavissima* lateral; **202**, *Antonia suavissima* posterior. Scales 0.5 mm.

THORAX

McAlpine's (1981) terminology for sclerites of the thorax, as applied to a typical bombyliid, is shown in figure 224.

50. Shape of basicosta. The basicosta is primitively a small, rounded structure at the base of the costa which usually bears a number of short hairs (fig. 225). In *Eurycarenus*, *Bombylius androgynus*, *Cytherea* and the anthracines *Aphoebantus*, *Petrorossia*, and *Anthrax*, apomorphic state 1 occurs and the icosta is produced into an elongate thorn-shaped structure and its apex curves laterally (figs. 226–227). In apomorphic state 2 of *Villa* and *Exoprosopa* the basicosta is more elongate, with the apex more sharply pointed, and the distal curvature more pronounced (fig.



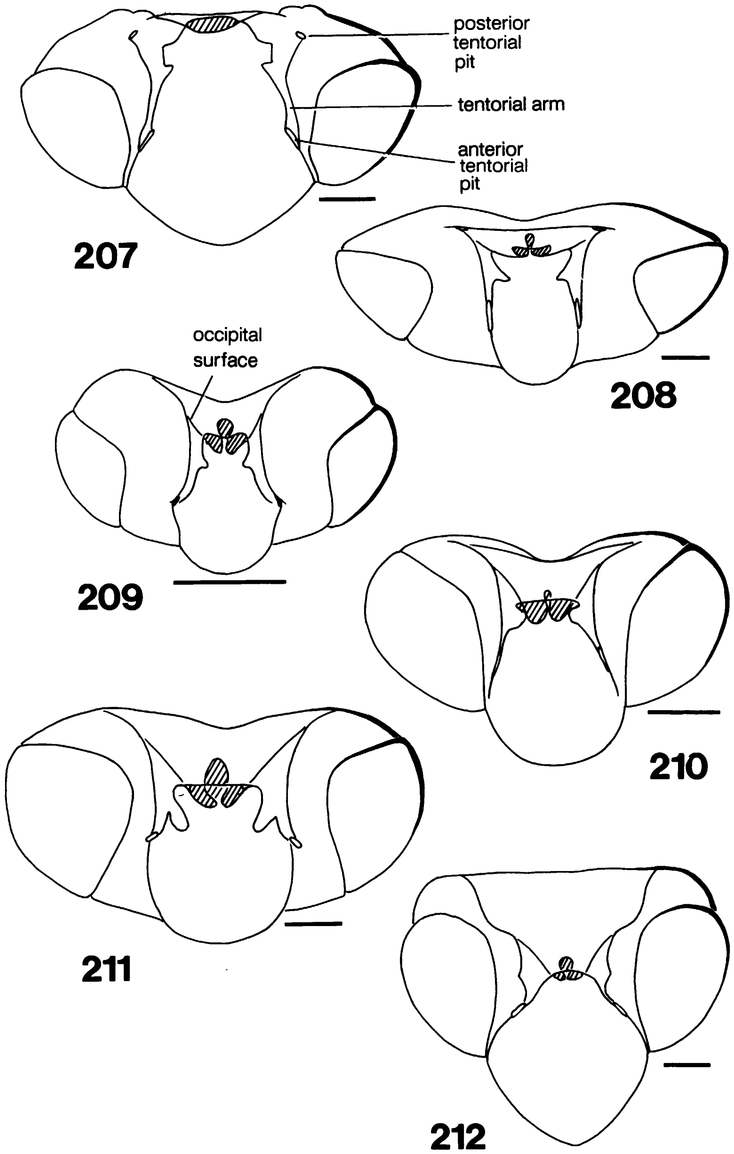
Figs. 203–206. Heads of Bombyliidae, lateral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **203**, *Plesiocera psammophila* lateral; **204**, *P. psammophila* posterior; **205**, *Exoprosopa caliptera* lateral; **206**, *E. caliptera* posterior. Scale for *Plesiocera* 0.5 mm, for *Exoprosopa* 1.0 mm.

228). State 2 appears to be a modification of state 1 confined to the Anthracinae and this character was coded additively. Bezzi (1924) and Hesse (1956b) termed the produced basicosta the basal hook and Hull (1973) termed it the costal hook.

51. Costal vestiture. The costa of most asiloids is covered in long hairs. In a disparate group of Bombyliidae the costal vestiture of males is modified so that it consists of shortened, blunt setae alone or among more sparse hairs. This advanced state was found in *Lordotus, Thevenetimyia* (fig. 222), *Cyrtomyia*, *Lepidophora*, and *Comptosia*. Within *Comptosia* the modified costal vestiture occurs in two species groups (Yeates, 1991b). Dodson and Yeates (1990) found that in *Comptosia* the spines were used in territorial interactions between males. *Thevenetimyia* may also have blunt tubercles in two mediolateral rows on the scutum (fig. 223). Modified costal spines also occur in some species of *Conophorus* (Hull, 1973). Thus this feature has evolved at least six times in the Bombyliidae.

52. Base of M. Plesiomorphically among asiloids the stem of M, between the arculus and the proximal corner of cell dm, is a well-developed tubular vein. In *Hilarimorpha*, and the mythicomyiine genera *Mythicomyia* (fig. 240), *Paraconsors* and *Cephalodromia* (fig. 238) the stem of M is reduced to a flattened, narrow line of sclerotization or absent altogether. This reduction was coded as the advanced state, and appears as an apomorphy for the Mythicomyiinae excluding *Acridophagus* (clade 25), reversing in *Glabellula*.

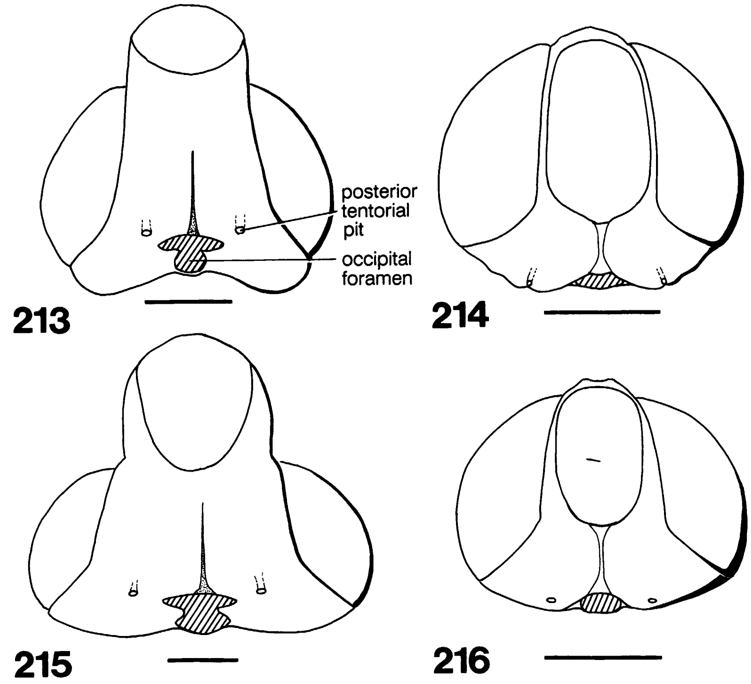
53. Branches of Rs. The radial sector of the "Orthorrhapha" plesiomorphically consists of three well-developed branches, R_{2+3}, R_4, and R_5. In the bombyliid subfamily Mythi-



Figs. 207–212. Heads of Bombyliidae, ventral views showing internal sclerotized structures, vestiture not shown, hatched area is occipital foramen: **207**, *Bombylius major*; **208**, *Pantarbes capito*; **209**, *Mariobezzia lichtwardti*; **210**, *Amictus validus*; **211**, *Cytherea obscura*; **212**, *Exoprosopa caliptera*. Scales 0.5 mm.

comyiinae R_4 and R_5 remain fused along their entire length and there are only two branches of Rs, R_{2+3}, and R_{4+5} (figs. 234, 236, 238, 240). This character was used by Becker (1913) to characterize the Mythicomyiinae (as Cyrtosiinae).

54. Base of R_{2+3}. In all the outgroups and most Bombyliidae R_{2+3} arises acutely from the stem of Rs (figs. 229–232). The advanced state, in which R_{2+3} arises at approximately 90° and then makes another sharp, approximately 90° distal turn shortly afterwards (figs. 241, 243), occurs in the Anthracinae scored here except *Aphoebantus* and *Petrorossia*. I define the advanced state narrowly and exclude those forms such as *Cytherea* and the



Figs. 213–216. Heads of Bombyliidae, ventral views showing features of the gena, vestiture not shown, hatched area is occipital foramen: **213**, *Eclimus gracilis*; **214**, *Zaclava clavifemorata*; **215**, *Thevenetimyia californicus*; **216**, *Dolichomyia gracilis*. Scales 0.5 mm.

Tomomyzinae, in which R_{2+3} arises "abruptly" but at less than a right angle. I also exclude *Aldrichia* which has a short stub vein extending proximally from the basal angle of R_{2+3}.

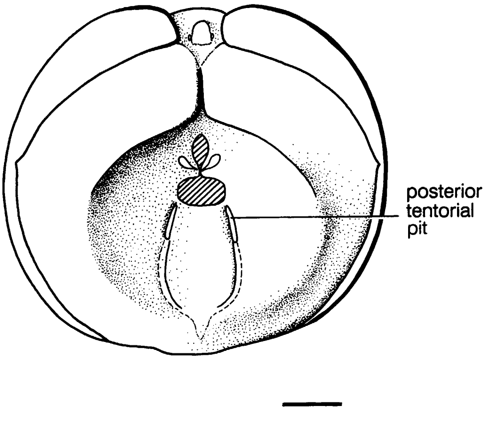
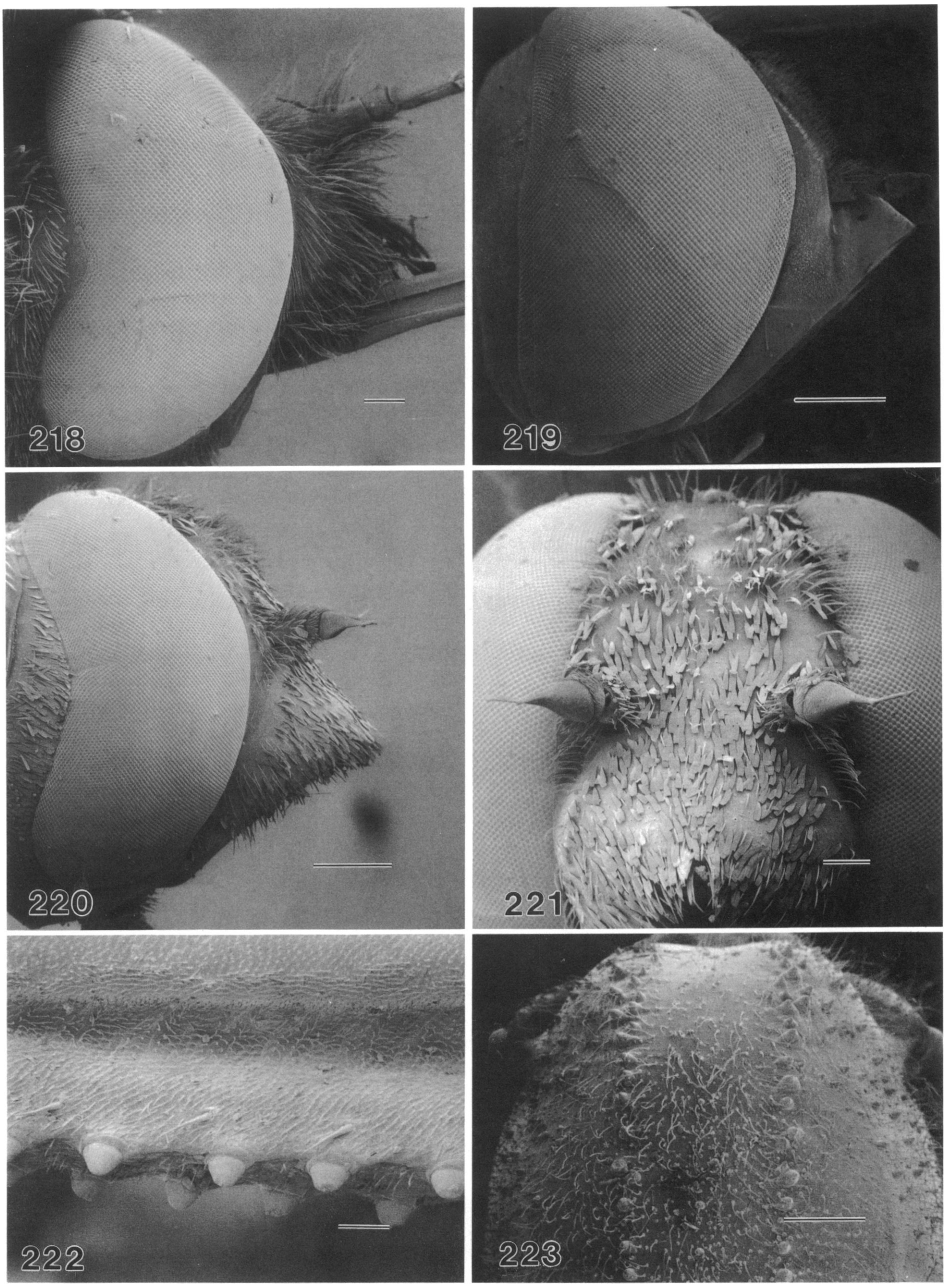


Fig. 217. Posterior view of the head of *Villa alterna* showing the modified postgena (character 47). Scale 0.5 mm.

Becker (1913) considered that this character, in combination with character 56 below, could provide a fundamental division in the Bombyliidae, and discussed the evolution of the apomorphic state. He hypothesized that the forms in which R_{2+3} arises at 90° evolved from bombyliids in which R_{2+3} arose at an acute angle and a short crossvein developed between the base of R_{2+3} and the base of R_{4+5}, arranged perpendicular to them. The original acute stem of R_{2+3} was lost (through intermediates that retain a portion of this stem, such as *Aldrichia*), leaving the perpendicular crossvein to form the base of R_{2+3}.

55. Apex of R_{2+3}. The plesiomorphic condition is for R_{2+3} to join the costal vein near the apex of the wing (figs. 229–232). In *Mythicomyia*, *Glabellula*, and *Paraconsors* of the Mythicomyiinae the advanced state occurs in which R_{2+3} is shortened and joins R_1 before the wing margin (figs. 236, 240). Hull (1973) used this characteristic as a distinguishing feature of his Mythicomyiinae (but it was absent in his Platypyginae which are now united



Figs. 218–223. Scanning electron micrographs of the head and thorax of Bombyliidae: **218**, *Heterostylum robustum* head, lateral, scale 200 μm; **219**, *Amphicosmus cincturus*, head, lateral, scale 500 μm; **220**, *Exoprosopa caliptera*, head, lateral, scale 500 μm; **221**, *E. caliptera*, head anterior, scale 200 μm; **222**, male *Thevenetimyia californicus*, anterior view of costa with modified setae, scale 50 μm; **223**, male *Thevenetimyia californicus*, dorsal view of scutum showing blunt tubercles, scale 500 μm.

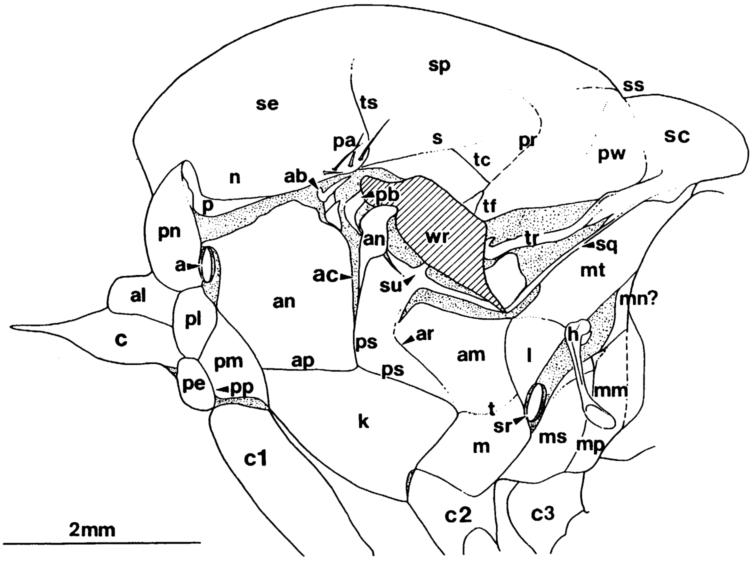
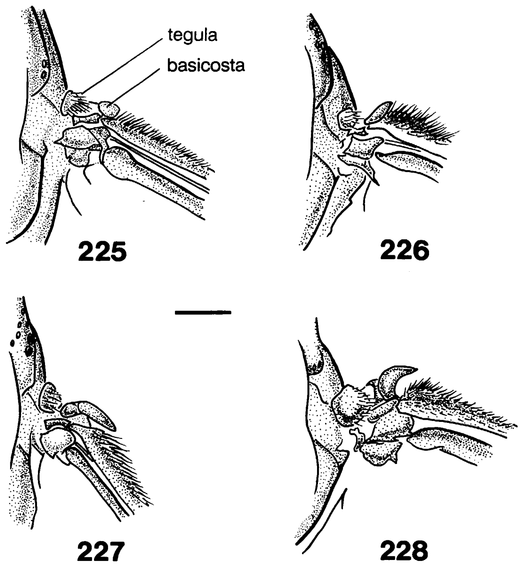


Fig. 224. Lateral view of the thorax of *Comptosia heliophila* Yeates showing terminology for the various sclerites and regions used in this work, vestiture not shown, membrane stippled and wing root cross-hatched. Terminology used by other authors such as Hesse, Hull, Hall and Evenhuis shown in parentheses. Abbreviations as follows:

a	anterior spiracle
ab	anterior basalare
ac	anepisternal cleft
al	antepronotum (median lobe)
am	anepimeron (pteropleuron)
an	anepisternum (mesopleuron)
ap	anapleural suture
ar	anepimeral ridge
c1	prothoracic (fore) coxa
c2	mesothoracic (mid) coxa
c3	metathoracic (hind) coxa
c	2nd laterocervical sclerite
h	haltare
k	katepisternum (mesosternum or sternopleuron)
l	laterotergite (metapleuron)
m	meropleurite (hypopleuron)
mm	metepimeron (posterior metasternum)
mn	metanotum
mp	metapleural suture
ms	metepisternum (metasternum)
mt	mediotergite (metanotum)
n	notopleuron
p	paratergite
pa	prealar bristles
pb	posterior basalare
pe	proepisternum
pl	antepronotum (lateral lobe)
pm	proepimeron (prosternum)
pn	postpronotal lobe (humeral callus)
pp	propleural suture
pr	postalar ridge
ps	mesopleural suture
pw	postalar wall
s	supra-alar area
sc	scutellum
se	presutural scutum (mesonotum)
sp	postsutural scutum (mesonotum)
sq	suprasquamal ridge
sr	posterior spiracle
ss	scutoscutellar suture
su	subalar sclerite
t	transepimeral suture
tf	tergal fissure
tc	tergal fulcrum
tr	tympanal ridge
ts	transverse suture
wr	wing root

with the Mythicomyiinae), and it will be an important feature in the phylogenetics and classification of that subfamily. The apomorphic state also occurs independently in the Apioceridae and Mydidae, but in these cases R_{2+3} is not shortened but joins R_1 near the apex of the wing.

56. Base of R_{2+3} in relation to the r-m crossvein. Vein R_{2+3} usually originates close to the base of Rs (e.g., fig. 239), however in

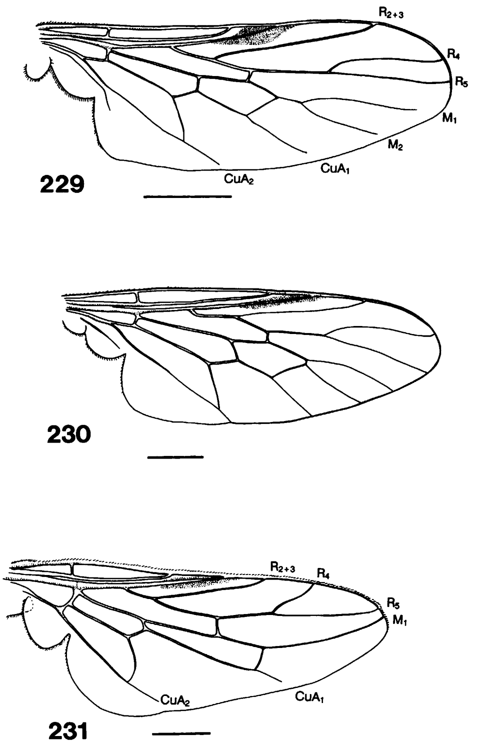


Figs. 225–228. Wing base of Bombyliidae, dorsal views showing tegula and basicosta: **225**, *Bombylius major*; **226**, *Cytherea obscura*; **227**, *Eurycarenus laticeps*; **228**, *Anthrax analis*. Scales 0.5 mm.

Anthrax, *Exoprosopa*, and *Villa* (clade 79) R_{2+3} originates in a more distal position, at or about the level of the r-m crossvein (fig. 243). These three genera also have the advanced state of character 54.

57. Inter-radial crossvein. The crossvein between R_{2+3} and R_4 or R_4 and R_5 is an apomorphic feature which has a scattered distribution among the Bombyliidae. I found it in *Toxophora, Lordotus, Conophorus*, *Aldrichia*, *Mariobezzia*, *Cytherea, Cyllenia*, *Neosardus, Pantarbes*, *Enica*, *Amphicosmus*, *Tomomyza*, *Antonia*, *Exoprosopa*, and *Comptosia*. This character is of uncertain cladistic value at this level because it is not a universal feature of many genera scored here, for example *Comptosia*, *Conophorus*, *Tomomyza*, and *Cytherea*.

58. Wing veins R_5 and M_1. Wing veins R_5 and M_1 plesiomorphically reach the margin of the wing posterior to its apex. In the Apioceridae and Mydidae these veins apomorphically curve strongly toward the anterior margin of the wing and end anterior to wing tip (Woodley, 1989). Nemestrinids and scenopinids also have R_5 and M_1 ending anterior to or at the wing tip, however the veins are not as strongly curved as in the apiocerids and mydids and I did not consider these conditions homologous.



Figs. 229–231. Right wings of various scenopinids: **229**, *Prorates frommeri*; **230**, *Caenotus hospes*; **231**, *Scenopinus fenestralis*. Scales 0.5 mm.

59. Wing vein M_3. Most Asiloidea have wing vein M_3 and its loss has been suggested as a synapomorphy of the Bombyliidae (Mühlenberg, 1971b). The advanced state of this character was found in all the Bombyliidae examined (figs. 233–243). Of the remaining asiloids, the scenopinids, *Hilarimorpha*, and *Apystomyia* (figs. 229–232) have

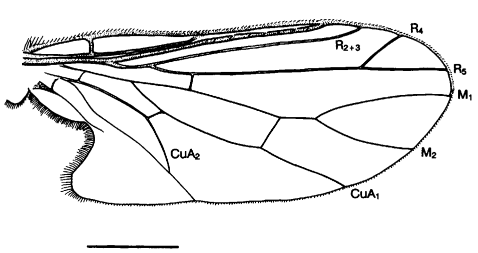


Fig. 232. Right wing of *Apystomyia elinguis*. Scale 0.5 mm.

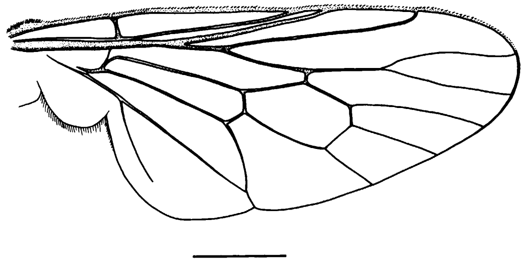


Fig. 233. Right wing of *Heterotropus gilvicornis*. Scale 0.5 mm.

also lost the vein M_3, as have the Muscoidea. Loss of wing veins is a trend throughout the Diptera, and a feature prone to much homoplasy.

60. Wing vein M_2. In addition to the loss of wing vein M_3, Bombyliidae belonging to the Oligodraninae, Usiini, and Toxophorinae have lost M_2 (figs. 235, 237, 242). The Scenopininae have also lost M_2 independently from the Bombyliidae.

61. Diagonal vein. The Nemestrinidae have a characteristic apomorphic conformation of wing veins termed the diagonal vein which crosses the wing obliquely and comprises elements of the R, M, and Cu fields (Bernardi, 1973; Woodley, 1989).

62. Cell r5. The plesiomorphic condition of cell r5 in asiloids is open with vein M_1 reaching the wing margin independently of vein R_5. In some Asiloidea cell r5 is apomorphically closed, with M_1 and R_5 joining before or at the wing margin. I found the apomorphic closed cell r5 in *Neorhaphiomidas*, *Propebrevitrichia*, *Bombylius* (fig. 239), *Heterostylum*, *Oniromyia*, *Amictus*, *Pantarbes*, *Peringueyimyia*, and *Antonia*. The feature is variable in at least the genera *Amictus and Antonia*. Hull (1973) proposed the Bombyliini for Bombyliinae with cell r5 closed, and Bowden (1985) further discussed the use of this character to distinguish tribes of Bombyliinae.

63. Cell m1. In most cases veins R_5 and M_1 are approximately parallel, however in the Scenopininae (fig. 231) they diverge strongly forming cell m1 which widens prominently toward the wing margin (Woodley, 1989). Since the inclusion of the Caenotinae and Proratinae in the Scenopinidae by Yeates (1992), this character becomes an apomorphy of the Scenopininae, not the Scenopinidae.

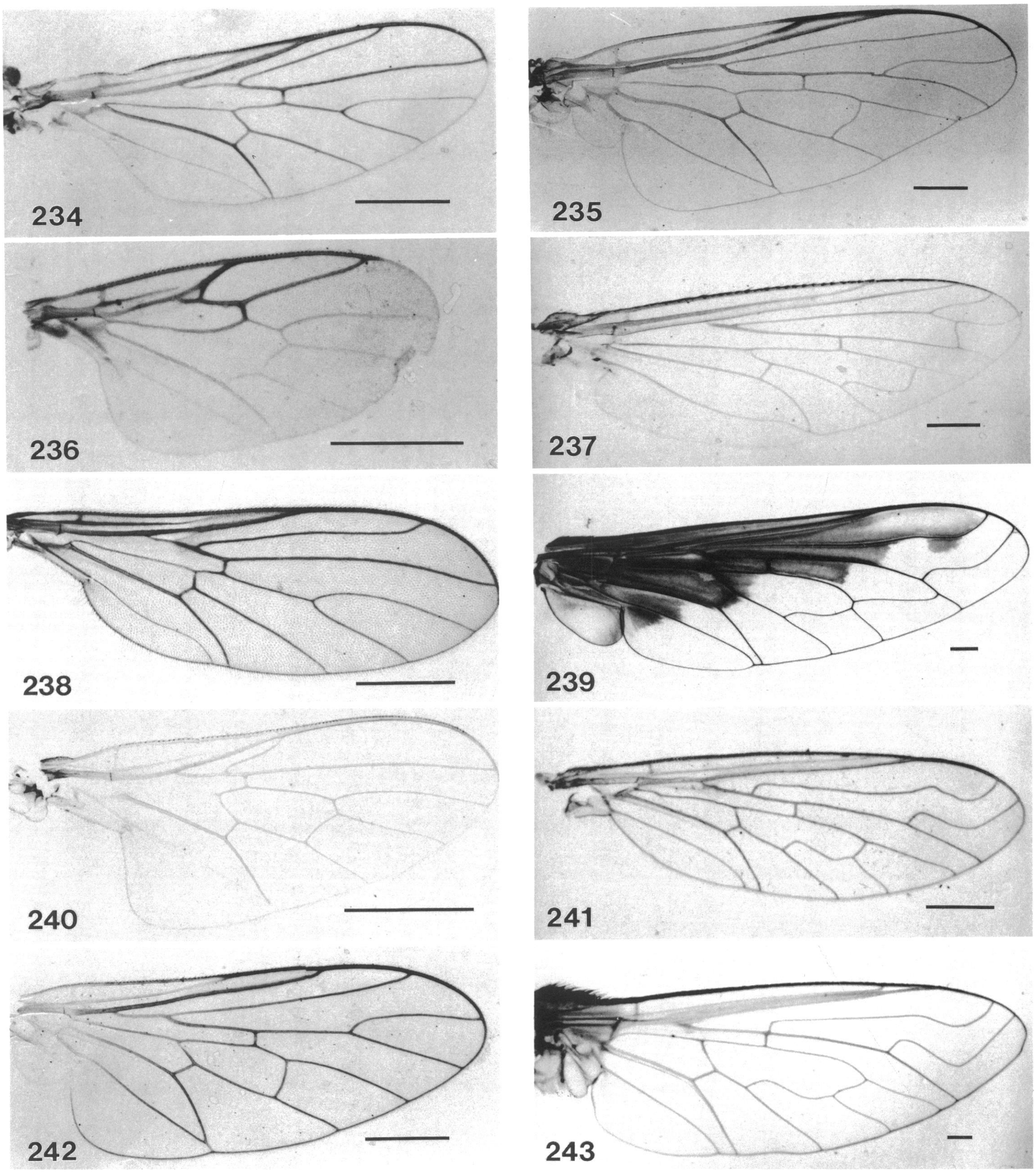
64. Discal or discal medial cell. The prominent wing cell in the center of the Dipteran wing blade is termed the discal cell if entirely within the M field and the discal medial cell if M_3 is lost and the cell is bounded posteriorly by CuA_1 (McAlpine, 1981). In the Bombyliidae M_3 is lost and there is plesiomorphically a discal medial cell (figs. 233, 237, 235, 239, 241–243). The discal medial cell can be lost because of the loss of the distal crossvein dm-cu which closes the cell. I found the discal medial cell absent in *Hilarimorpha* and the Mythicomyiinae examined (figs. 234, 236, 238) except *Mythicomyia* (fig. 240). Hull (1973) found that the discal medial cell was absent in many mythicomyiines and diagnosed the tribe Cyrtosiini on this basis. Evenhuis (1990) found the presence or absence of the discal cell to be variable in *Apolysis*; it was coded as present here.

65. Anal vein. The anal vein is usually present but is apomorphically lost as a tubular vein or reduced so that it does not reach the margin of the wing in the toxophorines *Dolichomyia* and *Zaclava* and in the mythicomyiines *Mythicomyia* (fig. 240), *Paracונsors*, and *Glabellula* (fig. 236).

66. Anal cell. As the anal vein approaches the wing margin it may unite with vein CuA_2 causing the anal cell to close. All asiloids examined had closed anal cells except for the asilids *Stenopogon*, *Leptogaster*, and *Dioctria*. Within the Bombyliidae the anal cell was closed in *Systropus*, the Gerontini, Toxophorini, Usiinae, *Oligodranes*, *Heterotropus*, *Ogcodocera*, and the Mariobezzinae (figs. 242, 235, 237). *Zaclava* and *Dolichomyia* do not have an anal cell due to the partial or complete loss of the anal vein and were coded as inappropriate here. In addition, Greathead (1988) found the anal cell closed in the eclimine *Palintonus* François.

67. Size of lower calypter. Only the acrocerids among the species examined here had the apomorphic state of this character (Woodley, 1989), an enlarged lower calypter.

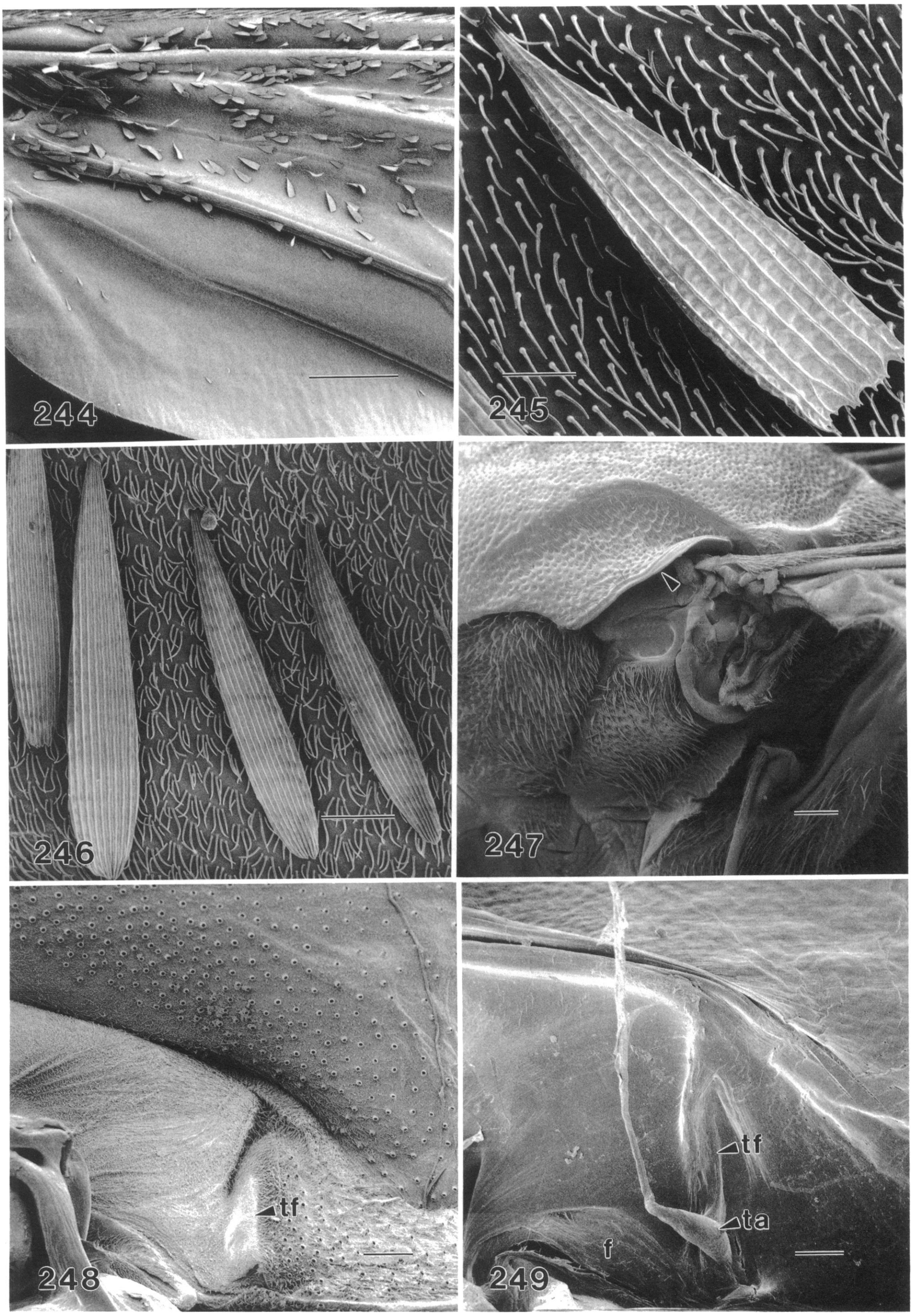
68. Squama (upper claypter). Plesiomorphically the squama is a rounded membranous lobe with the axillary cord running along its margin. I found the membrane of the squama to be apomorphically reduced in



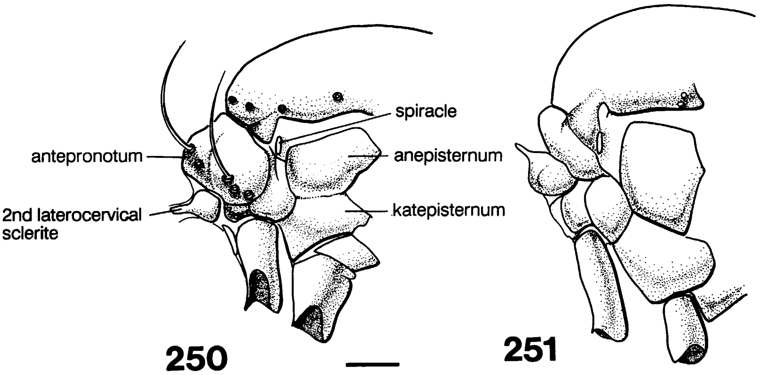
Figs. 234–243. Right wings of various Bombyliidae: **234**, *Acridophagus* sp.; **235**, *Apolysis* sp.; **236**, *Glabellula rotundipennis*; **237**, *Toxophora virgata*; **238**, *Cephalodromia fusca*; **239**, *Bombylius major*; **240**, *Mythicomyia illustris*; **241**, *Plesiocera psammophila*; **242**, *Oligodranes* sp.; **243**, *Villa alterna*. Scales 0.1 mm.

those asiloids with a particularly elongate bodies: *Apiophora*, *Leptogaster*, the Systropodini (fig. 281), *Eclimus*, and the Tomomyzinae. In association with this reduction the axillary cord is adjacent to the body wall.

69. Costal vein. Plesiomorphically the costal vein is complete around the margin of the wing and continues posteriorly as the axillary cord (figs. 230, 242, 239, 241, 243). In a small number of Asiloidea the costal vein is no



Figs. 244–249. Scanning electron micrographs of bombyliid wings sq suprasquamal ridge and thoraces: **244**, *Lepidophora lutea* wing showing scales, scale 500 μm; **245**, *L. lutea* detail of single scale, scale 20 μm; **246**, *Toxophora virgata* thorax, detail of scale, scale 20 μm; **247**, *Systropus macer*, lateral view of wing base, arrow indicates scutal flange, scale 200 μm; **248**, *Bombylius major*, lateral view of thorax just above and behind wing base, tf = tergal fulcrum, scale 50 μm; **249**, *B. major*, image taken



Figs. 250–251. Lateral views of the prothorax of two Bombyliidae: **250**, *Toxophora virgata*; **251**, *Bombylius major*. Scales 0.5 mm.

longer circumambient and I divided this apomorphic condition into two states analyzed nonadditively. In advanced state 1, found in *Geron*, the Phthiriini, *Usia*, *Lepidophora*, and *Cyrtomyia*, the costal vein ends at or near A_1 (fig. 235). In advanced state 2, found in *Hilarimorpha*, *Apystomyia*, the Mythicomyiinae, and all Scenopinidae except *Caenotus*, the costal vein is much shorter and ends at or near vein R_{4+5} (figs. 229, 231–232, 234, 236, 238, 240).

70. Veins of R and M field. Plesiomorphically the veins of the radial and medial field reach the wing margin, however in the Scenopininae and *Prorates* these veins taper and are eventually lost before the wing margin (figs. 229, 231).

71. Wing scales. The wing membrane of asiloids usually have a covering of microtrichia, with larger setae occasionally present on the wing veins. In the Bombyliidae *Lepidophora*, *Cyrtomyia*, *Enica*, and *Toxophora* there are flattened scales present on the wing blade (figs. 244–246). Greathead (1988) also found scales on the wing in the eclimine *Palintonus*.

Under high magnification these scales are similar to but more simple than typical lepidopteran scales, for example those figured by Miller (1987). Lepidopteran scales are characterized by longitudinal ridges connected at intervals by transverse crossribs. Small windows open to the interior of the scale between the crossribs (Ghiradella, 1985). The scales on the wing of *Lepidophora* (fig. 245) have six or seven parallel longitudinal ridges separated by a greater distance than typical lepidopteran scales, and the scales lack crossribs and windows.

72. Prothorax size. Plesiomorphically the prothorax is small and inconspicuous, almost hidden by the vestiture of the postcranium in lateral view (fig. 251). Bezzi (1924) first pointed out that *Toxophora* has an apomorphically enlarged prothorax (fig. 250), as does *Lepidophora*. This enlargement is caused primarily by an elongation of the proantepronotum, and has occurred independently in the two genera.

Zaytsev (1986) examined the morphology of the thorax in the Bombyliidae, Nemestrinidae, and Acroceridae in detail. Much of his discussion concerned the prothorax and the cervical sclerites in particular. Zaytsev (1986) noted the enlarged cephalinger of the second laterocervical sclerites in the Tomophthalmae (figs. 224, 253). I did not code this character because I believe it is completely correlated with the deep postcephalic lobes found in this same group of subfamilies. Once the lobes developed in the Tomophthalmae and the occipital foramen receded deeper into

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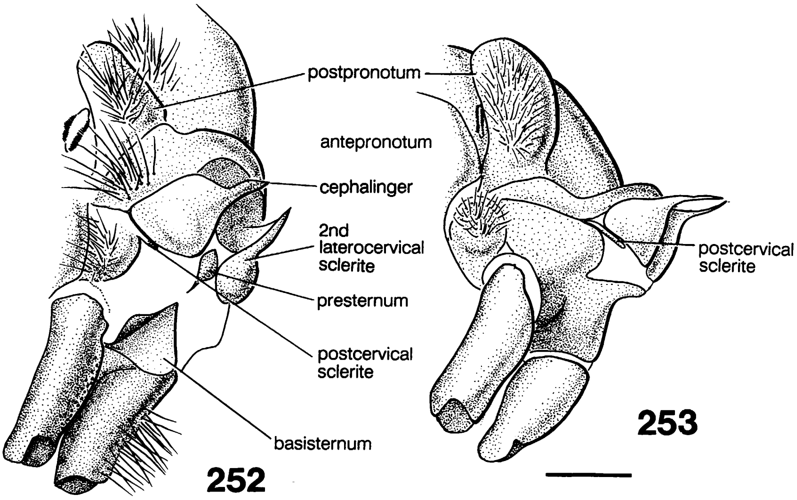
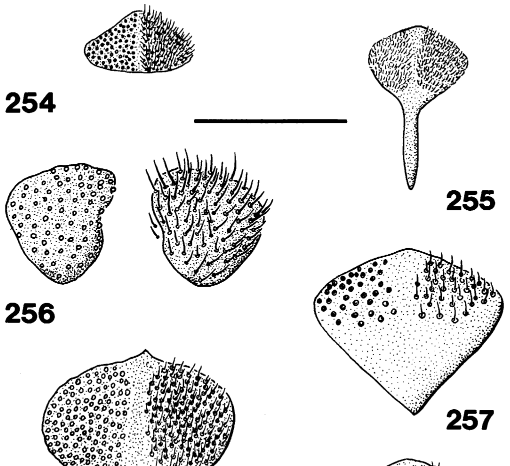
from same position as fig. 248 except inside the thorax, f = tergal fissure, ta = tergal apodeme, tf = tergal fulcrum, scale 50 μm.



Figs. 252–253. Anterolateral views of the cervical region and prothorax of two Bombyliidae: **252**, *Bombylius major*; **253**, *Amphicosmus cincturus*. Scales 0.5 mm.

the back of the head, an elongation of the cervical sclerites was required to maintain a sclerotized articulation between head and thorax.



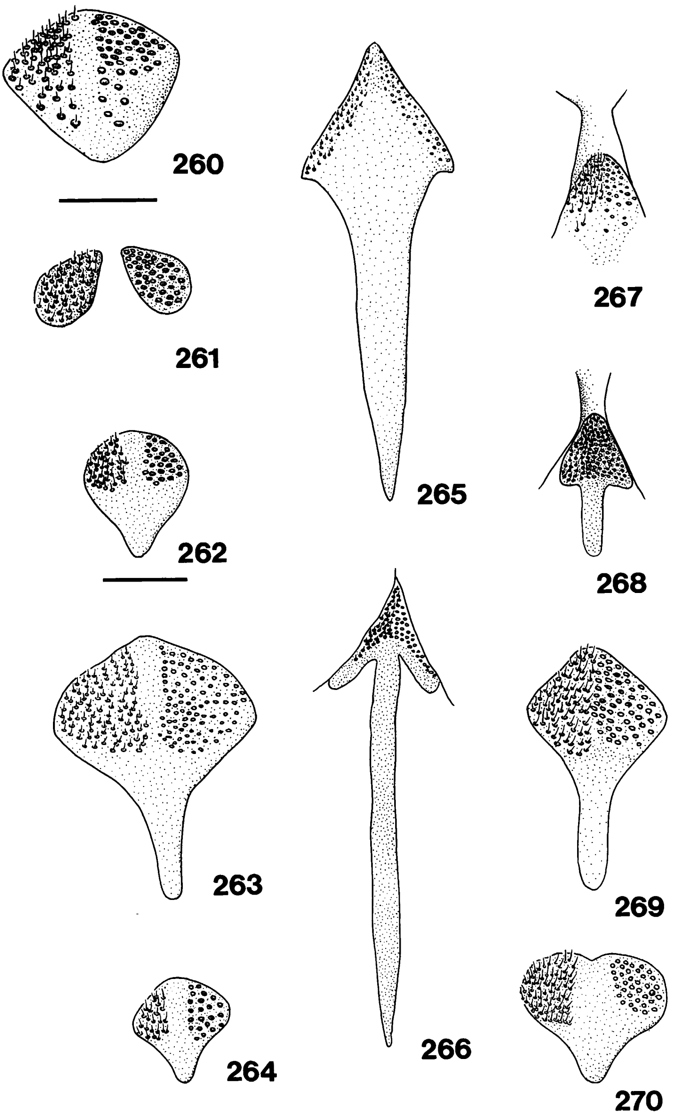
Figs. 254–259. Propresternums of various asiloids: **254**, Rhagionidae, *Rhagio mystaceus*; **255**, Therevidae, *Thereva fucata*; **256**, Asilidae, *Stenopogon inquinatus*; **257**, Scenopinidae, *Scenopinus fenestralis*; **258**, Apioceridae, *Apiocera aldrichi*; **259**, Apsilocephalidae, *Apsilocephala* sp. Scale 0.25 mm except figures 257 and 259 0.1 mm.

73. Form of postcervical sclerites. Zaytsev (1986) noted that the postcervicals become modified within the Tomophthalmae. They separate and shift from a position close to the propleura to lie along the second laterocervical sclerites (figs. 252–253). I found this modification in *Antonia*, the Tomomyzinae, and the Anthracinae except *Aphoebantus*, and it is an apomorphy for clade 72.

Marina (1987) examined the cervix and prothorax of 12 Bombyliidae from both the Homeophthalmae and Tomophthalmae and observed similar modifications to the propresternum and postcervical sclerite as did Zaytsev.

74. Antepronotum vestiture. Plesiomorphically the antepronotum has a covering of soft hairs. In *Apiocera*, *Neorhaphiomidas*, *Toxophora*, *Lepidophora*, *Cyrtomyia*, and *Marmasoma* large setae are also present (fig. 250). Bezzi (1924) used this feature as a characteristic of the Toxophorinae (then containing *Toxophora* and *Lepidophora*) in his key to subfamilies. Greathead (1988) found spines on the prothorax of the eclimine *Palintonus*.

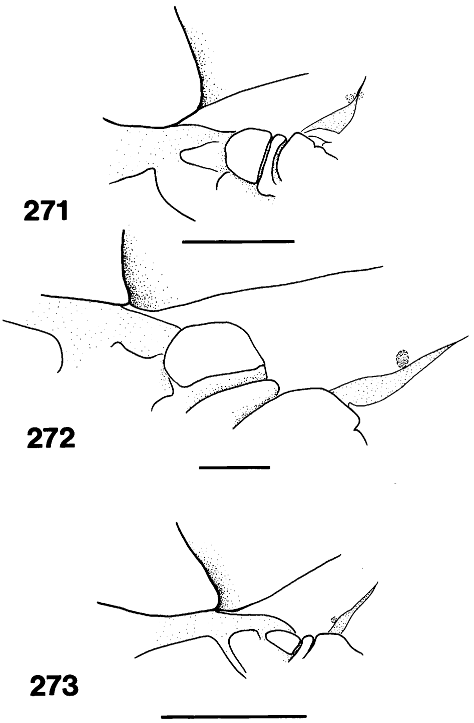
75. Propresternum shape. The propresternum is plesiomorphically rounded or pear shaped with two areas of microtrichia (figs. 254–264, 269–270). In the Asilidae and Mythicomyiinae the sclerotized area of the propresternum has been reduced to two rounded areas of microtrichia (256, 261). In the advanced state, found in the Lomatiinae, To-



Figs. 260–270. Propresternums of various Bombyliidae: **260**, *Heterotropus gilvicornis*; **261**, *Mythicomyia illustris*; **262**, *Geron grandis*; **263**, *Bombylius major*; **264**, *Oniromyia pachycerata*; **265**, *Lomatia belzebul*; **266**, *Exoprosopa caliptera*; **267**, *Cytherea obscura*; **268**, *Sericosoma furva*; **269**, *Corsomyza brevicornis*; **270**, *Usia atrata*. Scale for figures 260 and 261 0.05 mm, scale for remainder same as figure 262 0.1 mm.

momyzinae, and Anthracinae (clade 68) the propresternum is arrow-shaped, with one or two areas of microtrichia (figs. 265–266). Ahmed (1982) first discussed this character and considered that it could be useful in dividing the subfamilies of Bombyliidae into two groups, and Marina (1987) has examined the shape of the propresternum in 12 species of Bombyliidae. Zaytsev (1986) may have overlooked the narrow propresternum of the Anthracinae when he wrote that it was absent in that subfamily. In the Cythereinae the two areas of microtrichia may fuse and the posterior tail become more elongate (figs. 267–268), perhaps anticipating the advanced state.

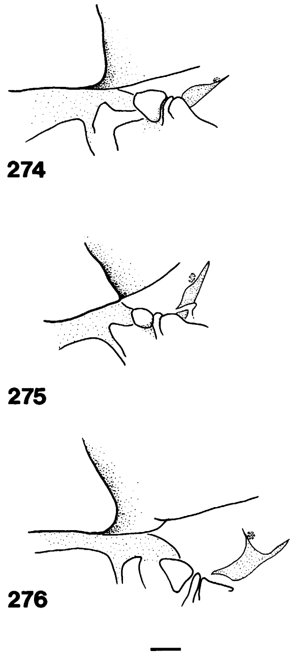
76. Preprocoxal bridge. Zaytsev (1986) discussed the distribution of the preprocoxal bridge in the Diptera, and followed Speight



Figs. 271–273. Tergal fissures of various asiloids: **271**, Rhagionidae, *Rhagio mystaceus*; **272**, Nemestrinidae, *Hirmoneura exotica*; **273**, Scenopinidae, *Scenopinus fenestralis*. Scale 0.5 mm.

(1969) in his conclusion that the bridge has arisen a number of times. He concluded that the preprocoxal bridge was plesiomorphic within the Bombyliidae because of its presence in the Anthracinae and Lomatiinae, subfamilies which he characterized as plesiomorphic. The preprocoxal bridge was absent in the Rhagionidae, Nemestrinidae, and Acroceridae and I coded this as the plesiomorphic state. A preprocoxal bridge was present in all the Apioceridae, Mydidae, Scenopinidae, *Apsilocephala* and Therevidae examined except *Caenotus* and *Apiocera*, and I coded this as the apomorphic state.

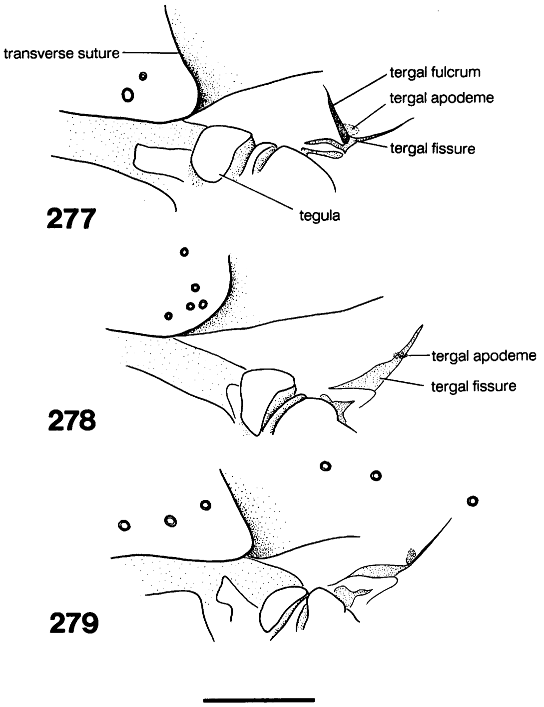
Speculation on the plesiomorphic state of this character in the Asilidae has occupied many journal pages. Hardy (1934) produced a key to tribes and subfamilies of Asilidae which relied heavily on the form of the prothorax. Clements (1951) remarked on the variation in the form of the preprocoxal bridge in the Asilidae, and considered that it was of no use at higher levels. Papavero (1973 a, b) considered that the presence of a preprocoxal bridge was plesiomorphic within the Asilidae but found that among the primitive asilid subfamily Dasypogoninae, only the New World *Blepharepium* Rondani had preprocoxal bridges. Among the Asilidae examined I found a preprocoxal bridge only in *Leptogaster*.



Figs. 274–276. Tergal fissures of various asiloids: **274**, Scenopinidae, *Caenotus hospes*; **275**, Bombyliidae, *Heterotropus gilvicornis*; **276**, Bombyliidae, *Acridophagus* sp. Scale 0.5 mm.

Within the Bombyliidae, I found preprocoxal bridges in *Eurycarenus*, the Tomomyzinae (fig. 253), *Antonia*, *Petrorossia*, and *Anthrax*. Thus the preprocoxal bridges are relatively derived within the Bombyliidae, in contrast to Zaytsev's (1986) conclusion.

77. Anapleural suture. The anapleural suture divides the mesothoracic episternum into dorsal an- and ventral kat- sclerites (fig. 250–251). In the Rhagionidae and most asiloids the anapleural suture is present, however Zaytsev (1986) discussed its apomorphic absence in a number of families. I found the anapleural suture to be lacking in the Nemestrinidae, Acroceridae, *Leptogaster*, and in the bombyliids *Oniromyia* and *Corso-*



Figs. 277–279. Tergal fissures of various asiloids: **277**, Bombyliidae, *Bombylius major* showing tergal fulcrum; **278**, Asilidae, *Leptarthrus brevirostris*; **279**, Therevidae, *Thereva fucata*. Scale 0.5 mm.

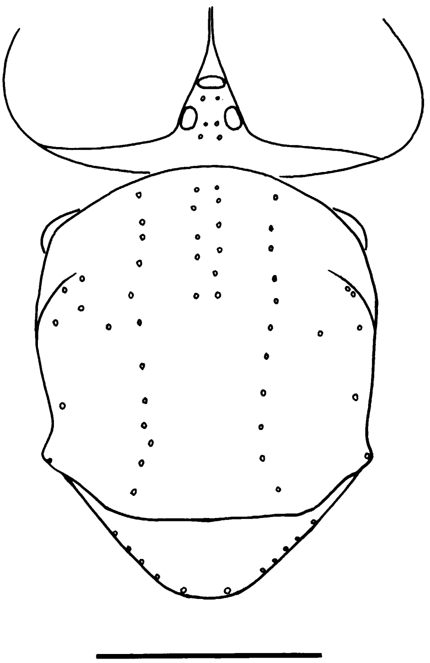


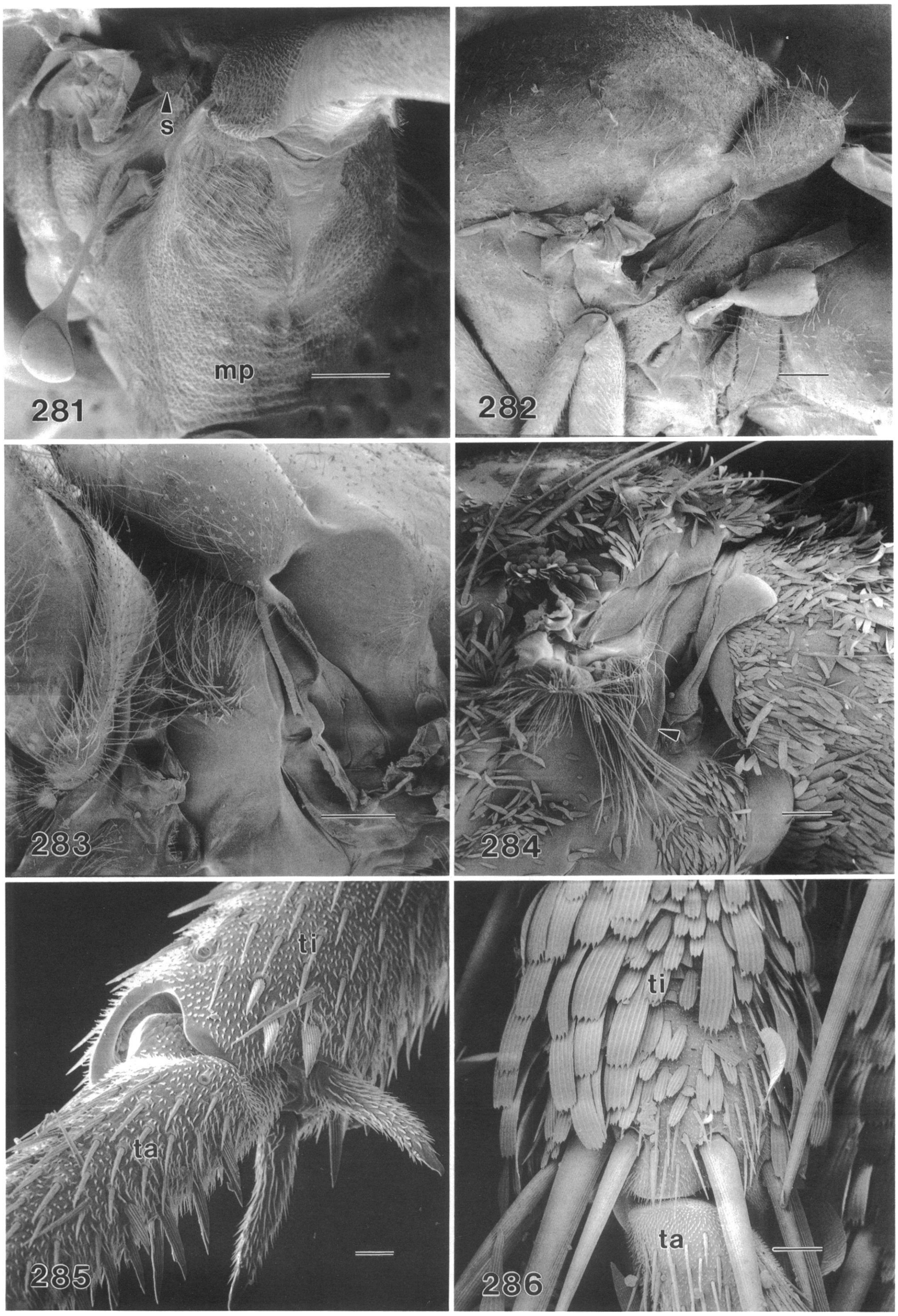
Fig. 280. Dorsal view of head and thorax of *Apystomyia elinguis* showing the position of the setae; some setae adjacent to notopleuron not shown. Scale 0.5 mm.

myza. Within the plesiomorphic state I occasionally found the suture to be weak or lost on its anterior one-quarter, for example, in the Mydidae and Anthracinae. Zaytsev (1986) recorded the anapleural suture absent in the Toxophorini and Heterotropinae, however I found it weak but present (fig. 250).

78. Supra-alar area. The scutum of the Systropodini and Toxophorini has a flange just above the wing base (fig. 247). Painter and Painter (1963) indicate that this apomorphy is "often" present in *Systropus*, indicating its absence in some species. Due to the occurrence of this character in *Zaclava* and *Docidomyia*, I suspect that the absence of a flange in some *Systropus* is derived. Ahmed (1982) described this character and Nagatomi et al. (1991) noted a lateral concave area just above the wing base which is associated with the flange in *Systropus*.

79. Position of tergal apodeme. On the supra alar area is the membranous tergal fissure with its base between the median and posterior notal wing processes and continuing dorsoposteriorly (figs. 271–279). Plesiomorphically the tergal apodeme is placed on the anterior margin of the fissure (figs. 278–279). Bonhag (1949) noted that the posterior tergal muscle (his muscle No. 32) of the basalare originates on the tergal apodeme, and the tendon of this muscle, can be seen in figure 249. Ahmed (1982) first described the apomorphic modification of the tergal fissure found in most Bombyliidae. In all Bombyliidae except the Mythicomyiinae, *Desmatomyia*, and *Heterotropus* the tergal apodeme is found on a small, separate, wedge-shaped sclerite, termed the tergal fulcrum, which runs anteriorly forward from the tergal fissure (figs. 248, 277). *Acridophagus* of the Mythicomyiinae exhibits a bifurcate tergal fissure, with the tergal apodeme lying between the two arms (fig. 276). This may represent a modification of the tergal fulcrum, however was coded as the plesiomorphic state.

The posterior tergal muscle of the basalare is a direct flight muscle and functions in wing



Figs. 281–286. Scanning electron micrographs of the thorax and legs of various Bombyliidae: **281**, *Systropus macer*, posterolateral view of thorax showing postmetacoxal bridge, s = strigilis, ms = metepimeron, scale 500 μm; **282**, *Desmatomyia anomala*, dorsolateral view of thorax, scale 200 μm; **283**, *Thevenetimyia californicus*, posterolateral view of thorax, scale 500 μm; **284**, *Toxophora virgata*, lateral view of meso- and metathorax, arrow indicates laterotergite, scale 200 μm; **285**, *D. anomala*, apex of

extension (Bonhag, 1949). It is tempting to speculate on the functional significance of the modification of the tergal apodeme in Bombyliidae. While Diptera generally fold their wings over the abdomen at rest, most Bombyliidae hold their wings outstretched when at rest (Yeates, personal obs.; photographs of living Bombyliidae as in Batra, 1965; Deyrup, 1988; Du Merle, 1966; 1971; Leech and MacDonald-Leech, 1989). The exceptions to this generalization recorded in the Bombyliidae lack the tergal fulcrum: the Mythicomyiinae (Mühlenberg, 1973), *Heterotropus* (Irwin, personal commun.), and *Desmatomyia* (Yeates and Irwin personal obs. June 1992). Thus the modification of the tergal apodeme may be associated with the modified wing position of most bee flies at rest.

Vestiture on the pleural regions of the meso- and metathorax of Bombyliidae varies in its distribution and is coded in characters 80, 82, and 83 below.

80. Anepimeron vestiture. The Rhagionidae examined lack hairs on the anepimeron; hence this were considered plesiomorphic. The Nemestrinidae and Acroceridae have hairs on the anepimeron, and were coded as the apomorphic state. A minority of Asiloidea had haired anepimera: *Mydas*, *Apiophora*, *Apiocera*, *Phthiria*, *Bombylius*, *Eurycarenus*, *Oniromyia*, *Cytherea*, *Enica*, *Ylasoia*, *Ogcodocera*, *Villa*, *Anthrax*, and *Exoprosopa*.

81. Strigula. Apomorphically present is a membranous flap on the tympanal ridge just beneath the sides of the scutellum of the Systropodini (fig. 281). The strigula was first described by Williston (1901), and the various subsequent terminologies are detailed by Painter and Painter (1963). I coded the much smaller structure in *Toxophora* 0.

82. Laterotergite vestiture. Plesiomorphically the laterotergite has a tuft of long hairs (fig. 283), however it has apomorphically lost the vestiture in numerous Asiloidea. Among the Bombyliidae I found a bare laterotergite to be most common, however the plesiomorphic state was present in *Lordotus, Bombylius*, *Eurycarenus*, *Marmasoma*, *Sericosoma*, *Oniromyia*, *Cytherea*, *Ogcodocera,* the Tomomyzinae and Antoniinae, and all the Anthracinae except *Exoprosopa* and *Villa*. Bowden (1985) placed great importance on this character in distinguishing tribes of the Bombyliinae. He diagnosed the Bombyliini as possessing a dense, prominent hair tuft and cell r5 closed. Among the lomatiines, *Ogcodocera* has the plesiomorphic state and Yeates (1989) found a haired laterotergite only in *Lyophlaeba* Rondani and *Doddosia* Edwards. Evenhuis (1990) found micropubescence on the laterotergite (as metapleuron) in the genera of the subtribe Phthiriini, however his data matrix codes *Acreophthiria* Evenhuis as having a bare laterotergite. I do not consider this micropubescence to be homologous with hairs because each filament lacks a basal articulation (see Yeates, 1988).

83. Mediotergite vestiture. The mediotergite plesiomorphically lacks hairs, however a tuft of hairs is apomorphically present in the Acroceridae, *Neorhaphiomidas*, *Lordotus, Marmasoma*, *Thevenetimyia* and *Eclimus*, the Lomatiinae, *Antonia*, *Plesiocera*, *Exoprosopa*, and *Villa*. Yeates (1989) also found a haired mediotergite in *Ligyra*.

84. Mediotergite and laterotergite shape. The medio- and laterotergite are usually rounded sclerites, the mediotergite being somewhat tumid. In *Toxophora* these sclerites are modified into an angled ridge (fig. 284). The laterotergite of *Systropus* is also produced into a ridge (fig. 247), but is not as sharply produced as in *Toxophora*.

85. Metepisternum and metepimeron size. A prominent apomorphy of the Systropodini is their enlarged metapleuron (fig. 281). This character was first used by Bezzi (1924).

86. Postmetacoxal bridge. In *Systropus* the metepimera becomes so enlarged that they meet behind the coxae forming a postmetacoxal bridge (fig. 281; Yeates and Hagan, 1988).

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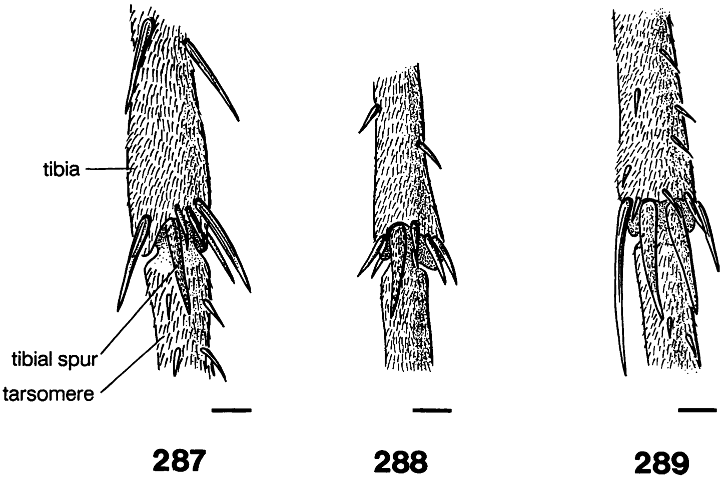
midtibia showing tibial spurs, ti = tibia, ta = 1st tarsomere, scale 20 µm; **286**, *T. virgata*, apex of midtibia showing setae inserted on tibia, ti = tibia, ta = 1st tarsomere, scale 50 µm.



Figs. 287–289. Apex of the midtibia of three Bombyliidae showing tibial spurs: **287**, *Conophorus fenestratus*; **288**, *Crocidium karooanum*; **289**, *Amictus validus*. Scales 0.1 mm.

87. Prealar bristles. The prealar bristles are large setae found laterally on the mesonotum just anterior to the transverse suture (figs. 277–279). They are present in most asiloids, although absent in Scenopinidae (but weakly present in *Prorates*); among the Bombyliidae they are present in *Oligodranes*, *Poecilognathus*, *Toxophora*, the Bombyliinae, *Crocidium*, *Megapalpus*, and clade 61 except *Ogcodocera* and the Tomomyzinae.

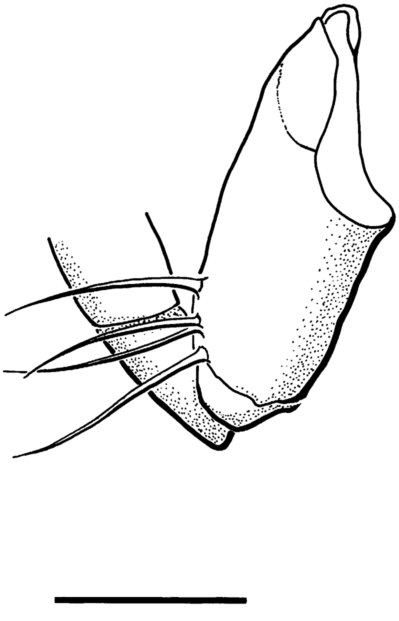
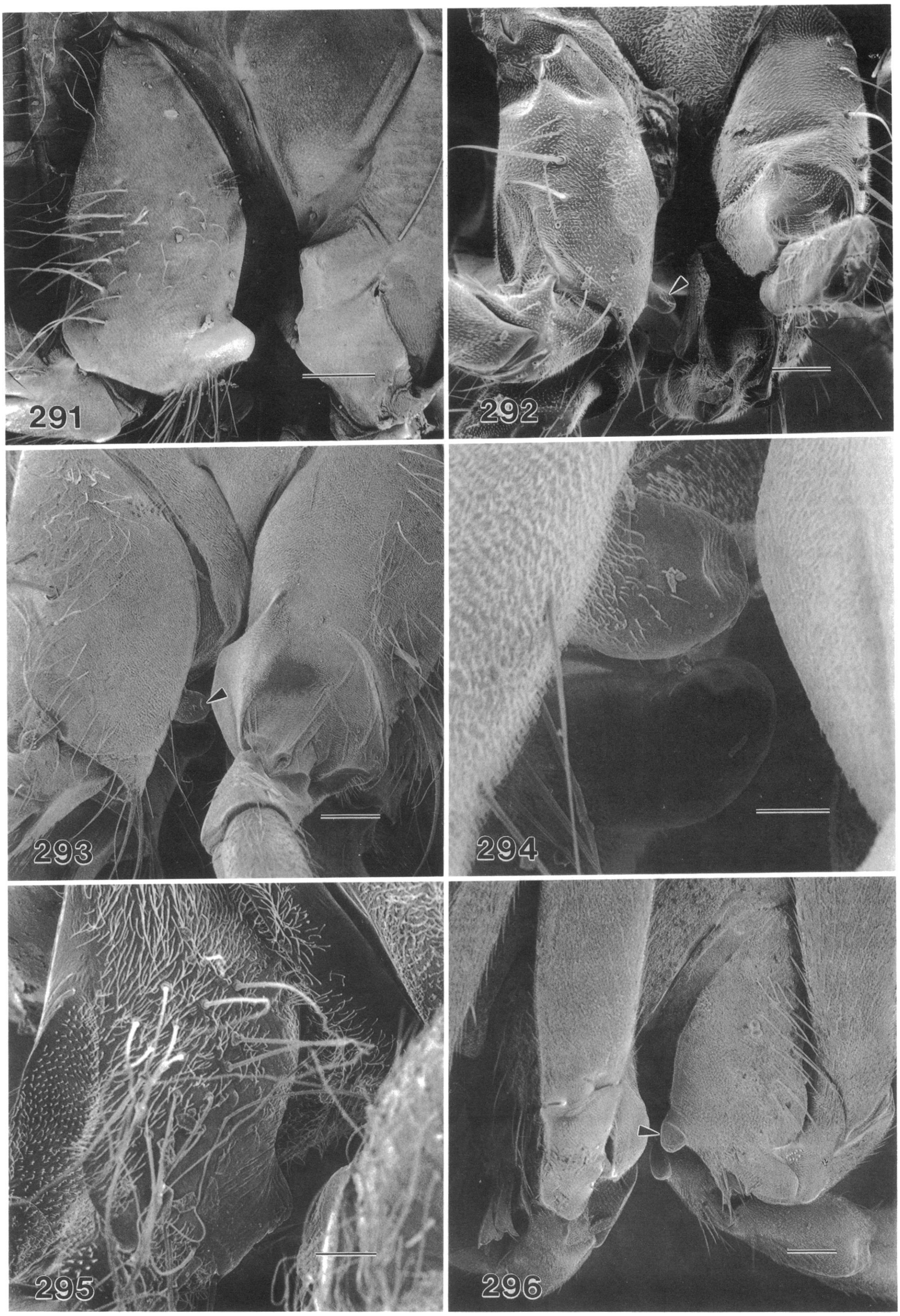


Fig. 290. Right forecoxa of the therevid *Thereva fucata* showing strong setae on apical half. Scale 0.5 mm.

88. Transverse suture. The transverse suture of the mesoscutum is plesiomorphically present, but is often reduced medianly. In *Neorhaphiomidas* and the Acroceridae examined (and other more divergent acrocerids such as *Ogcodes* and *Megalybus*), the transverse suture is completely absent, even laterally. This provides another synapomorphy for the Acroceridae.

89. Fore and hind tibial spurs. Woodley (1989) differentiated tibial spurs from other tibial setae by their point of origin: true tibial spurs are inserted on the membrane between the tibia and first tarsomere, rather than on the tibia itself. Fore and hind tibial spurs were only found in the rhagionids examined, and their loss provides a synapomorphy for the Muscomorpha as Woodley (1989) proposed. Midtibial spurs, however, were found in some Bombyliidae (character 90).

90. Midtibial spurs. Among the asiloids, true mesothoracic tibial spurs, coded the plesiomorphic state, were found in the rhagionids and in a number of bombyliid genera, where their presence is interpreted as an independent apomorphic origin. Two pairs of midtibial spurs were found in *Lordotus*, *Desmatomyia* (fig. 285), *Aldrichia*, *Eclimus*, and



Figs. 291–296. Hind coxae of Rhagionidae and various asiloids, posterior to left except figure 296 posterior to right: **291**, Rhagionidae, *Rhagio mystaceus*, scale 200 μm; **292**, Apsilocephalidae, *Apsilocephala* sp., arrow indicates coxal peg, scale 100 μm; **293**, Therevidae, *Anabarhynchus* sp. arrow indicates coxal peg, scale 200 μm; **294**, detail of coxal peg in figure 293, scale 50 μm; **295**, *Caenotus hospes*, scale 50 μm; **296**, *Desmatomyia anomala*, arrow indicates coxal peg, scale 100 μm.

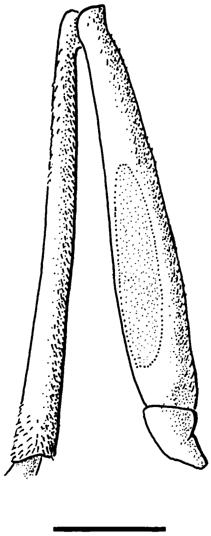


Fig. 297. Foretrochanter, coxa, and tibia of *Systropus macer* showing sensory area. Scale 0.5 mm.

Amictus (fig. 289) and a single midtibial spur was found in *Conophorus* (fig. 287) and *Crocidium* (fig. 288). Woodley (1989) considered the loss of tibial spurs apomorphic for the Muscomorpha, however only the loss of fore and hind tibial spurs is apomorphic for the Muscomorpha. It appears from the discussion in Woodley (1986) that stratiomyids have also lost the fore and hind tibial spurs.

In distinguishing the Phthiriini (as Phthiriinae) from the Usiini (as Usiinae), Evenhuis (1990) found that the Phthiriini have the forecoxae well separated at their bases in anterior view, whereas the Usiini have the bases of the forecoxae approximated. I was unable to use this character because I found it difficult to distinguish discrete states among the wide variety of asiloids coded here. Forecoxal separation appears to vary in relation to the width of the prosternum, those species with a deep median cleft in the prosternum having coxae which are more closely approximated than those species with a flat prosternum.

91. Coxal vestiture. The coxal vestiture of asiloids includes hairs, scales, and occasionally a few scattered setae. In the Therevidae examined the apex of each coxa has a distinct group of stout setae on the anterior face (fig. 290). These stout setae often differed in color from the other hairs on the coxa, and may be present on all three coxae, the mid and hind, or hind only. Other asiloids (e.g., asilids and apiocerids) may have stout setae on the coxae, however they are scattered all over each coxa, both apically and basally. Stout setae were also found restricted to the apex of the coxa in the eclimines *Marmasoma*, *Lepidophora*, and *Cyrtomyia*, however these have developed independently from those found in the Therevidae.

92. Shape of the hind coxae. The hind coxae of the Therevidae plus *Apsilocephala*, *Hilarimorpha*, *Desmatomyia*, *Crocidium* and *Oligodranes* all have a short peg on the anterior face of the hind coxa (figs. 292–294, 296; also Irwin and Lyneborg, 1981b, figs. 9 and 10). A similar protuberance is also known in many Rhagionidae, Athericidae, and Xylophagidae (fig. 291), however I do not consider the tabanomorph protuberance homologous with the one found in the Asiloidea because of its more rounded shape and its position closer to the apex of the coxa.

93. Femur vestiture. The femora of asiloids are most often armed with one or more longitudinal rows of setae (fig. 341), however these setae are absent in rhagionids, nemestrinids and acrocerids and this was coded as the plesiomorphic state. Many Bombyliinae and some members of clade 62 including the Tomomyzinae, *Cyllenia* and *Pantarbes* lack these stout setae. Greathead (1988) found that the eclimines except *Eclimus* had spines on the femora.

94. Forefemur. The forefemur of *Systropus* has an elongate, rounded "sensory" area on its outer face which is not found in other Asiloidea (fig. 297; Painter and Painter, 1963).

95. Hind femur vestiture. A characteristic feature of the Mydidae is the presence of a ventral row or rows of thick, shortened bristle-like pegs on the hind femur (Wilcox, 1981; Woodley, 1989). *Neorhaphiomidas* has a row of bristles ventrally on the hind femora (fig. 341), however these were coded the plesiomorphic state because they were more slender and longer than those found in the Mydidae.

96. Pulvilli. Primitively the pulvilli are flattened, rounded lobes about as long as the tarsal claws (figs. 299–301). In *Leptogaster*, *Heterostylum*, *Cytherea*, *Enica*, *Neosardus*, *Exoprosopa*, and *Villa* the pulvilli are re-

duced to one-half the tarsal claw length or less (figs. 303–304). They are also reduced in some genera not coded here, e.g., *Anastoechus* Osten Sacken.

97. Empodium shape. Woodley (1989) considered a bristleform empodium to be apomorphic for the Muscomorpha excluding the Nemestrinoidea. I have found the descriptive term "bristleform" inadequate to describe many asiloid empodia. They are most often reduced in size and triangular in shape with an acute apex but bearing small setae (figs. 298–299). No asiloids were found with pulvilliform empodia in this study. Some asiloids have lost the empodium: Mydidae (Wilcox, 1981); some Apioceridae (Peterson, 1981b); four genera of leptogastrine Asilidae (Martin, 1968), and *Hilarimorpha* (Webb, 1974).

98. Foretarsal claw size. Plesiomorphically all tarsal claws are approximately the same size (figs. 300–301). The anthracine genera *Plesiocera*, *Villa*, and *Exoprosopa* have the foreclaws reduced and much smaller than the mid and hind claws (figs. 302–303). This reduction in the pretarsus is associated with an overall reduction in size of the foreleg.

99. Pulvillus shape. Many authors (e.g., Hull, 1973; Hall, 1976) have mistaken the modified, cone-shaped pulvilli underneath the tarsal claws of the Exoprosopini (figs. 303–304) as basal teeth on the claw itself. Not surprisingly, these genera are also described as having lost the pulvilli. Spinelike pulvilli are also present in the bombyliine *Zinnomyia* Hesse.

ABDOMEN

100. Abdominal tergite 2. Theodor (1983) was the first to notice the sensory areas on abdominal tergite 2 of the Scenopininae and *Prorates*. Woodley (1989) was not convinced that this similarity indicated a relationship between *Prorates* and the Scenopininae because of the different shape of the sensory areas in the two groups and the wing venation of *Prorates* which is dissimilar to that of the Scenopininae.

Scanning electron microscopy indicates that the position, size, and shape of the sensory patches in the Scenopininae, *Caenotus*, and *Prorates* are similar and I consider them homologous. This was part of the evidence which led me to remove the Proratinae (excluding *Apystomyia*) from the Bombyliidae to the Scenopinidae (Yeates, 1992a).

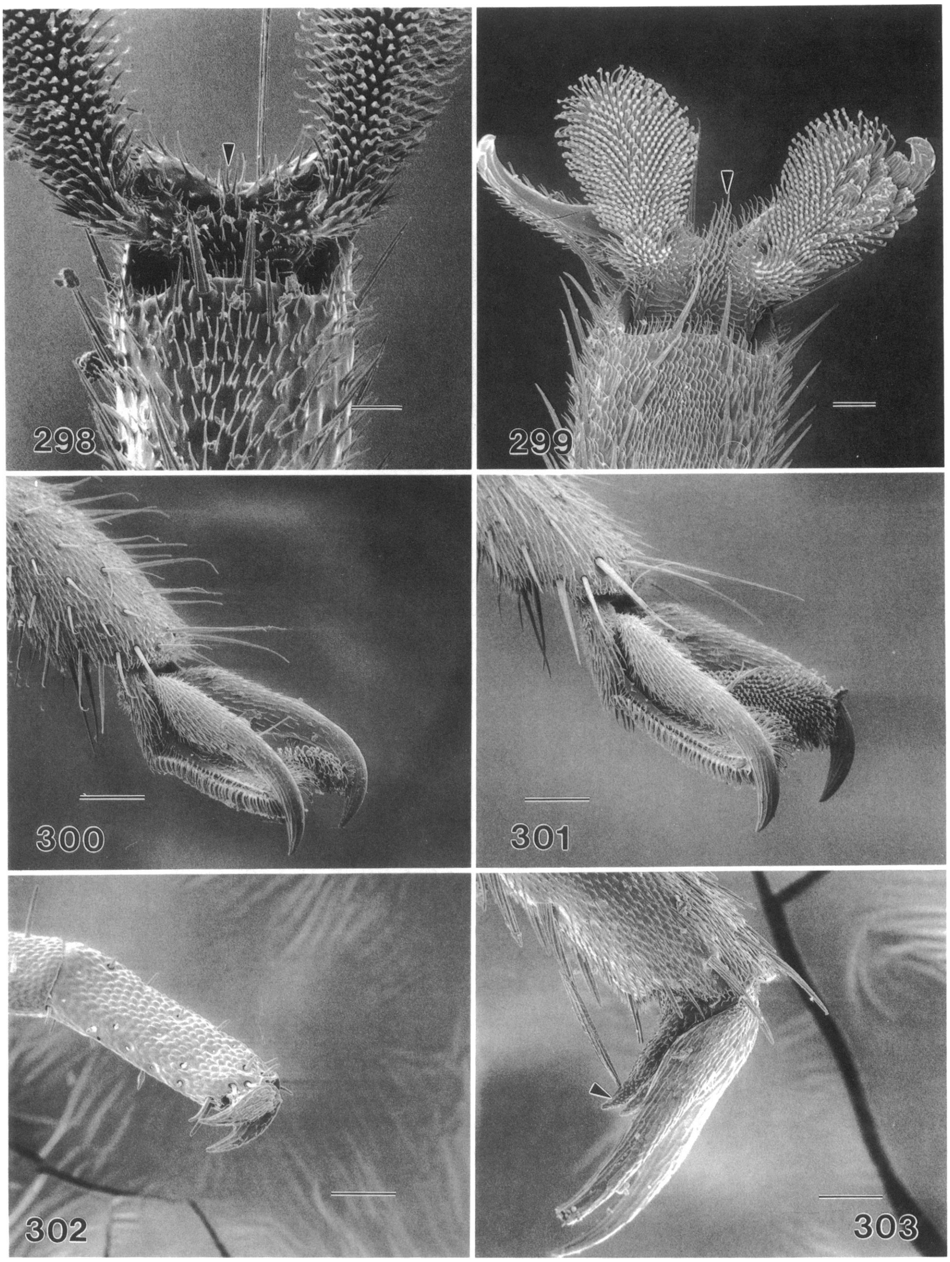
The sensory area of the Scenopininae and *Caenotus* is made up of two semicircular areas of enlarged setae (figs. 306–309) while in *Prorates* the sensory area consists of a triangular area of enlarged setae (fig. 305). The setae comprising the sensory patch in *Prorates, Caenotus,* and the Scenopininae are all similarly fluted. In *Prorates* the setae are truncate, whereas those of *Caenotus* and the Scenopininae are evenly tapered.

101. Abdomen shape. Most asiloids have cigar-shaped abdomens which taper toward the apex, which I considered the plesiomorphic state. In some Bombyliidae, particularly the Bombyliinae, the abdomen is short and rounded. In *Leptogaster* of the Asilidae and the Systropodini the abdomen is apomorphically very narrow and elongate, often with a slight widening apically.

102. Position of abdominal spiracles. All species examined here have functional abdominal spiracles on abdominal segments 1–7. Primitively, all abdominal spiracles are located in the pleural membrane. Occasionally in the Asiloidea they have migrated dorsally into the tergite above. This was found to be the case in the spiracles of segments 2–7 in the therevid *Phycus* and in all the abdominal spiracles of the Mythicomyiinae (figs. 312, 429). This character provides a useful synapomorphy for the Mythicomyiinae (Zaytsev, 1992), and Mühlenberg (1971b) used it as his character 9; however he mistook segment 7 for 8. The abdominal spiracles of Acroceridae are located in the tergites, sternites, or pleural membrane (Schlinger, 1981). I found abdominal spiracle 1 of both *Eulonchus* and *Lasia* located on the tergite, however I do not consider this condition to be homologous with the condition found the Asiloidea.

MALE GENITALIA

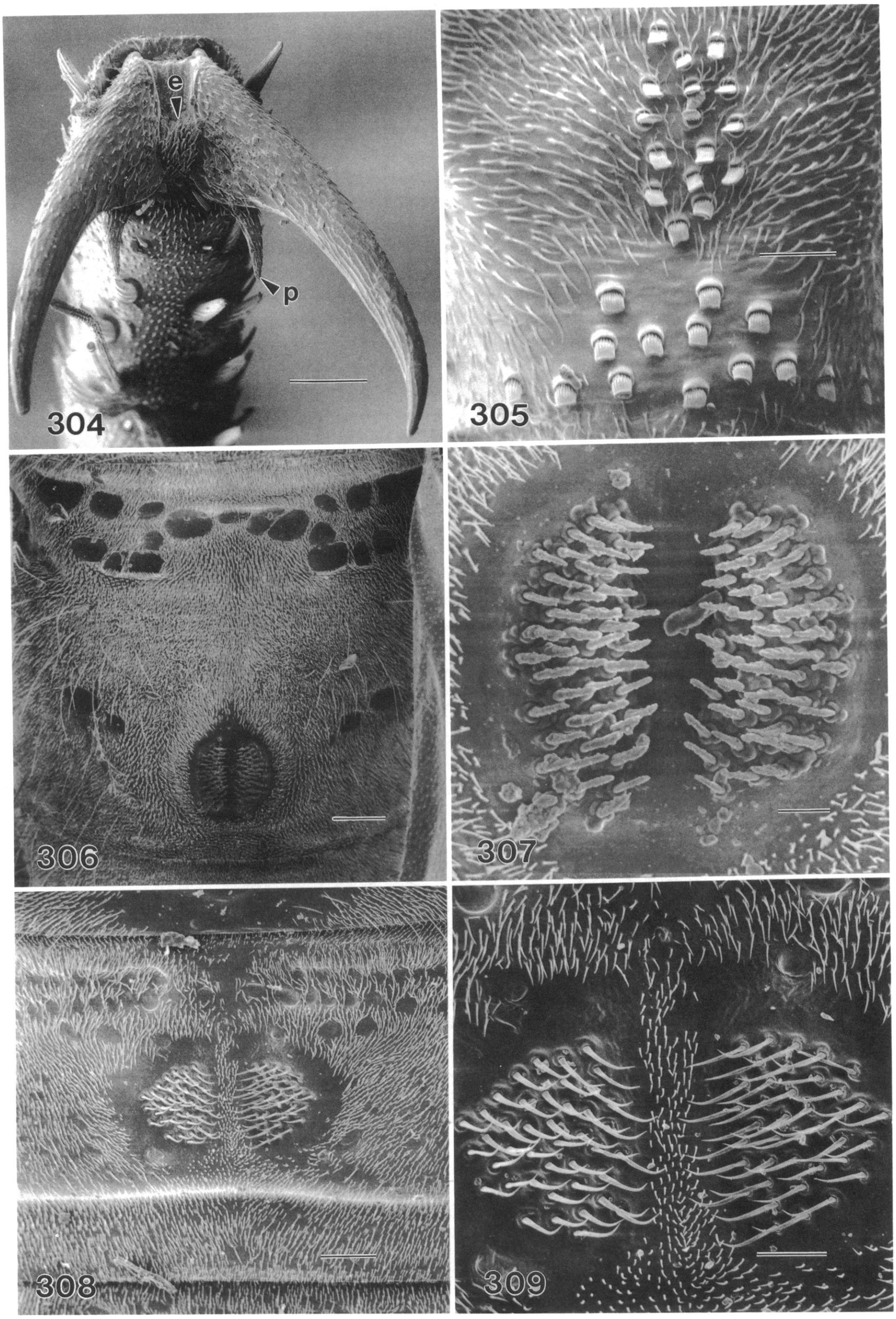
The male genitalia of Asiloidea are complex and contain much phylogenetic information. While much of this variation is useful at lower taxonomic levels than those of concern here, I have scored 22 characters which describe more conservative modifications. The terminology used here for male



Figs. 298–303. Pretarsus of various Bombyliidae: **298**, *Heterotropus gilvicornis*, arrow indicates empodium, scale 10 μm; **299**, *Desmatomyia anomala*, arrow indicates empodium, scale 20 μm; **300**, *Bombylius major*, fore pretarsus, scale 50 μm; **301**, *B. major*, hind pretarsus, scale 50 μm; **302**, *Exoprosopa caliptera* fore pretarsus, scale 50 μm; **303**, *E. caliptera* hind pretarsus, arrow indicates pulvillus, scale 50 μm.

genitalia is compared to that of previous authors in table 2.

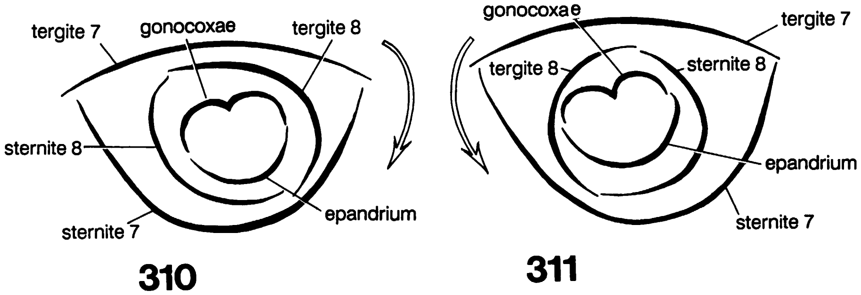
One particular aspect of male genitalic variation which I did not score was the rotation of the genital capsule. Within the Asiloidea, genitalic rotation appears to be an advanced feature derived independently in a number of families (McAlpine, 1981).



Figs. 304–309. Pretarsus of a bombyliid and abdominal tergite 2 of various Scenopinidae: **304**, *Exoprosopa caliptera* hind pretarsus, e = empodium p = pulvillus, scale 50 μm; **305**, *Prorates* sp., detail of sensory area on abdominal tergite 2, scale 20 μm; **306**, *Caenotus hospes*, abdominal tergite 2, scale 100 μm; **307**, *C. hospes*, detail of sensory area in figure 306, scale 20 μm; **308**, *Scenopinus fenestralis*, abdominal tergite 2, scale 100 μm; **309**, *S. fenestralis*, detail of sensory area in figure 308, scale 50 μm.

TABLE 2
Terminology for Structures of the Male Genitalia Used Here in Comparison with Those of Previous Authors
Dashes indicate that the relevant structure could not be found in the work cited

Term used here	Hesse, 1938	Bowden, 1964	Hull, 1973	Hall, 1976	Hall + Evenhuis, 1980–1987	Theodor, 1983
epandrium	last sternite	—	epandrium	epandrium	epandrium	epandrium
hypandrium	—	—	9th sternum	—	—	hypandrium
gonocoxite	basal parts	basimere	basistylus	basistylus	basistylus	gonocoxa
gonostylus	beaked apical joint	telomere	dististylus	dististylus	dististylus	dististylus
aedeagal sheath	ventral aedeagal process	aedeagal sheath	epiphallus	aedeagus	epiphallus	aedeagus
basiphallus	aedeagus	aedeagus	aedeagus			
distiphallus						
lateral aedeagal apodeme	lateral strut	paraphysis	lateral ejaculatory apodeme	lateral wing	—	basal plate
ejaculatory apodeme	basal strut	aedeagal apodeme	basal ejaculatory apodeme	basal keel	basal apodeme	aedeagal apodeme
point where aedeagal sheath joins gonocoxite	ramus	lateral process	ramus	—	lateral rami	lateral strut



Figs. 310–311. Diagrammatic sections through the terminalia of two anthracine Bombyliidae, arrows indicate the direction of rotation: **310**, *Aphoebantus cervinus*; **311**, *Anthrax analis*.

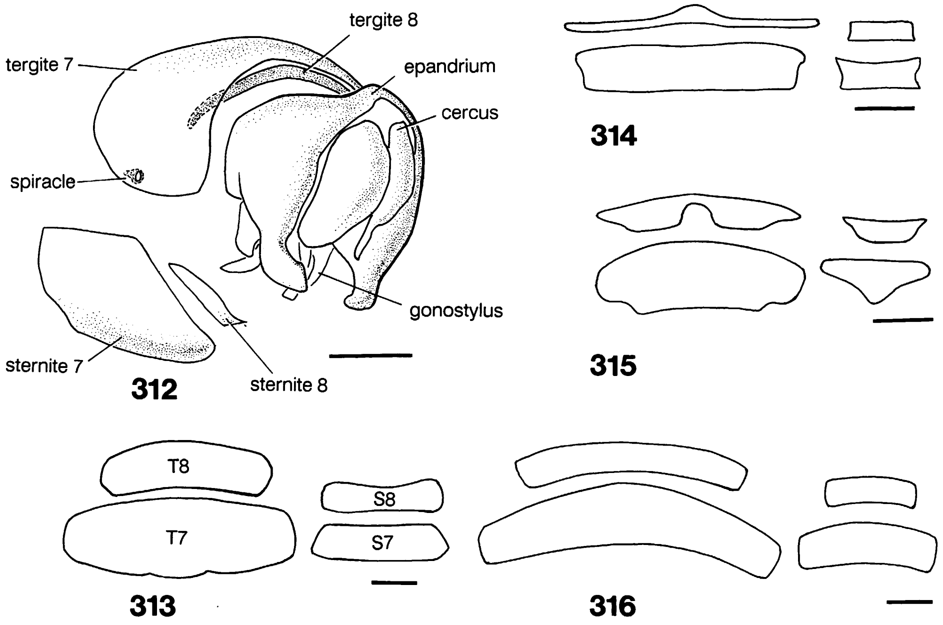
Among the subfamilies of Bombyliidae examined here, I found obligate male genitalic rotation through 90–180° in all Cythereinae, Mariobezziinae, Anthracinae and *Antonia*, some Mythicomyiinae, some Bombyliinae, and some Usiinae (Evenhuis, 1990). Distinguishing homologous states within the category of genitalic rotation requires more detailed study than I was able to perform here. It appears that obligate rotation of the genital capsule occurs in a number of Bombyliidae, however there is evidence that this rotation has been independently acquired a number of times, even within one subfamily.

McAlpine (1981) stressed the distinction between facultative rotation, which occurs only at the time of mating, and obligate rotation, in which the genital capsule is already rotated on eclosion. In the Bombyliidae there are two common types, one in which male genitalic rotation occurs only during copulation and another in which the genital capsule is rotated throughout adult life. I have not yet determined whether this latter "obligate" rotation is accomplished on eclosion, and hence conforms strictly to the definition of McAlpine (1981). Nevertheless, these two types of rotation are quite distinct, and should be scored as separate character states in a cladistic analysis. Facultative rotation may be mistaken for obligate if the specimens examined had just mated, however this difficulty should be overcome with the examination of a large number of specimens. Facultative rotation is common in the Bombyliidae, as it is associated with the tail-to-tail mating position (McAlpine, 1981) which is observed in the family (Du Merle, 1966; 1971; observations made during field work reported in Yeates and Dodson, 1990).

It may be possible to distinguish obligate from facultative rotation by the conformation of intersegmental muscles in the abdomen immediately preceding the genitalia. Ovchinnikova (1989) found that the intersegmental muscles M18 were asymmetrically developed in the anthracines *Villa* and *Hemipenthes*, whereas muscle M19 was asymmetrically developed in the bombyliine *Anastoechus*. These asymmetries serve the function of obligately rotating the genitalia, and species with facultative rotation, unfortunately not examined by Ovchinnikova, probably have symmetrical abdominal muscles. However, different muscles are involved in the obligate rotation of the male genitalia in Bombyliinae and Anthracinae; thus the rotation found in these two subfamilies is not homologous. In addition, within the Anthracinae, *Villa* has the left bundle of M18 broad and short while *Hemipenthes* has the right bundle broad and short. These asymmetries would have the effect of rotating the genitalia clockwise in *Villa* and counterclockwise in *Hemipenthes*, and thus they do not appear to be homologous.

Once the male genitalia has rotated through approximately 180° it is difficult to distinguish left hand rotation from right hand rotation. To overcome this difficulty, the direction of rotation may be inferred by the positions of sternite and tergite 8, which usually rotate only an intermediate angle in comparison to more posterior segments. For example, *Aphoebantus* male genitalia have rotated 180° clockwise whereas those of *Anthrax* appear to have rotated 180° counterclockwise (figs. 310–311).

In a few asiloids obligate genitalic rotation has caused segment 8 to become narrowed



Figs. 312–316. Terminal abdominal segments of various male Bombyliidae: **312**, *Mythicomyia illustris*; **313**, *Bombylius major*; **314**, *Usia atrata*; **315**, *Cyllenia maculata*; **316**, *Amictus validus*. Scales 0.5 mm except figure 313 0.1 mm.

into a thin band. The next two characters describe this modification.

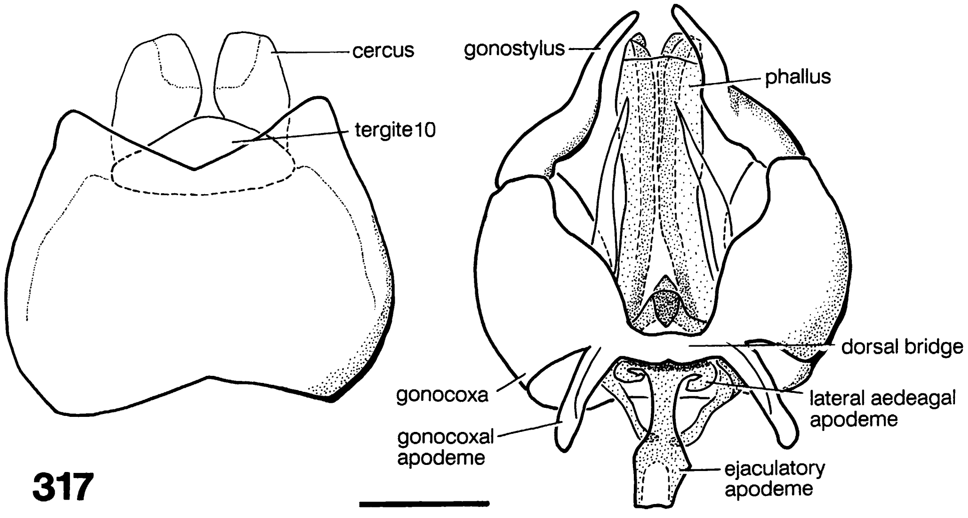
103. Shape of tergite 8. In the Scenopininae, Mythicomyiinae, *Amictus*, *Cyllenia*, and *Usia* tergite 8 is reduced to a very thin band (figs. 312, 314–316).

104. Shape of sternite 8. In the Scenopininae and Mythicomyiinae sternite 8 is also reduced into a very thin band. In the Mythicomyiinae sternite 8 is often so small that it is difficult to find (fig. 312).

105. Shape of epandrium. The epandrium forms a roof over the aedeagal complex and the gonostyli, and assumes a wide variety of forms. In particular, the posterior margin of the epandrium may be convex, concave, or the epandrium may be divided medially. The convex form was found in the outgroup and many Tabanomorpha and was considered primitive (figs. 321, 334, 350, 352, 356–357, 362–364). Many asiloids have a concave epandrium (coded 1) (figs. 312, 317, 322, 327, 330, 345, 351, 353–355, 358, 360–361, 365–366): the nemestrinids, *Thereva*, *Bonjeania*, *Dioctria*, *Apystomyia*, the Mythicomyiinae, the Oligodraninae, *Poecilognathus*, the Usiini, Toxophorini, Systropodini, *Lordotus*, *Acrophthalmyda*, *Eurycarenus*, *Thevenetimyia*, *Eclimus*, many Cythereinae, the Tomomyzinae, Antoniinae, *Plesiocera*, and *Aphoebantus*. A completely divided epandrium, coded 2, was found in the mydids (fig. 343), apiocerids (figs. 336, 340), scenopinids (fig. 333), and the asilids *Stenopogon* and *Leptogaster*, however not in any Bombyliidae. This character was analyzed in nonadditive form. Wiegmann et al. (1993) advanced the possibility that the concave posterior margin of the epandrium in *Apystomyia* was homologous with that found in primitive empidoids such as the Atelestidae.

106. Apical margin of epandrium. The apical margin of the epandrium is smoothly rounded plesiomorphically, however in a number of cases a small, narrow median notch has developed. This notch appears in two forms and two advanced states were coded and analyzed nonadditively. A simple notch (fig. 356), coded 1, was found in *Leptarthrus*, *Lordotus*, and the Conophorini. A more compex notch, with a thickened margin, (figs. 359, 363–364) was found to be a synapomorphy for the Lomatiinae and the Mariobezziinae.

107. Anteroventral corners of epandrium. The epandrium is loosely connected to the anterodorsal region of the gonocoxites in all



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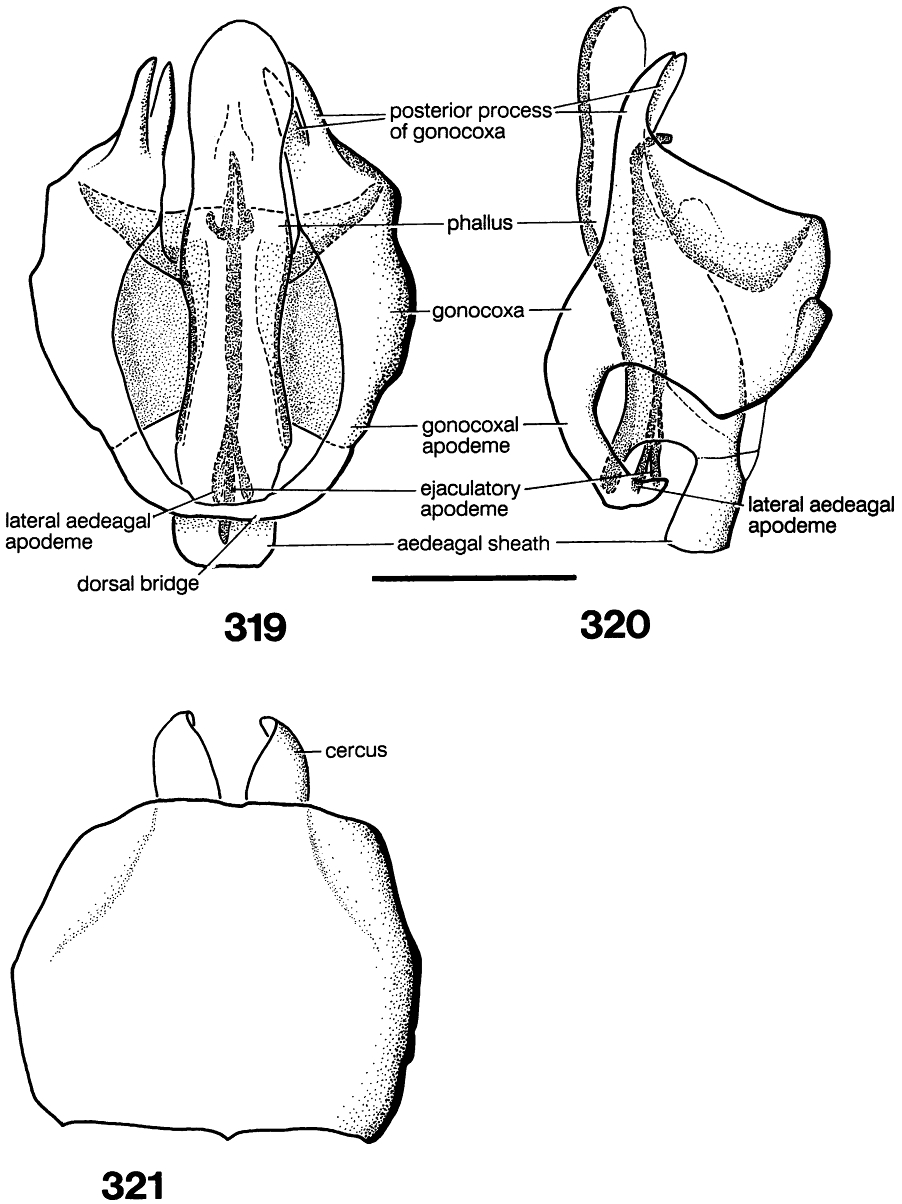
Figs. 317–318. Dorsal views of the male genitalia of the nemestrinid *Hirmoneura exotica*, vestiture not shown: **317**, epandrium and associated sclerites; **318**, genitalia with epandrium removed. Scale 0.5 mm.

families examined except the Asilidae. In the Asilidae the anteroventral corners of the epandrium are articulated on and may be directly connected to the lateral margins of the hypandrium, so that segment 9 forms a complete ring (Karl, 1959; Adisoemarto and Wood, 1975; Griffiths, 1986). This feature appears to be an apomorphy for the Asilidae.

108. Male epandrium. As indicated under character 107, the epandrium is loosely connected to the gonocoxites in the plesiomorphic condition. In the genus *Toxophora* only, I found that the epandrium has a strong, sclerotized connection with the posterodorsal region of the gonocoxites (fig. 367).

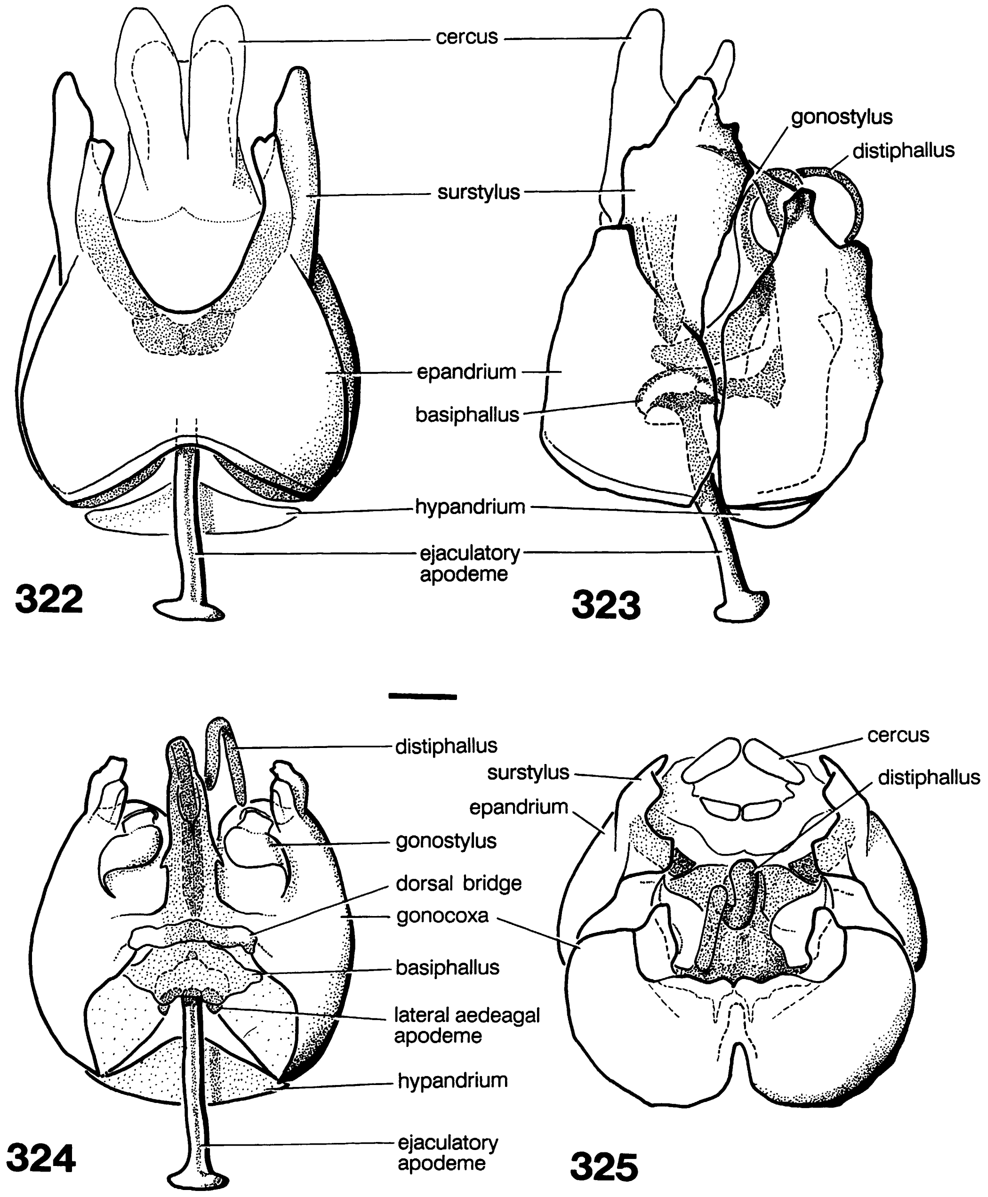
109. Surstyli. Hennig (1976) considered the surstyli of higher Diptera to be derivatives of tergite 10, as did McAlpine (1981). Griffiths (1972, 1981), citing ontogenetic evidence, concluded that they are derivatives of segment 9, a view with which I concur. In any case, the surstyli are closely associated with, or articulate on, the epandrium (tergite 9). McAlpine (1989) reported that they were an apomorphic feature of the Muscoidea [his Muscomorpha] and also occurred in various families of Asiloidea and Empidoidea such as the Asilidae, Empididae, and Dolichopodidae. Cumming and Sinclair (1990) interpreted the presence of surstyli in various subfamilies of Empididae and in the Dolichopodidae as homoplasious. McAlpine (1989) considered that the surstyli were "more or less homologous" in all the groups in which they occur. Nagatomi et al. (1991b) concluded that the surstyli of the Apsilocephalidae indicated that they may have a close relationship with the Muscoidea [their Muscomorpha]. Surstyli were only found in *Apsilocephala* here (figs. 322, 323, 325). I consider that the surstyli found in some Tabanomorpha, Asiloidea, Empidoidea, and Muscoidea have been independently derived.

110. Male hypandrium. In *Rhagio* and many other Tabanomorpha and the Nemestrinidae the hypandrium (sternite 9) is a separate sclerite lying just anterior to the base of the gonocoxites (figs. 322, 326, 328, 334, 337, 338). However, in the Acroceridae and various asiloids the hypandrium has become lost or fused to the gonocoxites. Among the asiloids the loss or fusion of the hypandrium has apparently occurred independently in a number of families. Among the asiloid families excluding the Bombyliidae, the hypandrium is lost or fused in *Phycus*, the Mydidae except *Neorhaphiomidas*, *Hilarimorpha* (fig. 348–349), *Apystomyia* (figs. 344–345), and all scenopinids except *Caenotus* (Yeates, 1992a). Within the Bombyliidae the hypan-



Figs. 319–321. Male genitalia of the acrocerid *Eulonchus smaragdinus*, vestiture not shown: **319**, dorsal view with epandrium removed; **320**, lateral view with epandrium removed; **321**, dorsal view of epandrium and cerci. Scale 0.5 mm.

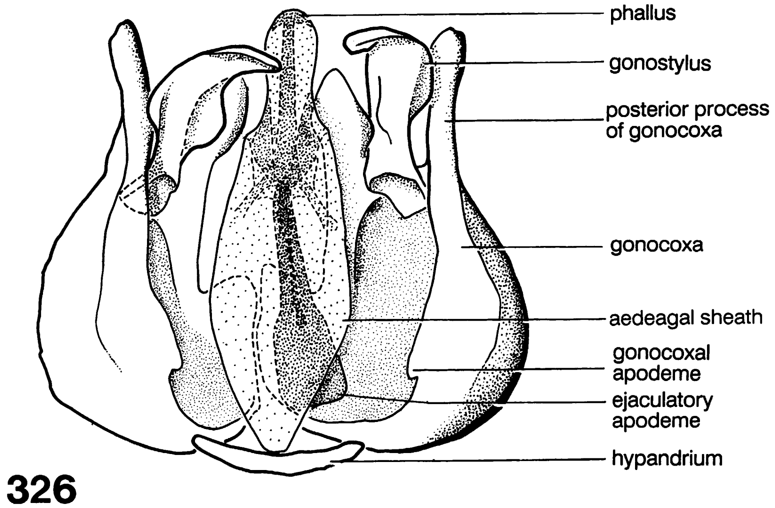
drium is present in a number of subfamilies (figs. 373–377, 380) and has presumably been lost independently a number of times (figs. 367–372, 378–379, 381). By itself, the presence or absence of the hypandrium as a separate sclerite is of little use at the subfamily level. It is present in *Oligodranes* (fig. 373), *Apolysis*, *Heterotropus* (figs. 385, 387–388), the Conophorini and many Bombyliini and Eclimini (figs. 374–375), *Cyllenia*, *Amictus* (fig. 377), *Neosardus*, *Pantarbes*, *Cytherea* (fig. 376), and among the Anthracinae, *Plesiocera* (fig. 380) and *Aphoebantus*. In *Caenotus* and *Heterotropus* the hypandrium appears joined

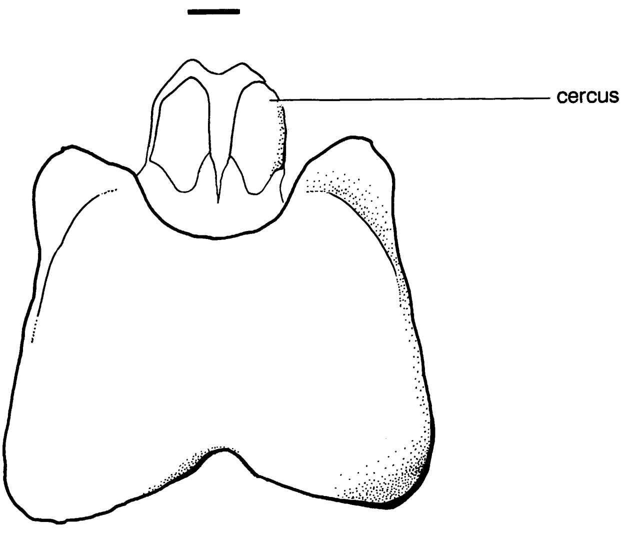


Figs. 322–325. Male genitalia of the apsilocephalid *Apsilocephala* sp., vestiture not shown: **322**, dorsal view with epandrium in place; **323**, lateral view with epandrium in place; **324**, dorsal view with epandrium removed; **325**, posterior view with epandrium in place. Scale 0.5 mm.

to the gonocoxites but a distinct, membranous line of weakness is present (fig. 385). These cases were considered plesiomorphic and coded 0. It is plausible to assume that this is an intermediate stage in the fusion of the hypandrium with the bases of the gonocoxites. In other examples such as *Cytherea* and *Plesiocera* (figs. 376, 380), the hypandrium is quite distinct from the gonocoxites but very reduced in size. In these cases it is plausible to postulate that the hypandrium will become completely lost rather than become fused with the gonocoxites.

111. Gonocoxal fusion. In the Rhagionidae examined the gonocoxites are separated from each other ventrally at the base by the hy-



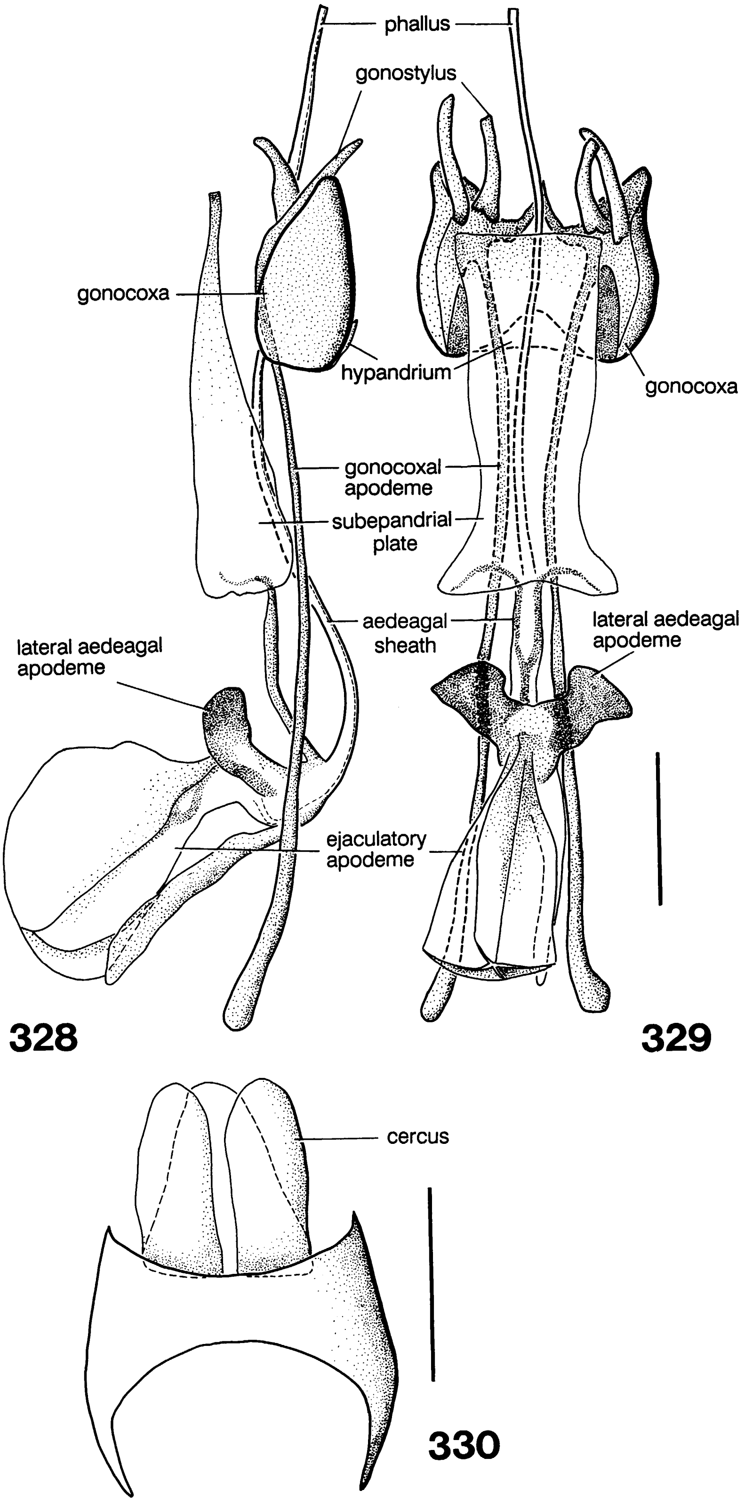


Figs. 326–327. Male genitalia of the therevid *Thereva fucata*, vestiture not shown: **326**, dorsal view with epandrium removed; **327**, epandrium and cerci. Scale 0.1 mm.

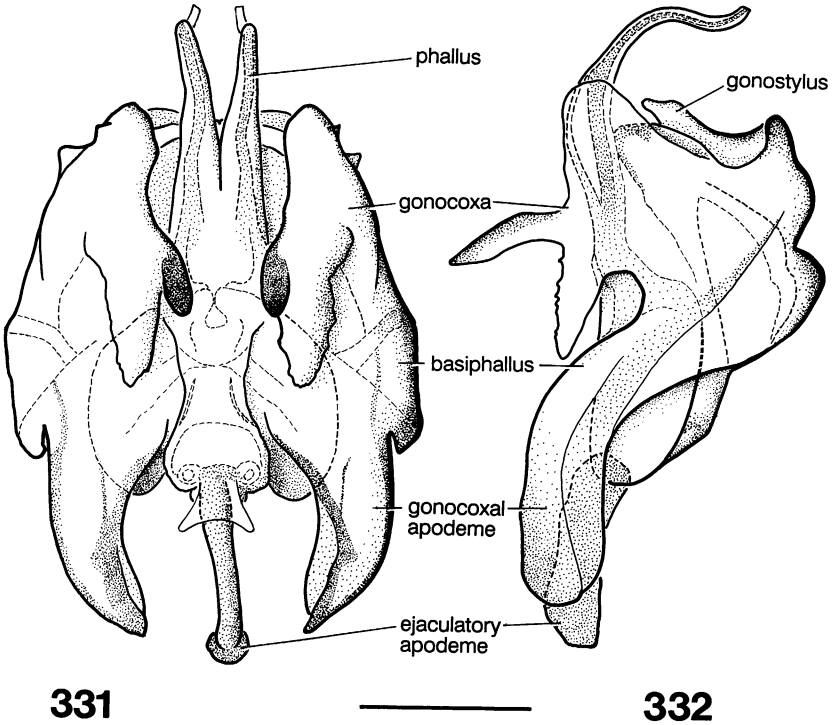
pandrium and are free at the apex and Nagatomi (1984) showed that this is the case in many Tabanomorpha. In many asiloids, including all Bombyliidae except *Heterotropus*, the gonocoxites are fused together ventrally. This fusion was coded as two advanced states, those with a ridge marking the line of fusion being scored 1, and those fused smoothly so that they lack this line of fusion being scored 2. State 2 was only found in the following Bombyliidae taxa: all Toxophorinae (figs. 367, 370), *Poecilognathus*, some Mythicomyiinae, the Tomomyzinae (fig. 378), *Enica*, *Sericosoma*, *Marmasoma*, and *Desmatomyia*.

112. Ventral gonocoxal rod. The fused gonocoxites of the mythicomyiinae genera *Acridophagus*, *Cephalodromia*, and *Mythicomyia* each have a ventral, median rod which articulates with the gonostyli (fig. 369).

113. Gonocoxal apodemes. The gonocoxal apodemes are elongate sclerotized lobes extending anteriorly from the anterodorsal margin of the gonocoxites (figs. 318, 320, 328, 335, 337, 339, 342, 345), and are plesio-

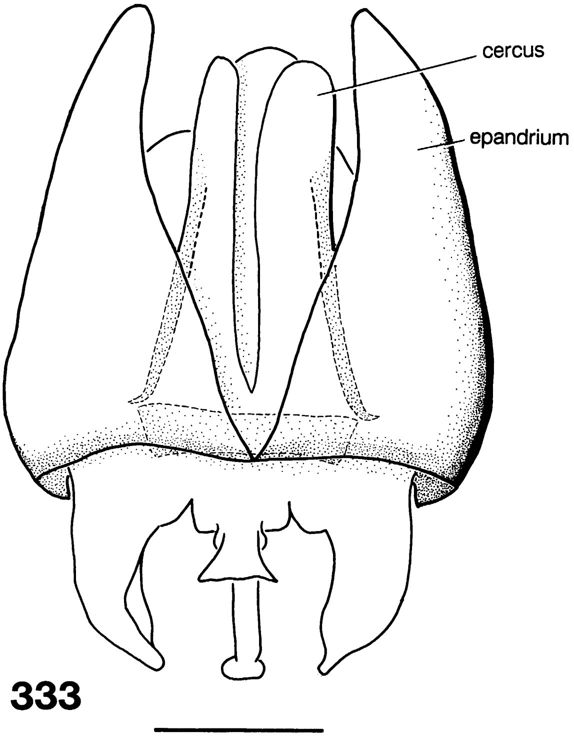


Figs. 328–330. Male genitalia of the therevid *Bonjeania* sp. 1, vestiture not shown: **328**, lateral view with epandrium removed; **329**, dorsal view with epandrium removed; **330**, dorsal view of epandrium and cerci. Scale 0.5 mm.


phallus
gonostylus
gonocoxa
basiphallus
gonocoxal apodeme
ejaculatory apodeme

331

332


cercus
epandrium

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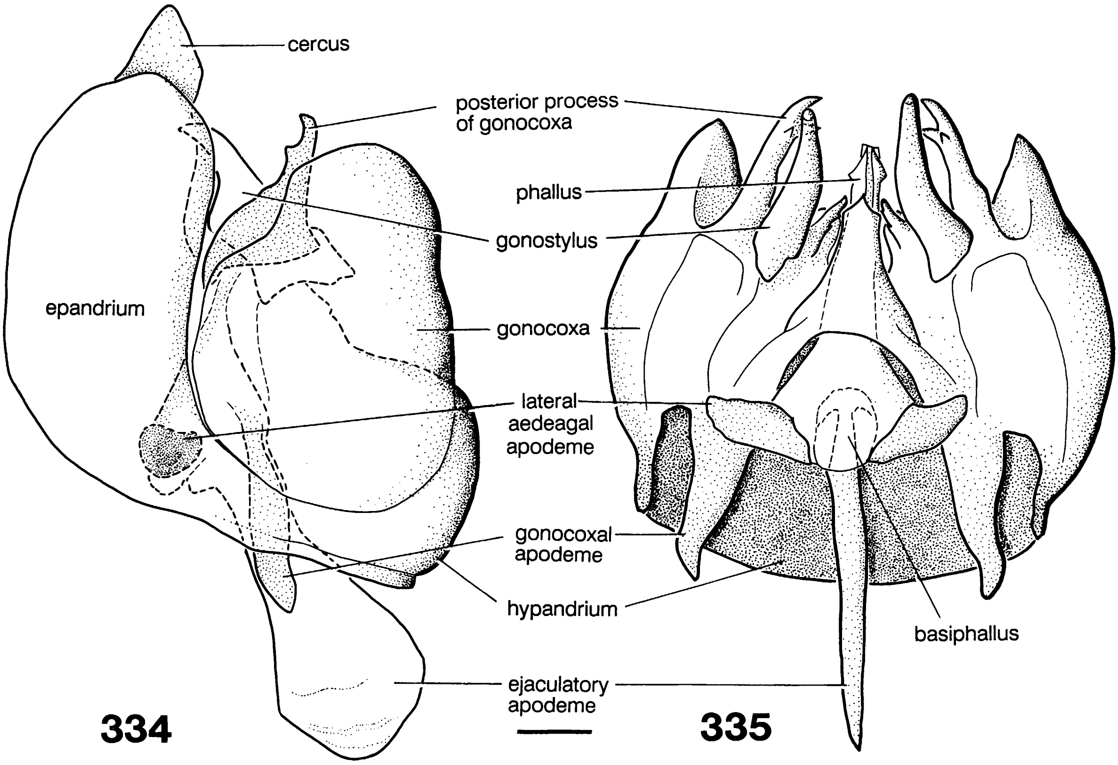

Figs. 334–335. Male genitalia of the asilid *Leptarthrus brevirostris*, vestiture not shown: **334**, lateral view with epandrium in place; **335**, dorsal view with epandrium removed. Scale 0.1 mm.

morphically present in the Asiloidea. They were found to be lost in most Bombyliidae and *Apsilocephala* (fig. 324) and very small in *Thereva* (fig. 326). When present in the Bombyliidae I found the gonocoxal apodemes to be small and often directed ventrally rather than anteriorly (figs. 372, 376–377, 386).

McAlpine (1989) considered that primitively throughout the "Orthorrhaphous" Brachycera (and perhaps the entire Diptera) the gonocoxal apodemes and the rims of the gonocoxites were fused to form a bridge behind the aedeagus. I could not find a sclerotized dorsal bridge between the gonocoxal apodemes in the Rhagionidae, but one is present in *Vermileo comstocki* Wheeler, and the Nemestrinidae and Acroceridae examined (figs. 318–319).

I did not include this character because of the uncertainty in polarity assignment and the different form of the bridge in the Nemestrinidae and Acroceridae. The bridge between the gonocoxal apodemes in the Nemestrinidae (fig. 318) is similar to that found in *Vermileo*: it is situated between the bases of the gonocoxal apodemes and above the basiphallus, and only has a small median connection to the aedeagal sheath. The sclerotized bridge in the Acroceridae occurs at the very ends of the gonocoxal apodemes (fig. 319) and is not connected to the aedeagal sheath. The distribution of this bridge in the Tabanomorpha and the homology of the bridge in the Nemestrinidae and Acroceridae require further evaluation. In *Apsilocephala* the gonocoxal apodemes are absent and the

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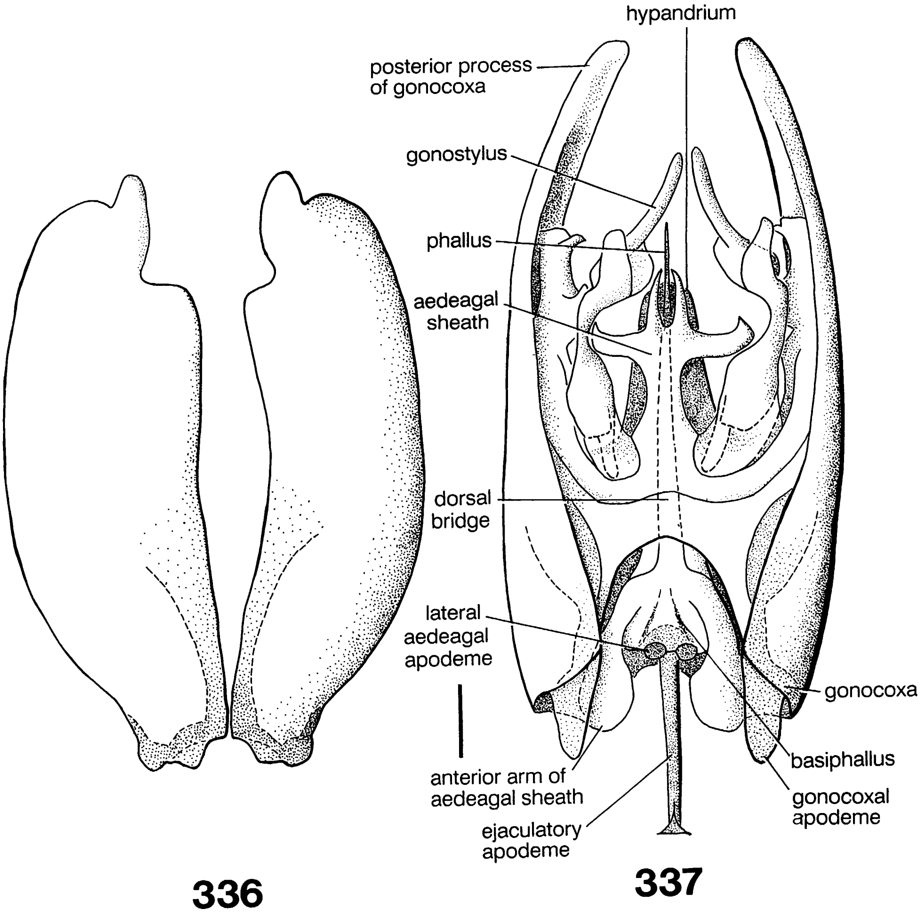
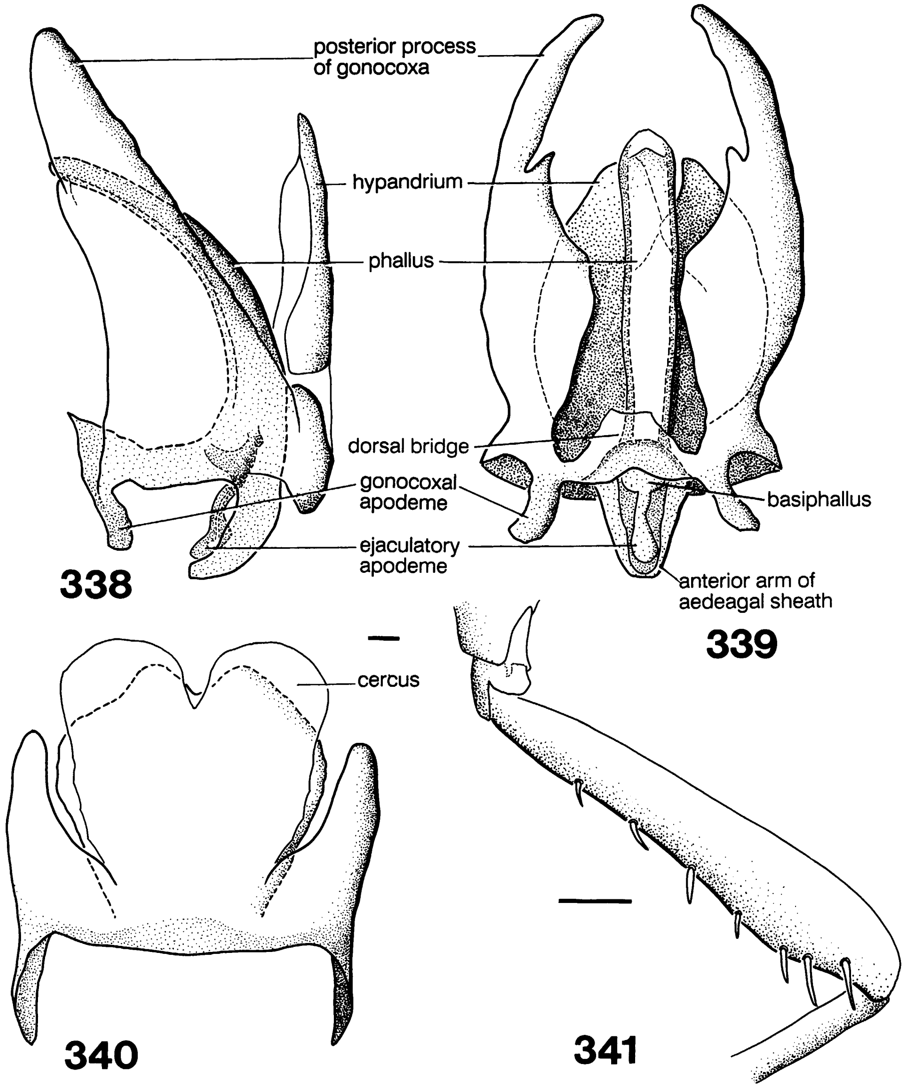
Figs. 331–333. Male genitalia of the scenopinid *Propebrevitrichia* sp., vestiture not shown: **331**, dorsal view with epandrium removed; **332**, lateral view with epandrium removed; **333**, dorsal view showing epandrium in place. Scales 0.1 mm.



Figs. 336–337. Male genitalia of the apiocerid *Apiocera aldrichi*, vestiture not shown: **336**, dorsal view of epandrium; **337**, dorsal view with epandrium removed. Scale 0.5 mm.

phallus sheath surrounding the basiphallus is heavily sclerotized, providing support for the surstyli (figs. 324–325). The dorsal bridge in *Vermileo*, *Apsilocephala*, and the Nemestrinidae and Acroceridae does not appear to be homologous with the dorsal bridge of Hennig (1976) because it is not connected to the hypandrium.

Hennig (1976) proposed that the Muscomorpha (in Woodley's sense) excluding the Bombyliidae, Acroceridae and Nemestrinidae differed from more plesiomorphic flies because the aedeagus (his endoaedeagus) and the aedeagal sheath (his phallus sheath) were fused to form the aedeagus. Griffiths (1986) discussed the Asiloidea (his Prophalanx Pleroneura which includes the Bombyliidae but excludes the Nemestrinidae and Acroceridae) and proposed, as a supporting apomorphy, the aedeagal sheath formed by fusion of the parameres (his gonites). He considered that the parameres were free in many Eremoneura, and the sheath over the aedeagus in the Tabanomorpha (his Tabaniformia) was formed by separate lobes which enclose the parameres and aedeagus. Wood (1990b) considered that the entire Muscomorpha (in Woodley's sense) were characterized by the parameres fusing over the aedeagus forming a parameral sheath, and termed the composite structure the phallus (Wood, 1990a). I prefer to name the sheath over the aedeagus in Muscomorpha the aedeagal sheath rather than the parameral sheath, because of the disputed

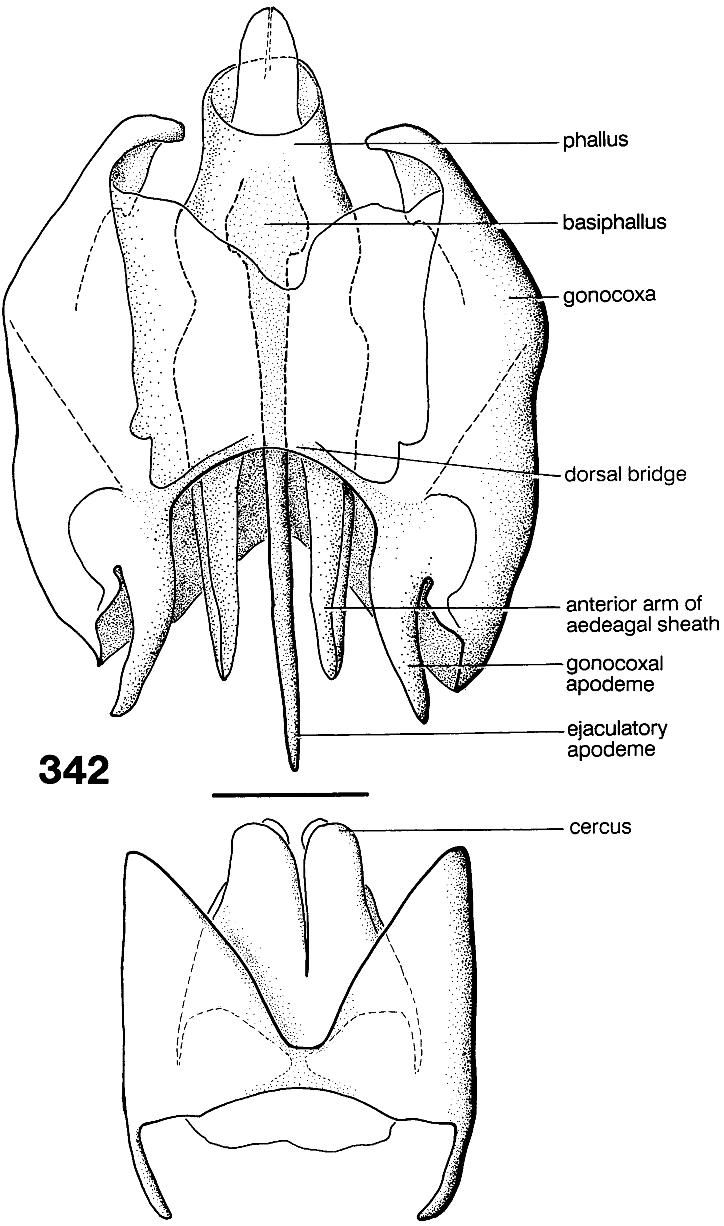


Figs. 338–341. Male genitalia and leg of the apiocerid *Neorhaphiomidas hardyi*, vestiture not shown: **338**, lateral view with epandrium in place; **339**, dorsal view with epandrium removed; **340**, dorsal view of epandrium and cerci; **341**, hind femur showing ventral row of strong setae. Scale 0.1 mm except figure 341 0.5 mm.

homology of the parameres in the endopterygote orders (Griffiths, 1981).

I found that the aedeagus of the Asiloidea was indeed covered with and fused to the aedeagal sheath, forming the phallus, however this sheath was identical to the one found in the Rhagionidae, Nemestrinidae, and Acroceridae. Hence I could not find any useful variation in this character.

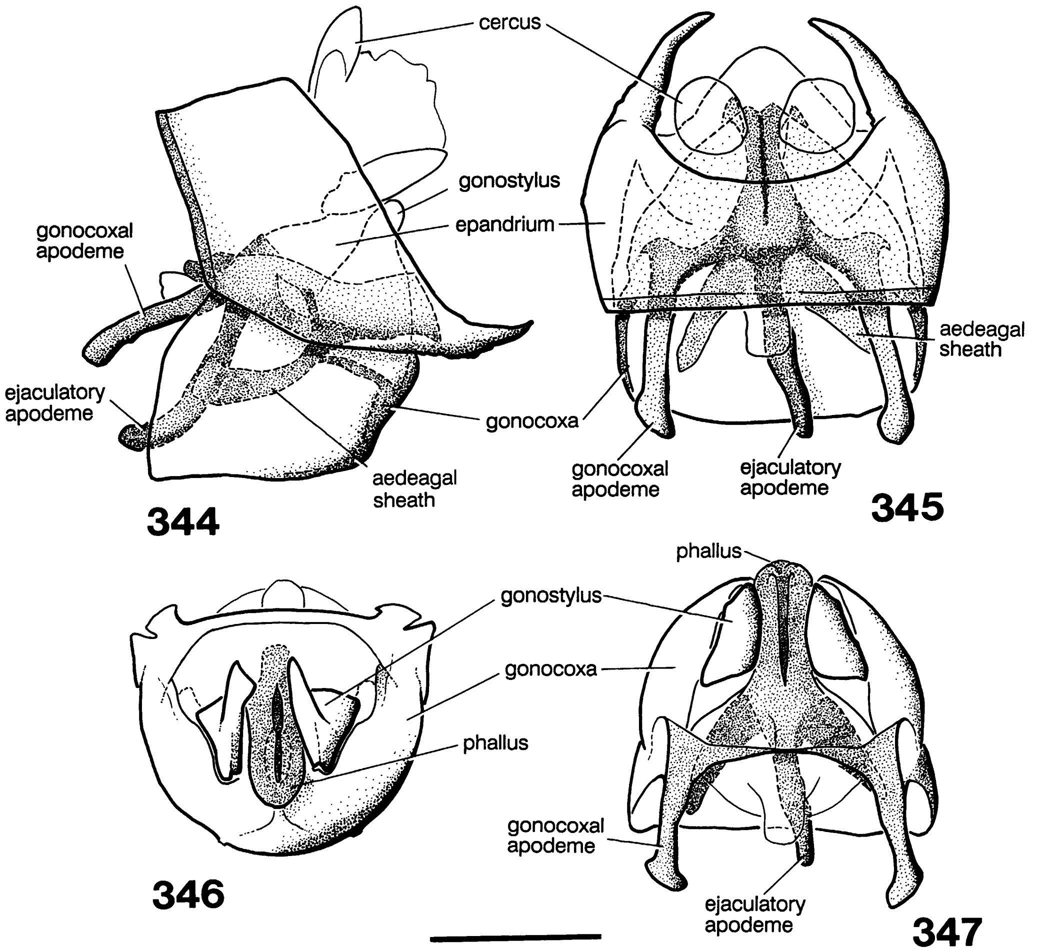
114. Form of the aedeagal sheath. The aedeagal sheath extends anteroventrally as two arms, and plesiomorphically these arms extend to a point not much beyond the basiphallus (figs. 345, 349, 394). In the Mythicomyiinae the aedeagal sheath is produced as two lobes extending anteriorly beyond the basiphallus and anterior margins of the gonocoxites (figs. 382–383, 395). Initially I homologized these long, anteriorly directed rods of the Mythicomyiinae as gonocoxal apo-



Figs. 342–343. Male genitalia of the mydid *Heteromydas bicolor*, vestiture not shown; **342**, dorsal view with epandrium removed; **343**, dorsal view of epandrium. Scale 0.5 mm.

demes, however they are extensions of the aedeagal sheath and not attached to the anterodorsal margins of the gonocoxites as are gonocoxal apodemes. Hall and Evenhuis (1986) apparently correctly identified these structures as part of the aedeagal sheath, and termed them the "epiphallus." Theodor (1983) perplexingly interpreted these structures as tergite 8.

115. Secondary division of gonocoxites. The gonocoxites of *Exoprosopa* have a secondary line of weakness about half way along

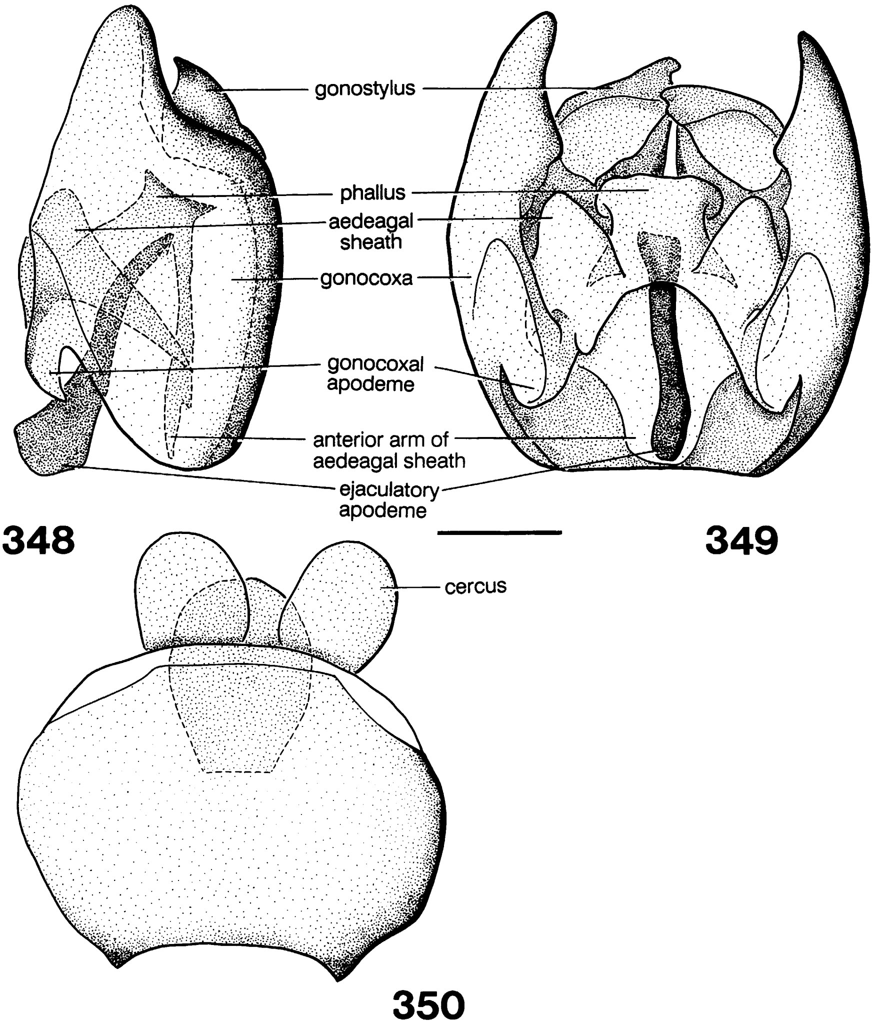


Figs. 344–347. Male genitalia of *Apystomyia elinguis*, vestiture not shown: **344**, lateral view with epandrium in place; **345**, dorsal view with epandrium in place; **346**, posterior view with epandrium removed; **347**, dorsal view with epandrium removed. Scale 0.1 mm.

the fused gonocoxites placed perpendicularly to their line of fusion (fig. 381). This feature may provide an apomorphy for the Exoprosopini or some internal clade thereof.

116. Aedeagal sheath. Plesiomorphically the aedeagal sheath forms a simple, snug-fitting covering over the aedeagus (figs. 399–400). Among some Bombyliidae the aedeagal sheath becomes more elaborate and is termed the epiphallus. I have divided the variation in the epiphallus into two apomorphic states, treated nonadditively. The distribution of the two states among the subfamilies indicates that the apomorphic states have been derived independently a number of times. Apomorphically, the aedeagal sheath is either a simple lobe whose apex is separate from, and above, the gonopore (figs. 397, 401–402, state 1), or a more complex group of lobes, with no apices corresponding to the gonopore (figs. 391, 396, state 2). State 1 was found in *Apiophora*, *Oligodranes*, *Apolysis*, *Geron*, many Bombyliinae, the Cythereinae, *Antonia* and the Anthracinae. State 2 was found in *Poecilognathus*, *Toxophora*, the Systropodini, and *Desmatomyia*.

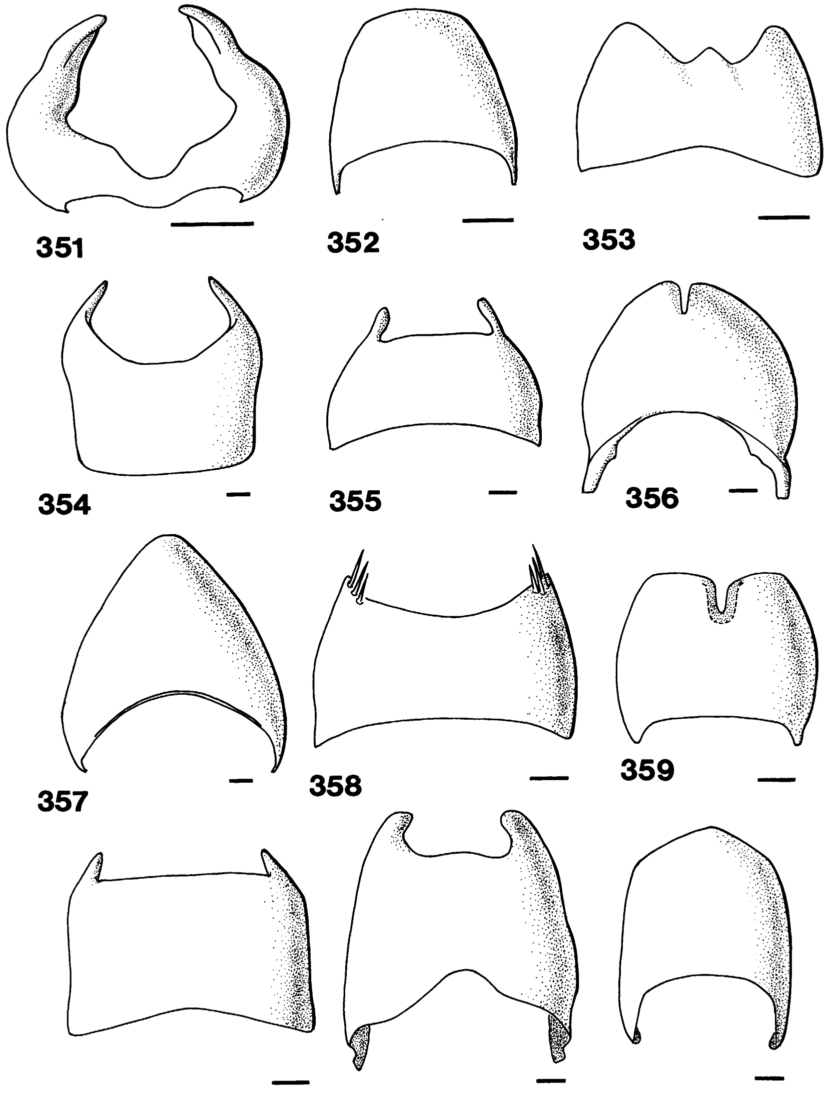
117. Distiphallus. Downes (1968) found a tripartite or bipartite aedeagus in various Nematocera, however Wood (1990a) concluded that a single opening at the apex of the distiphallus was most likely to be the primitive



Figs. 348–350. Male genitalia of *Hilarimorpha mentata*, vestiture not shown: **348**, lateral view with epandrium removed; **349**, dorsal view with epandrium removed; **350**, epandrium and cerci. Scale 0.1 mm.

state in the Diptera. I found a single gonopore in the outgroup and this state is widespread in Tabanomorpha (Nagatomi, 1984); thus I consider a single gonopore to be plesiomorphic for the Asiloidea.

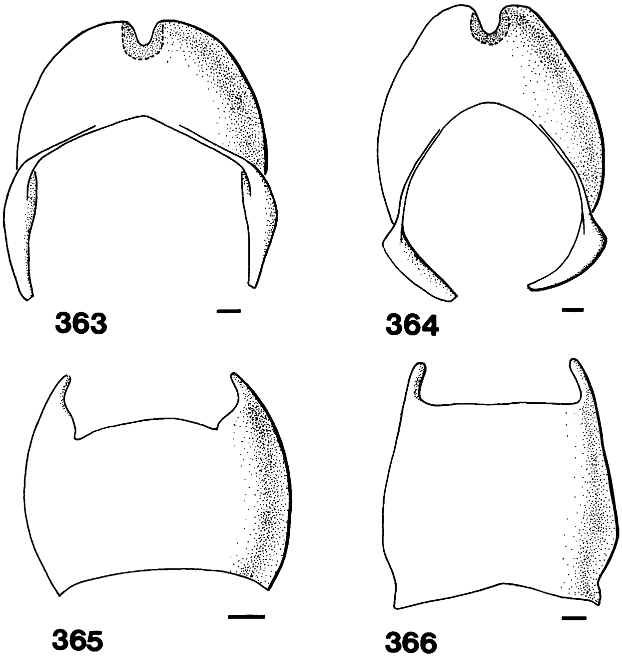
Among the asiloids, an occasional division of the distiphallus into two (state 1) or three (state 2) tubes was evident, and I analyzed this character nonadditively. The phallus of *Lasia* and *Caenotus* is bifid only at the apex. *Prorates* and *Propebrevitrichia* have the phallus bifid (fig. 331), and the bifurcation occurs in a position more basal than in *Lasia* or *Caenotus*. *Scenopinus* has a trifid phallus as have the bombyliid genera *Heterotropus*, *Acridophagus*, *Paraconsors*, and *Cyllenia* (figs. 382, 385, 403–404). Kelsey (1969) interpreted the trifid condition found in some scenopinids as a median phallus and two lateral aedeagal parameres, however all three processes have an apical opening. Some other asiloid families have developed a trifid phallus as follows. Theodor (1976) found a trifid phallus in some Asilidae (e.g. *Machimus* Loew, *Promachus* Loew); however this is assumed to be a secondary condition because



Figs. 351–362. Epandrium (tergite 9) of various Bombyliidae, vestiture not shown except strong setae in figure 358; **351**, *Mythicomyia illustris*; **352**, *Geron grandis*; **353**, *Toxophora virgata*; **354**, *Systropus macer*; **355**, *Apolysis mus*; **356**, *Conophorus fenestratus*; **357**, *Bombylius major*; **358**, *Eclimus gracilis*; **359**, *Mariobezzia lichtwardti*; **360**, *Pantarbes capito*; **361**, *Cyllenia maculata*; **362**, *Anthrax analis*. Scales 0.1 mm.

he found that all the primitive Dasypogoninae except *Holcocephala* Jaennike had a single gonopore. Hall and Evenhuis (1987, figs. 457 and 458) illustrated the apically trifid phallus of *Paraconsors scutellaris*, however other members of the genus illustrated have the plesiomorphic state.

118. Phallus shape. Most asiloids examined here have an approximately straight phallus, however in the Therevidae and Scenopinidae the aedeagus is frequently curved ventrally at its apex. Among the Bombyliidae the phallus is of a distinctive shape in the eclimine *Marmasoma*, and the cythereines



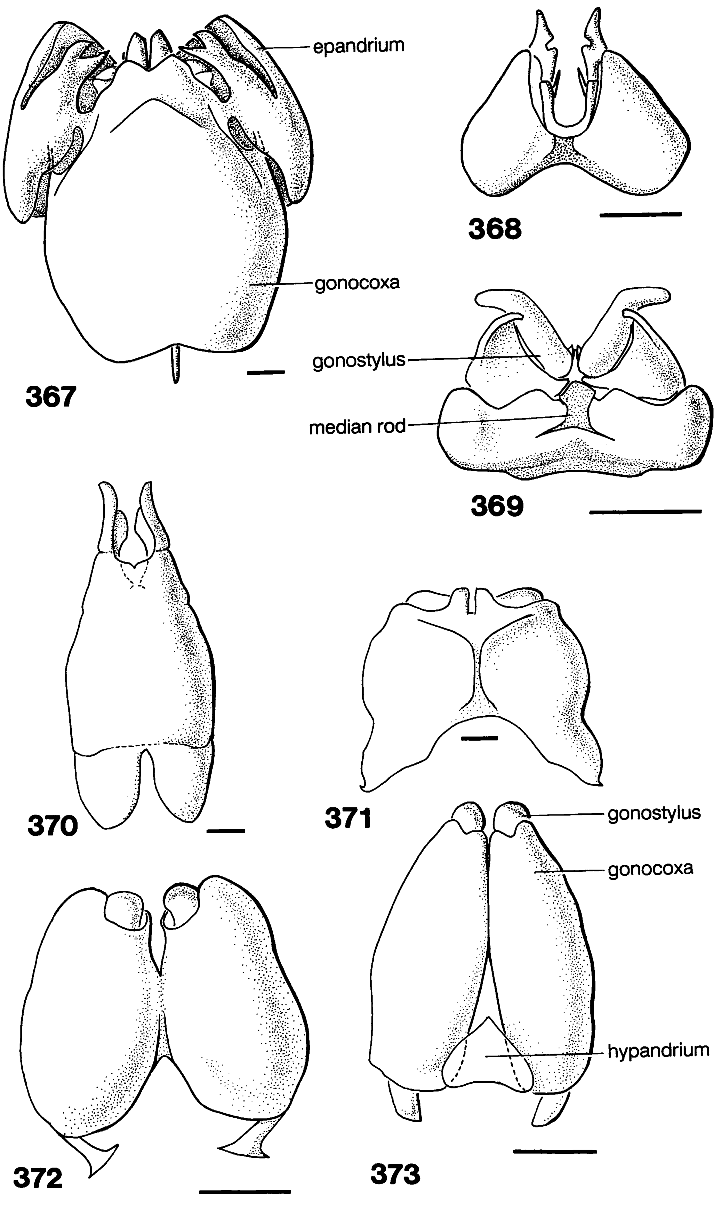
Figs. 363–366. Epandrium (tergite 9) of various Bombyliidae, vestiture not shown: **363**, *Peringueyimyia capensis*; **364**, *Comptosia fascipennis*; **365**, *Tomomyza anthracoides*; **366**, *Aphoebantus cervinus*. Scales 0.1 mm.

Amictus, *Cyllenia*, and the lomatiine *Peringueyimyia*. In these groups the distiphallus curves anteriorly underneath the basiphallus and then posteriorly (figs. 399–400), and this was coded the apomorphic state. This curvature causes the three apodemes emerging from the base of the basiphallus to be directed dorsally rather than anteriorly.

The form of phallus described here is quite distinct from the curvature found in *Heterotropus* (fig. 385), where the distiphallus curves dorsally then posteriorly, causing the apodemes emerging from the base of the basiphallus to be directed ventrally.

119. Lateral aedeagal apodemes. The lateral aedeagal apodemes are found in most Tabanomorpha and were present in the outgroup examined in this study. Nagatomi (1984) termed these sclerites either the aedeagal dorsoanterior plate or aedeagal dorsoanterior sclerite (adp or ads in his figures). Theodor (1976, figs. 6,7) termed them the basal plates in the Asilidae and Ovchinnikova (1989) termed them the ejaculatory sclerites. In the Bombyliidae they have various names (Table 2): lateral struts (Hesse, 1938); basal struts (Painter and Hall, 1960); paraphyzes (Bowden 1964); lateral ejaculatory apodemes (Hull, 1973); lateral wings (Hall, 1976); basal plates (Theodor, 1983), and aedeagal apodemes (Greathead, 1988). They arise from the basiphallus and should not be confused with various anteriorly directed lobes and outgrowths of the aedeagal sheath, as are found in *Caenotus*. The lateral aedeagal apodemes are homologized because of their position, slightly dorsal and lateral to the insertion of the ejaculatory apodeme.

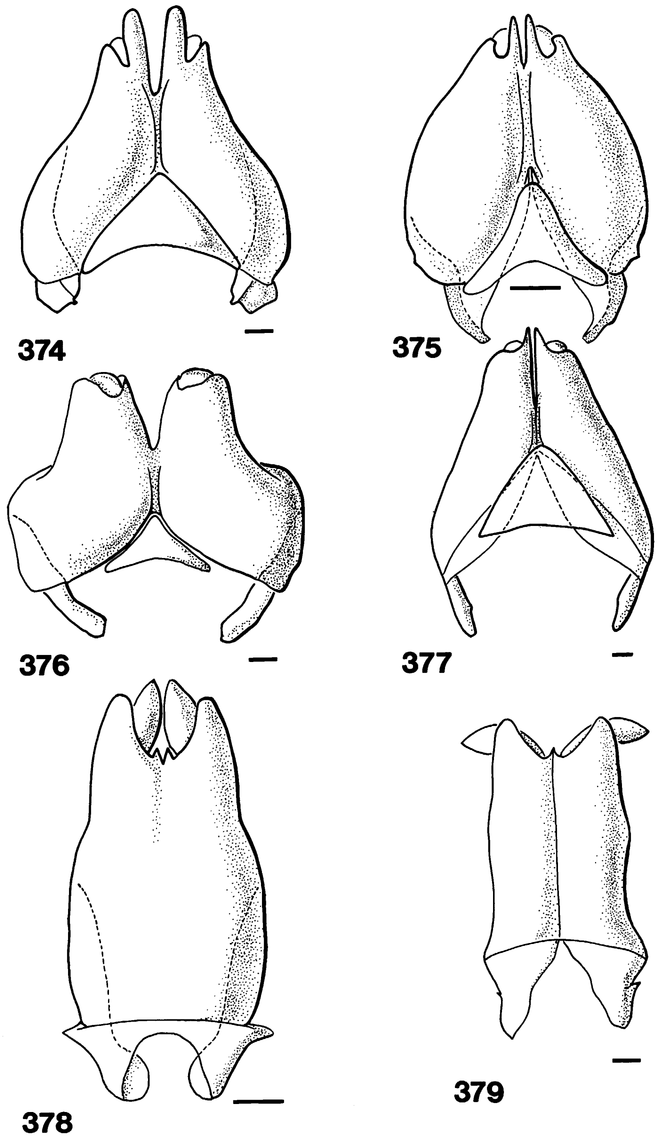
Griffiths (1986) considered the presence of lateral aedeagal apodemes (his transverse sclerites) an apomorphy for the Asiloidea (his Prophalanx Pleroneura). This is incorrect given their wide distribution in the Tabanomorpha. Lateral aedeagal apodemes are particularly prominent in the Bombyliidae (except the mythicomyiine *Paraconsors*) and Asilidae, and are present but reduced in *Apsilocephala* (fig. 324). The lateral aedeagal apodemes are absent in the Scenopinidae and the Therevidae examined except *Bonjeania*. The lateral aedeagal apodemes in *Bonjeania* (figs. 328–329) are solidly fused to (not ar-



Figs. 367–373. Ventral view of the male genitalia of various Bombyliidae, vestiture not shown: **367**, *Toxophora virgata* showing attachment of epandrium to gonocoxites; **368**, *Cephalodromia fusca*; **369**, *Mythicomyia illustris*; **370**, *Geron grandis*; **371**, *Phthiria gaedei*; **372**, *Crocidium karooanum*; **373**, *Oligodranes* sp. Scales 0.1 mm.

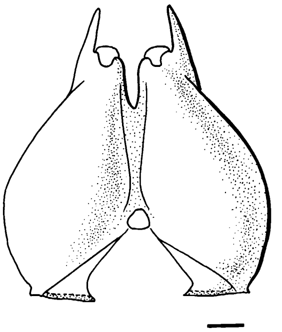
ticulated on) the basiphallus as they are in the Asilidae and Bombyliidae, but were considered homologous. Within the Apioceridae, *Apiocera* has small but reduced lateral aedeagal apodemes (fig. 337) and the Mydidae have lost them altogether (figs. 339, 342). *Hilarimorpha* and *Apystomyia* lack lateral aedeagal apodemes (figs. 347, 349), as do the Eremoneura.

The protractors of the ejaculatory apodeme (muscle M32) are attached to the lateral aedeagal apodemes (Ovchinnikova, 1989),



Figs. 374–379. Ventral view of the male genitalia of various Bombyliidae, vestiture not shown: **374**, *Bombylius major*; **375**, *Eclimus gracilis*; **376**, *Cytherea obscura*; **377**, *Amictus validus*; **378**, *Tomomyza anthracoides*; **379**, *Lomatia belzebul*. Scales 0.1 mm.

hence these muscles indicate the position of the apodemes. In all but one case examined by Ovchinnikova (1989) the lateral aedeagal apodemes are lost in association with the absence of the protractors of the ejaculatory apodeme. The one exception is the therevid *Euphycus bocki* Kröber in which the protractors of the ejaculatory apodeme are present but apparently attach to the aedeagus and a lobe of the aedeagal sheath. Further study of the homology of muscle M32 and the occurrence of the lateral aedeagal apodemes in the Therevidae is required. No structure that could be interpreted as the lateral aedeagal apodemes was present in the figures of Irwin and Lyneborg (1981a). However small, dorsally directed apodemes visible in *Spiriverpa candida* (Loew) illustrated by Irwin and Lyneborg (1981b, their fig. 20) may be lateral aedeagal apodemes.



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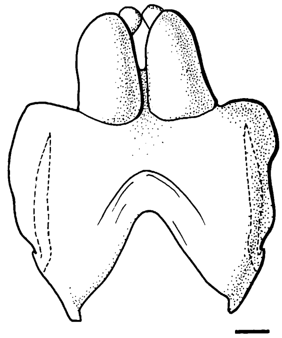

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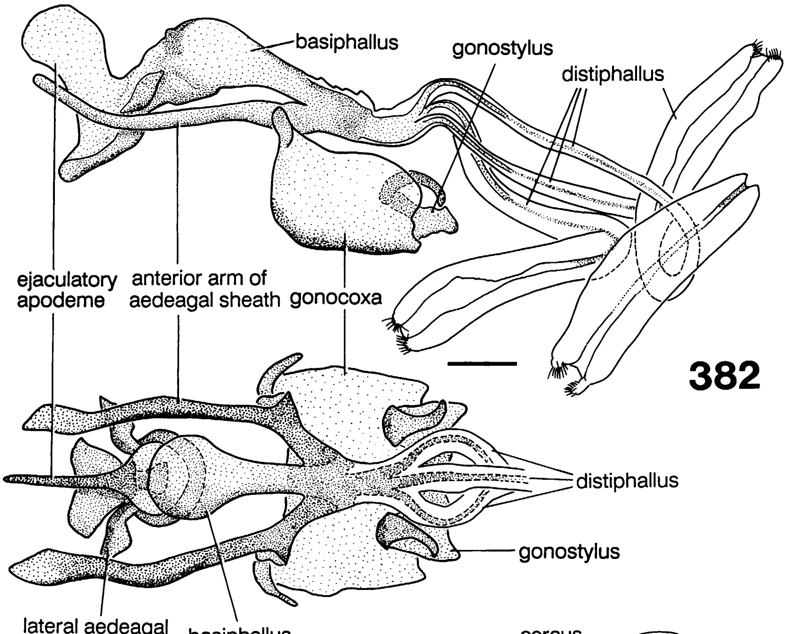
Figs. 380–381. Ventral view of the male genitalia of bombyliids, showing gonocoxites, vestiture not shown: **380**, *Plesiocera psammophila*; **381**, *Exoprosopa caliptera*. Scales 0.1 mm.



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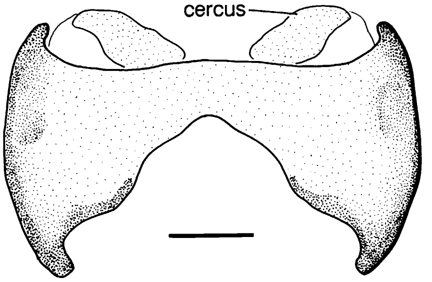

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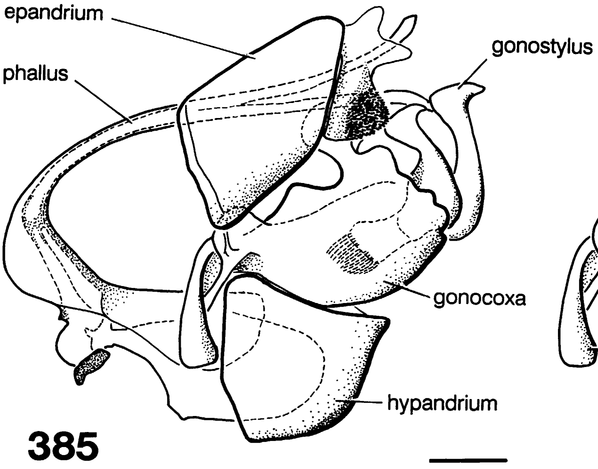
Figs. 382–384. Male genitalia of the mythicomyiine *Acridophagus* sp., vestiture not shown: **382**, lateral view with epandrium removed; **383**, dorsal view with epandrium removed; **384**, dorsal view of epandrium and cerci. Scales 0.1 mm.



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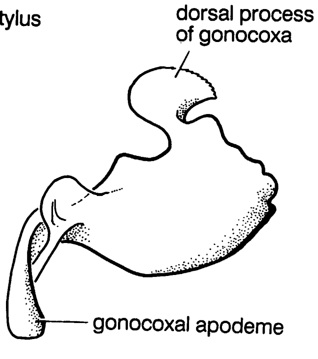

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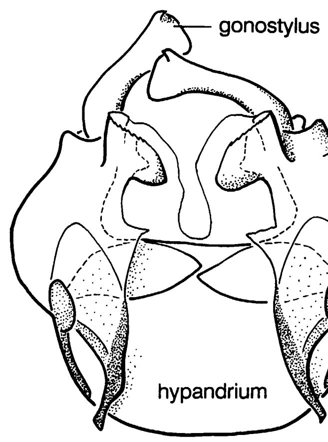

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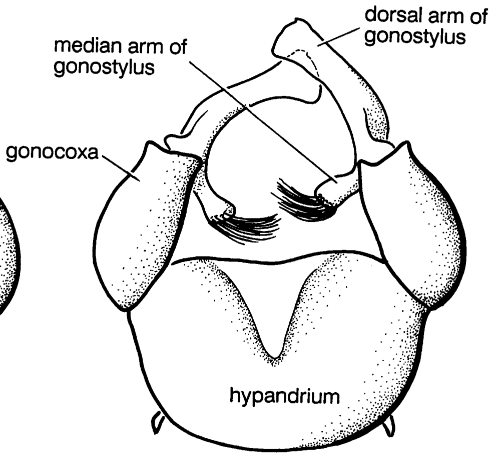

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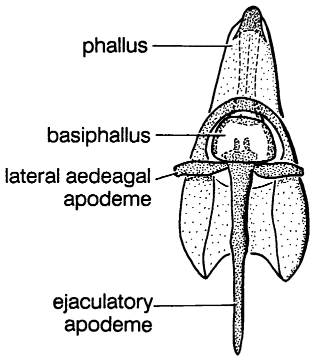

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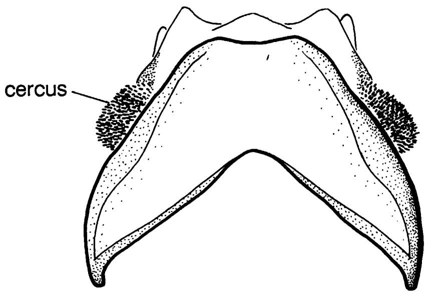

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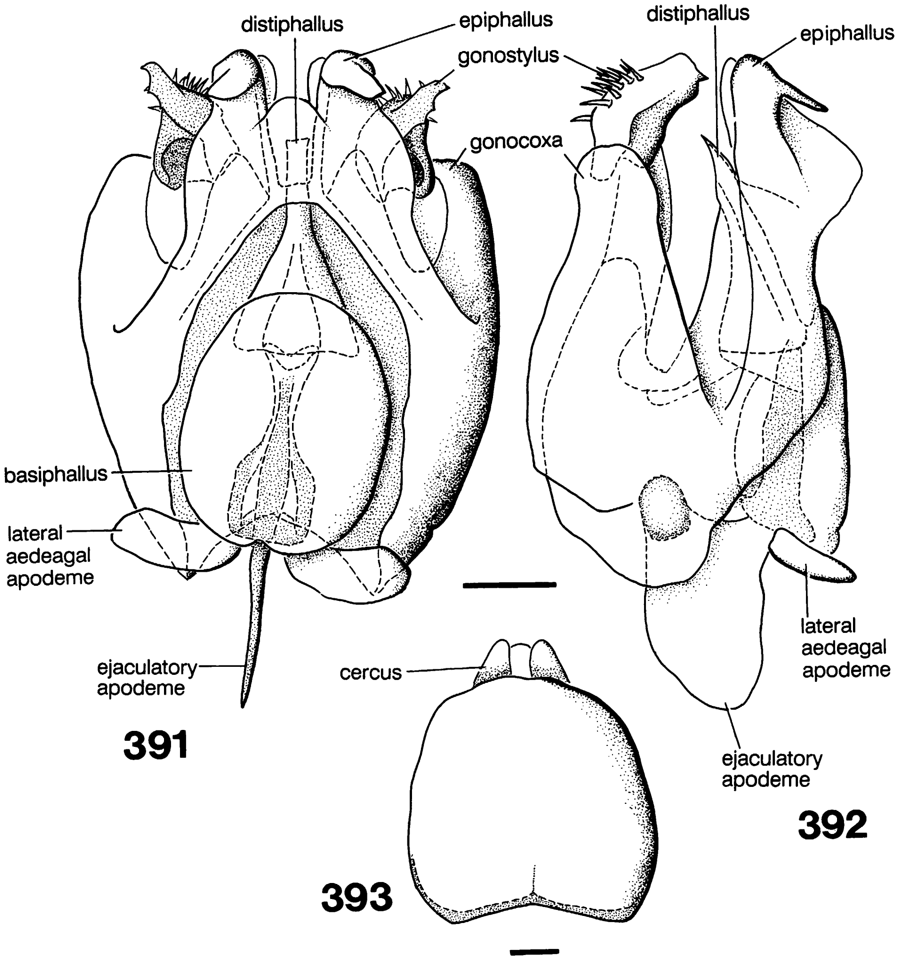
Figs. 385–390. Male genitalia of *Heterotropus gilvicornis*, vestiture not shown except on gonostyli: **385**, lateral view with epandrium in place; **386**, lateral view of gonocoxite; **387**, dorsal view with



Figs. 391–393. Male genitalia of *Desmatomyia anomala*, vestiture not shown: **391**, dorsal view with epandrium removed; **392**, lateral view with epandrium removed; **393**, dorsal view of epandrium. Scales 0.1 mm.

120. Form of ejaculatory apodeme. The ejaculatory apodeme in the Rhagionidae and Nemestrinoidea examined is rounded in cross section (figs. 318, 319), and this was considered the plesiomorphic state. Among the asiloids I found three separate advanced states treated nonadditively: laterally compressed (figs. 385, 392, 394–400, 402), coded 1; *Antonia* has three vanes (fig. 401), and was coded 2; *Caenotus* (Yeates, 1992a) *and Bonjeania* have four vanes (figs. 328–329), cross-shaped in section, and was coded 3.

The ejaculatory apodeme is laterally compressed in the Asilidae, Mydidae except *Neorhaphiomidas,* and *Apiocera. Apsilocephala* and the Therevidae (except *Bonjeania*) have rounded ejaculatory apodemes (figs. 323–324, 326). *Neorhaphiomidas* has a very reduced, rounded ejaculatory apodeme, coded 0 (fig. 339). In the panopine acrocerids

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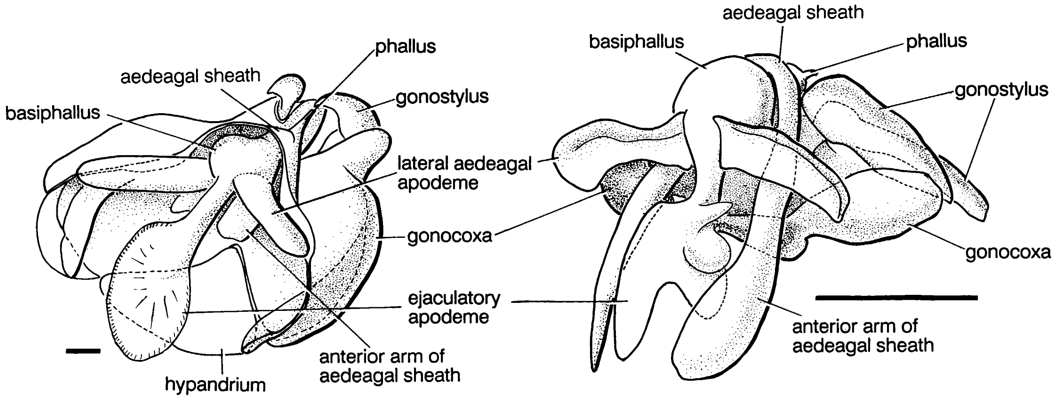
epandrium and aedeagal complex removed; **388**, ventral view with aedeagal complex removed; **389**, dorsal view of aedeagal complex; **390**, dorsal view of epandrium. Scale lines 0.1 mm.



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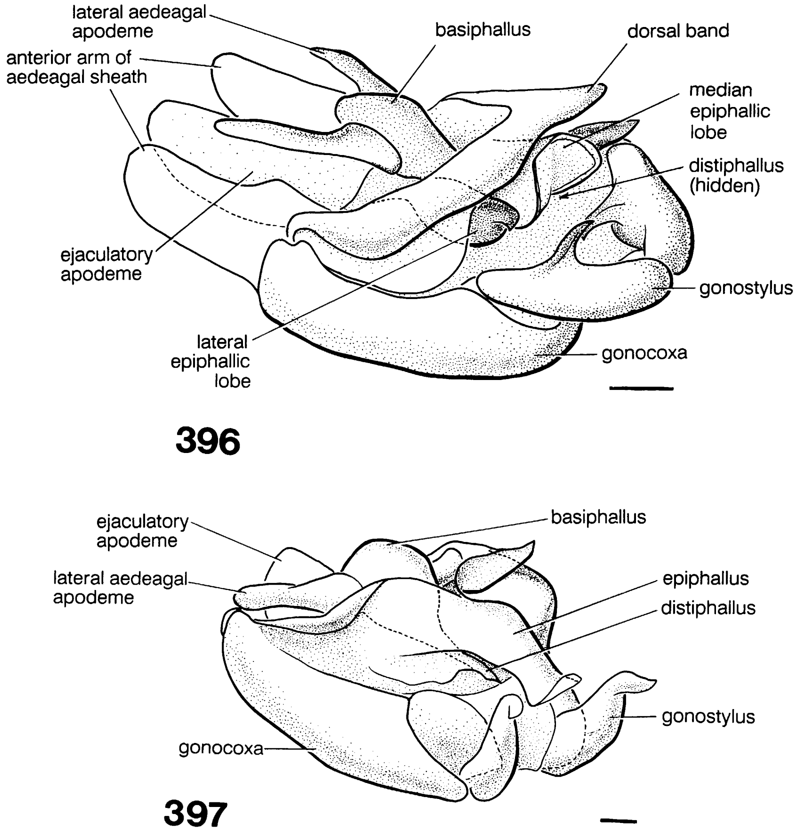
Figs. 394–395. Anterolateral view of the male genitalia of two Bombyliidae with epandrium removed and vestiture not shown: **394**, *Bombylius major*; **395**, *Mythicomyia illustris*. Scales 0.1 mm.



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Figs. 396–397. Posterolateral view of the male genitalia of two Bombyliidae with epandrium removed and vestiture not shown: **396**, *Systropus macer*; **397**, *Cytherea obscura*. Scales 0.1 mm.

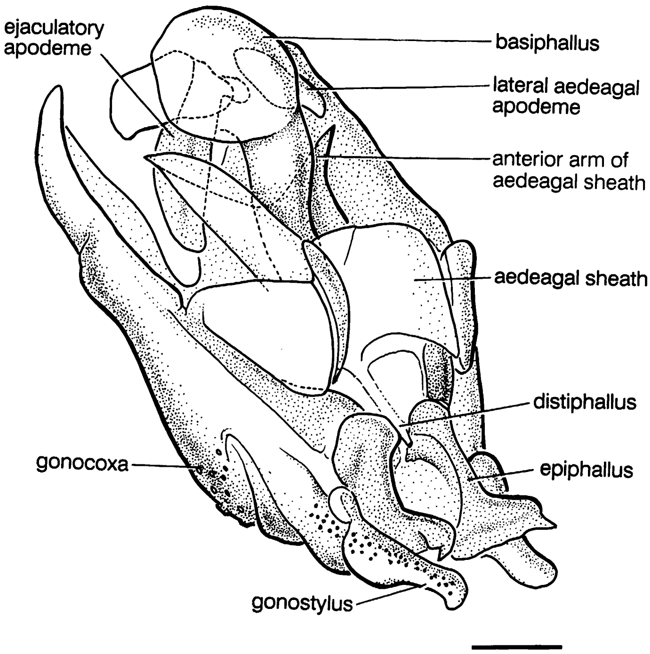


Fig. 398. Posterolateral view of male genitalia of *Geron grandis*, epandrium removed and vestiture not shown. Scale 0.1 mm.

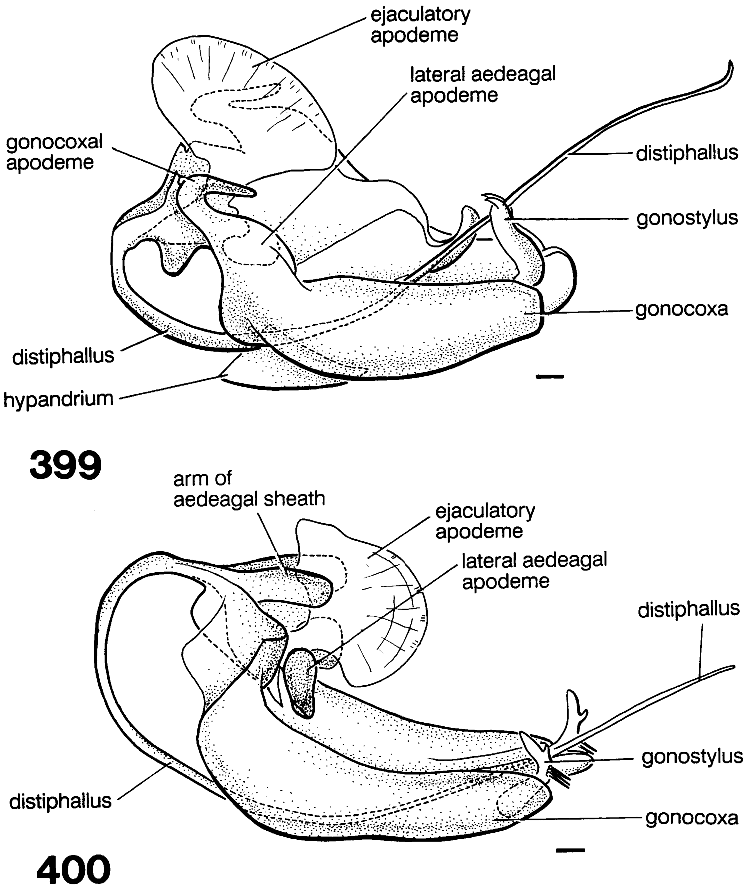
examined here the ejaculatory apodeme was rounded and coded 0, however, Schlinger (1960, e.g., figs. 83–94) illustrated some *Ogcodes* with lateral compression of the aedeagal apodeme. *Apiocera* has a lateral flange at the anteriormost end of the laterally compressed ejaculatory apodeme (fig. 337).

121. Gonostyli. Gonostyli articulating on the apex of the gonocoxites (figs. 318, 323, 326, 329, 332, 335, 337, 346, 349, 369, 373, 382, 388, 392, 396–402) are a primitive feature of the Asiloidea and found in the outgroup and more plesiomorphic flies. The Acroceridae (fig. 319), Mydidae (fig. 342), and *Neorhaphiomidas* (fig. 339) were found to have lost the gonostyli.

122. Gonostyli articulation. Plesiomorphically the gonostyli have points of articulation on the dorsal and ventral surface and they move in a horizontal plane. Among the Asiloidea the articulations of the gonostyli are on the ventral surface, allowing them to move in a dorsoventral plane relative to the gonocoxites (figs. 323, 326, 329, 332, 335, 337, 346, 349, 369, 373, 382, 388, 392, 396–402). The Nemestrinidae (fig. 318) have the plesiomorphic state, and the Acroceridae were coded -, as were other taxa lacking gonostyli (see character 121). This apomorphy was used by Hardy (1953) to distinguish the Asiloidea and other higher flies from the Nemestrinidae, Acroceridae, Tabanomorpha, and Stratiomyomorpha. Wood (1990a) considered it an apomorphic feature of the Muscomorpha.

123. Form of the gonostyli. In most Tabanomorpha and asiloids there is a single pair of gonostyli articulating on the gonocoxites. In a minority of examples examined here there appear to be two pairs of gonostyli. I have coded *Bonjeania* (fig. 329) and the Mythicomyiane (fig. 369, 382) as possessing the advanced state. However, differences in form of the gonostyli in these groups make me uncertain about their homology.

Bonjeania (fig. 329) has four articulating lobes at the apex of the gonocoxites, and this is a feature of many other Therevidae from the Southern Hemisphere (M. E. Irwin, personal commun.). In this case it appears that those of the most lateral pair are actually articulating lobes of the gonocoxites, and the median pair is homologous with the gonostyli of other flies. The Mythicomyiinae also appear to have four lobes extending from the



Figs. 399–400. Posterolateral views of male genitalia of two Bombyliidae with epandrium removed and vestiture not shown: **399**, *Amictus validus*; **400**, *Paratoxophora cuthbertsoni*. Scale 0.1 mm.

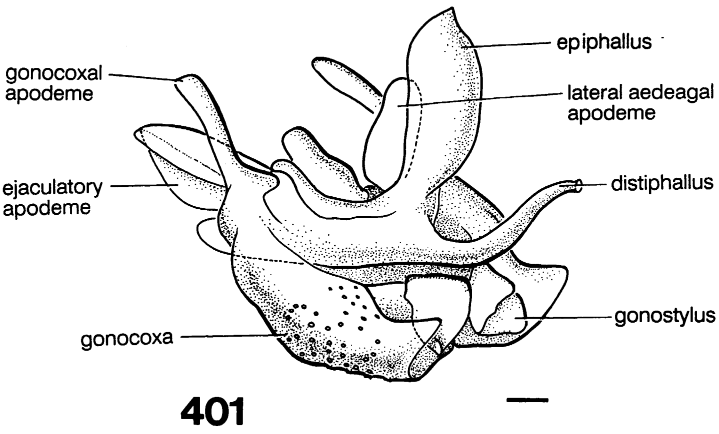
apex of the gonocoxites (figs. 369, 382), with their bases one above the other. They may be articulating lobes of the gonocoxites as found in *Bonjeania*, however they may also be secondarily divided gonostyli, or lobes of the aedeagal sheath.

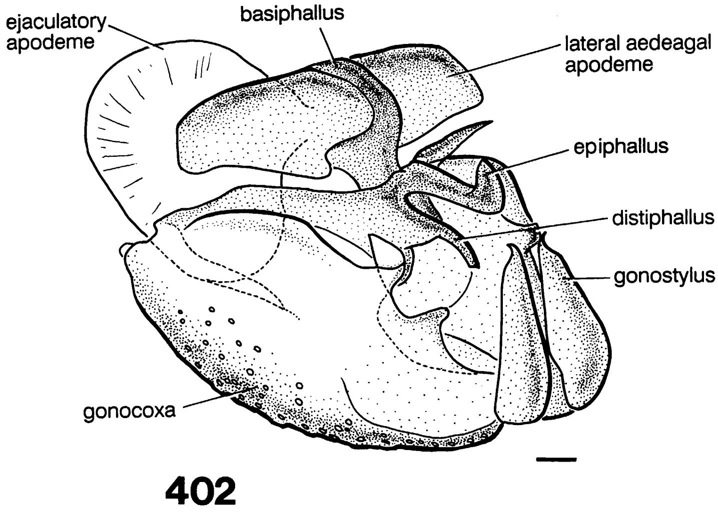
Geron has four or more lobes extending from the apex of the gonocoxites (fig. 398), however only the most ventral lobes articulate with the gonocoxites and are homologous with the gonostyli. The remaining lobes are modified extensions of the aedeagal sheath termed the epiphallus (character 116, state 2).

124. Tergite 10. I identified a small, undivided sclerite behind the epandrium and anterior to the cerci as the tergite of segment 10 (fig. 317). I found tergite 10 only in the Rhagionidae and Nemestrinidae, thus the absence of this sclerite is an apomorphy of the Acroceridae and Asiloidea and Eremoneura. I consider the surstyli of *Apsilocephala* (fig. 323) to be lobes differentiated from tergite 9, the epandrium (character 109).

FEMALE GENITALIA

While such works as Nagatomi and Iwata (1976, 1978) have surveyed female terminalia in more plesiomorphic Brachycera, no such survey exists for the Asiloidea. However, surveys of varying extent have been conducted within some families. Irwin (1976) made a pioneering study of therevid female genitalia and correlated oviposition behavior. The Bombyliidae have fared better than other asiloids as Mühlenberg (1971a) made detailed examinations of a broad spectrum



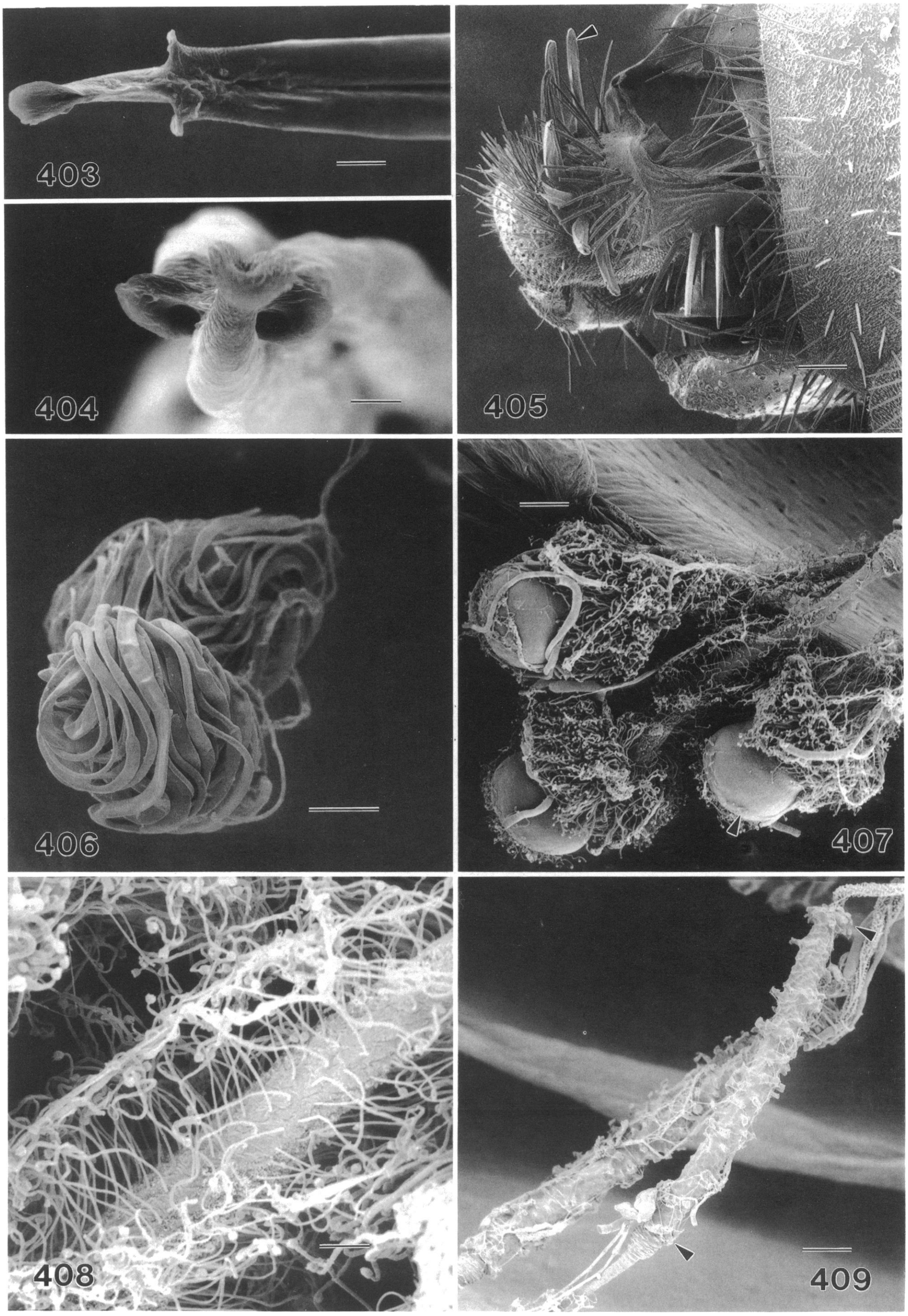


Figs. 401–402. Posterolateral view of the male genitalia of two Bombyliidae with epandrium removed and vestiture not shown: **401**, *Antonia suavissima*; **402**, *Aphoebantus cervinus*. Scales 0.1 mm.

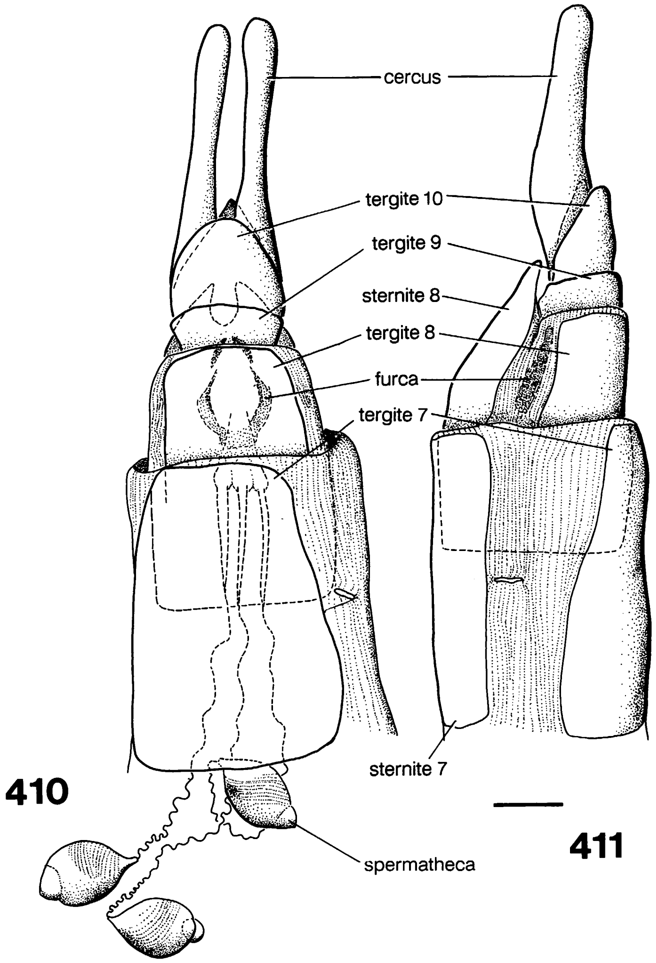
of Bombyliidae, and his phylogenetic conclusions (1971b) are based largely on female genitalic characters. Theodor (1983) has also examined and illustrated the male and female genitalia of a large sample of bombyliid taxa, but his phylogenetic speculations were limited.

The main theme in the modification of female terminalia within the Asiloidea concerns the acquisition and loss of acanthophorites and their accompanying spines (character 139). Within the Bombyliidae, the female terminalia have undergone striking changes in association with the development of the sand chamber. The sand chamber is a complicated, composite structure comprising elements from a number of segments, and its evolution is described in a number of characters below. The sand chamber subfamilies are the Bombyliinae, Crocidiinae, Mariobezzinae, Oniromyiinae, Cythereinae, Lomatiinae, Tomomyzinae, and Anthracinae. Where appropriate, I have indicated the character number used by Mühlenberg (1971b) in square brackets.

125. Shape of tergite 8. Plesiomorphically the anterior margin of tergite 8 is simple, however in some therevids and many bombyliids a strongly sclerotized apodeme is present which is directed anteriorly. In the



Figs. 403–409. Scanning electron micrographs of male and female genitalia and spermathecae of Bombyliidae and a therevid: **403**, dorsal view of the tip of the phallus of *Cyllenia maculata*, scale 10 μm; **404**, posterior view of the tip of the phallus of *C. maculata*, scale 5 μm; **405**, lateral view of the tip of the abdomen of a therevid *Anabarhynchus* sp., arrow indicates an acanthophorite spine, scale 100 μm; **406**, spermathecae of *Geron grandis*, scale 50 μm; **407**, spermathecal bulbs and apical spermathecal



Figs. 410–411. Female genitalia of the nemestrinid *Hirmoneura exotica*, vestiture not shown: **410**, dorsal view; **411**, lateral view. Scale 0.5 mm.

Bombyliidae, Mühlenberg (1971a) found that muscle M14 had its origin on this apodeme [his rostrum and his character 15] and was inserted on the lateral margin of tergite 9.

I divided the form of the apodeme into two states and coded a laterally compressed apodeme 1, and a dorsoventrally compressed apodeme 2. Within the Therevidae, *Bonjeania* had state 1 and *Thereva* (fig. 446) had state 2. Within the Bombyliidae, all the sand chamber subfamilies had advanced states except *Bombylius androgynus*, *Lepidophora*, *Cyrtomyia*, *Myonema*, and *Anthrax* (figs. 436–445). Of the sand chamber subfamilies with advanced states, all had state 1 except *Exoprosopa* (fig. 445), *Aphoebantus*, *Pantarbes*, *Cytherea*, *Corsomyza*, *Paratoxophora*, and *Megapalpus* (fig. 441) with state 2. Within the Bombyliidae, this feature is closely correlated with the sand chamber, and

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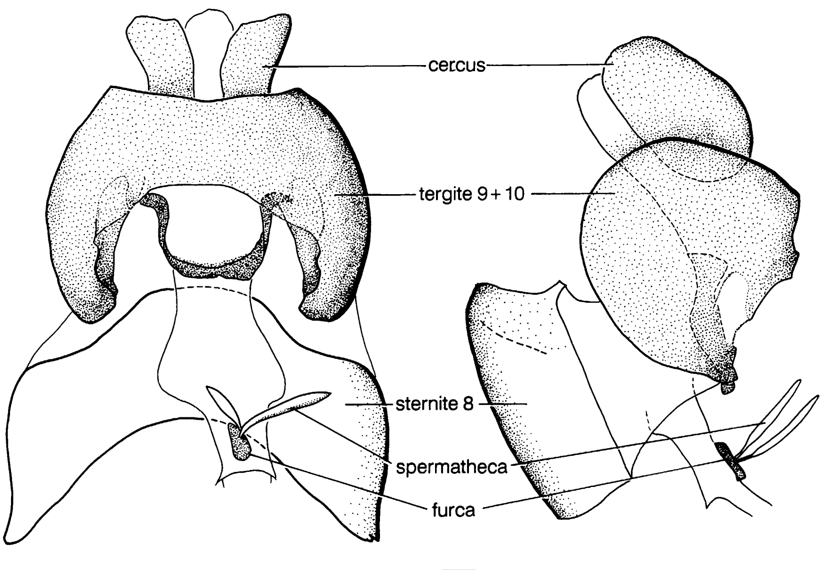
ducts of *Bombylius major*, arrow indicates spermathecal bulb, scale 50 μm; **408**, detail of tubules surrounding spermathecal bulb and ducts in figure 407, scale 10 μm; **409**, sperm pump of *Bombylius major*, arrows indicate sclerotized discs at each end of pump, scale 50 μm.



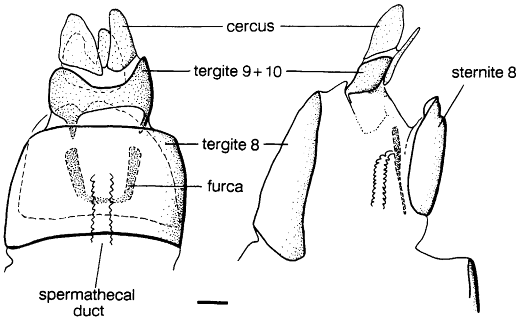
412 **413**

Figs. 412–413. Female genitalia of the acrocerid *Eulonchus smaragdinus*, vestiture not shown: **412**, dorsal view; **413**, lateral view. Scale 0.5 mm.

both features appear to be lost together. For example, *B. androgynus* has lost the apodeme and sand chamber but has close relatives with both.

Havelka (1974) reported that *Crocidium* lacked the apodeme on the anterior margin of tergite 8, however Theodor (1983) and I (fig. 440) found it to be present in this genus.

126. Shape of tergite 9 + 10. *Systropus* alone has a small, dorsally directed apodeme medially on the anterior margin of tergite 9 + 10 [Mühlenberg (1971b) character 15a; he erroneously considered it an anterior apodeme of tergite 8].

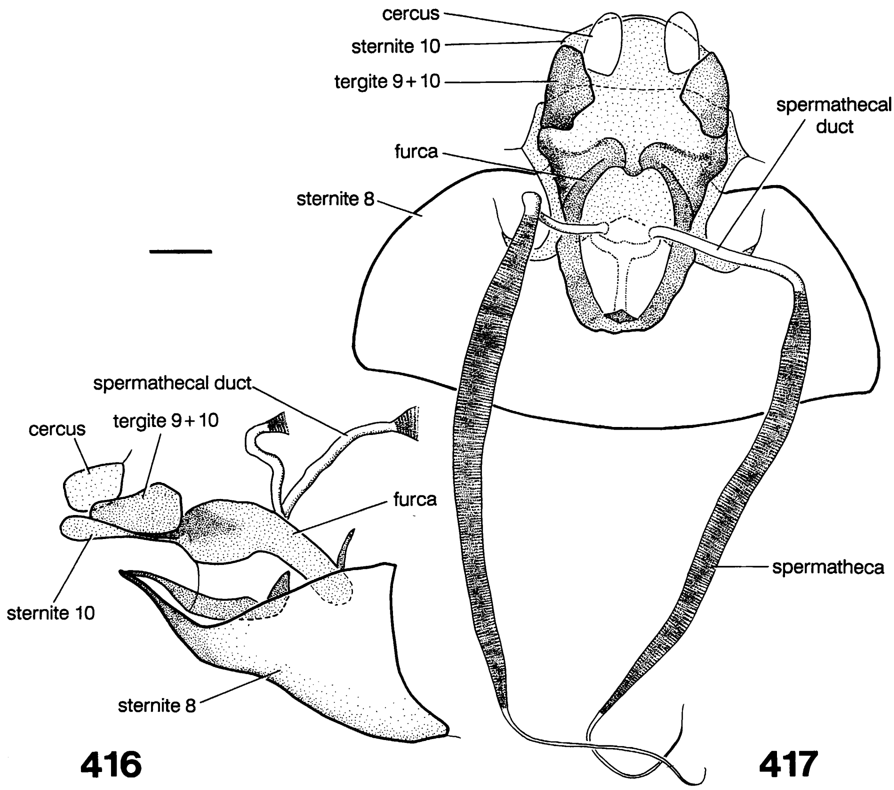


414 **415**

Figs. 414–415. Female genitalia of the apsilocephalid *Apsilocephala* sp., vestiture not shown: **414**, dorsal view; **415**, lateral view. Scale 0.1 mm.

127. Tergite 8 vestiture. Plesiomorphically tergite 8 is clothed with hairs, those on the posterior margin being approximately the same length as the remainder (figs. 436, 438–439). In the advanced state of this character, the hairs on the anterior portion are reduced or absent and the hairs on the posterior margin of the tergite become dense and lengthened (figs. 437, 440–442, 444–445). I found this feature to be present in all the sand chamber subfamilies except *Mariobezzia* (fig. 443) and *B. androgynus*. As in character 125, this feature appears to be closely associated with the sand chamber. [Mühlenberg (1971b) character 13].

128. Tergite 8 vestiture. The eclimines *Thevenetimyia* and *Eclimus* have the lateral margins of tergite 8 curved ventrally and medially (fig. 485). These lateral margins have dense, long vestiture which extends underneath the cerci. Instead of hairs, *Eclimus* has thick setae on the posterior margin of tergite 8, which may be autapomorphic for the genus [Mühlenberg (1971b) character 14].

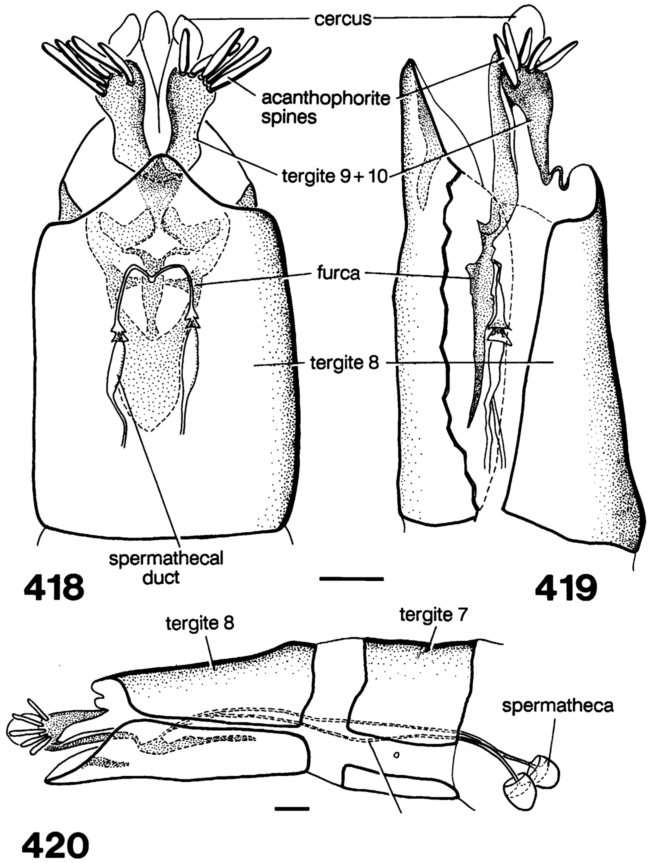


Figs. 416–417. Female genitalia of the scenopinid *Scenopinus fenestralis*, vestiture not shown: **416**, lateral view; **417**, dorsal view. Scale 0.1 mm.

129. Tergites 8 and 9. Plesiomorphically tergites 8 and 9 are separate, however, in *Caenotus, Prorates*, *Propebrevitrichia*, *Thereva*, and *Bonjeania* these two sclerites are joined in the midline by a narrow sclerotized strap (figs. 418–419; Yeates, 1992a). This character is one of the few adult apomorphies only found in the Therevidae and Scenopinidae, and it appears to be only found in species with well-developed acanthophorite spines.

The chorion surrounding the eggs of most insects is not in itself waterproof, and egg desiccation is a problem which insects overcome in a variety of ways. Many asiloids protect their eggs by inserting them in the substrate (e.g. Irwin, 1976). The Bombyliidae belonging to the sand chamber subfamilies, which includes most of the species in the family, coat the eggs in sand before depositing them on the wing. A notable exception is the genus *Lordotus* and its relatives, which have an elongate, telescoping abdomen and acanthophorites modified into flattened digging blades (figs. 430–431). *Lordotus* oviposits by thrusting the abdomen into loose sand [J.W. McSwain personal obs. *in* Hull (1973)]. Although there have been very few observations made, more primitive Bombyliidae appear to have a more simple oviposition behavior and eject naked eggs from the abdomen onto the ground while at rest (e.g., *Usia*, Du Merle, 1971).

The female sand chamber (Schremmer, 1964) functions as a receptacle where the eggs can be coated in sand (Mühlenberg, 1971a; Theodor, 1983). It is a large pouch formed ventrally by the invagination of sternite 8 (character 130) and dorsally by tergite 8 and the long hairs extending from its margin (character 127). In addition, the segments posterior to 7 become invaginated inside segment 7, providing additional support for the sand chamber.



Figs. 418–420. Female genitalia of the scenopinid *Propebrevitrichia sp.*, vestiture not shown: **418**, dorsal view; **419**, lateral view; **420**, lateral view showing tergite 7 and spermathecal bulbs. Scale 0.1 mm.

130. Sternite 8 position. Plesiomorphically sternite 8 is external and oriented similarly to the more anterior abdominal sternites. Among the sand chamber subfamilies sternite 8 is invaginated and its posterior margin becomes elevated so that it effectively forms the anterior wall of the sand chamber (figs. 479, 483). I found sternite 8 to be invaginated in *Geron* and all the sand chamber subfamilies except *Antonia.* Mühlenberg (1971b) considered that *Geron* represented an intermediate stage in the development of a sand chamber because of the invagination of sternite 8. The invagination seen in *Geron* is at least partially caused by the large lateral expansions of tergite 8 (fig. 475) and the posterior margin of the sternite does not become elevated, as in the sand chamber subfamilies. On the cladogram the advanced state of this character in *Geron* has been reached independently of the advanced state found in the sand chamber subfamilies. *Antonia* has lost the sand chamber and sternite 8 has reversed to an external position. [Muhlenberg (1971b) character 16].

131. Vestiture of sternite 8. In those asiloids without a sand chamber the vestiture of sternite 8 is simple and similar to that found on the more anterior sternites. In most of the forms with an invaginated sternite 8, the vestiture of this sclerite becomes more elaborate, with a band of hairs adjacent to the anterior margin (figs. 461–468). An autapomorphy of *Marmasoma* is a median row of long hairs on sternite 8 (fig. 460).

132. Shape of sternite 8. In most asiloids sternite 8 is simple and has a similar shape to sternite 7 (figs. 447–458). Within the Bom-

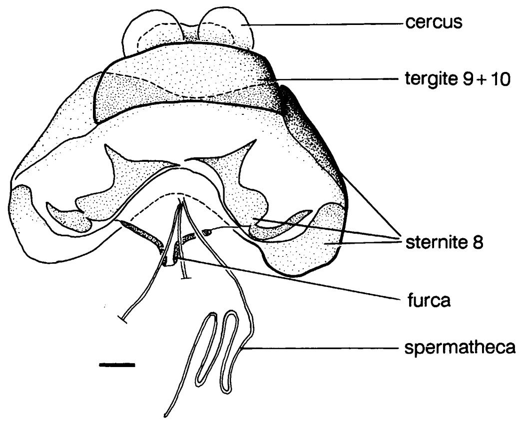
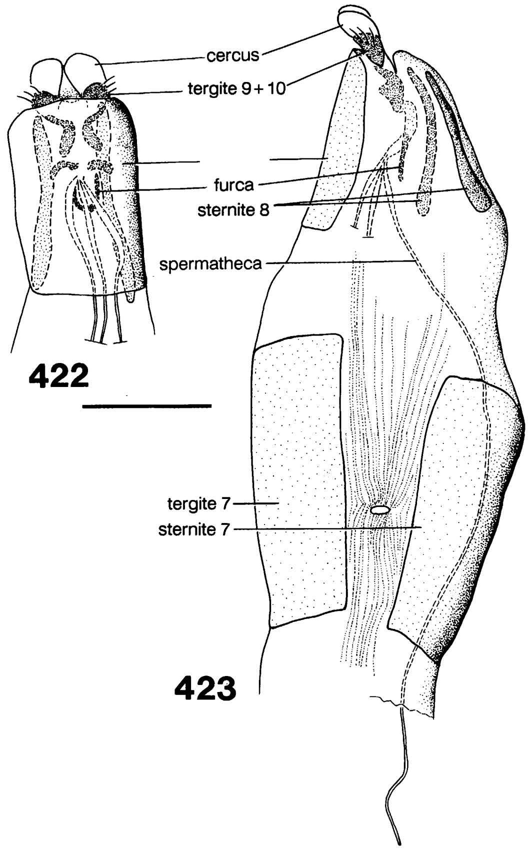


Fig. 421. Female genitalia of the asilid *Dioctria atricapilla*, vestiture not shown. Scale 0.1 mm.



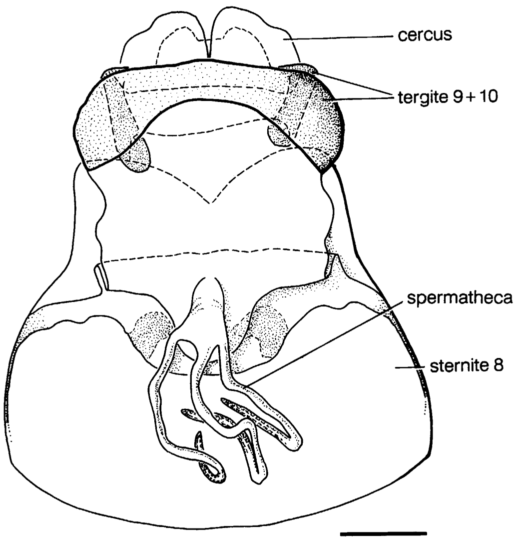
Figs. 422–423. Female genitalia of the asilid *Leptarthrus brevirostris*, vestiture not shown: **422**, dorsal view; **423**, lateral view. Scale 0.5 mm.

byliidae, however, sternite 8 has undergone much modification in association with the development of the sand chamber. These modifications were coded into three apomorphic states and analyzed additively. The eclimine *Marmasoma* and the bombyliine *Paratoxophora* have sternite 8 modified into an internal concave sheet (figs. 459–460) with a strong median ridge, coded 1. Most members of clade 42 have sternite 8 divided into three sclerites (figs. 461–467); one narrow, transverse sclerite near the base, and two longitudinally orientated sclerites which are separated by a narrow, median desclerotized area, coded 2. Members of clade 42 possessing a simple sternite 8 include the eclimines except *Marmasoma*; *Crocidium*, and the Antoniinae. In state 3, found in *Exoprosopa* and *Villa*, the sand chamber is large and vaulted and sternite 8 is composed of a single, well-sclerotized, concave sheet (fig. 468). [Mühlenberg (1971b) termed this a semispherical 8th sternite, character 11b].

133. Posterior margin of sternite 8. In the Phthiriini examined the posterior margin of sternite 8 has one pair of enlarged hairs medially (fig. 451). This feature appears to be a synapomorphy of the Phthiriinae, however it will require verification in *Australiphthiria* Evenhuis, an Australian phthiriinae with highly modified, laterally compressed female genitalia.

Some confusion exists in the literature as to the segmental origin of the sclerites of the female terminalia of Bombyliidae. Mühlenberg (1971a, b) consistently referred to the fused tergites 9 and 10 as tergite 9 alone, and confused the cerci with tergite 10. Crampton (1942), Colless and McAlpine (1970), and Hennig (1976) considered that the acanthophorites (see character 134) represented the 9th tergite, not the 10th as is currently recognized (Adisoemarto and Wood, 1975; Irwin, 1976; McAlpine, 1981; Griffiths, 1986).

134. Tergites 9 and 10. In the outgroup and commonly in Tabanomorpha, tergite 9 is quite separate from tergite 10 (Nagatomi and Iwata, 1976), and I considered this the plesiomorphic condition (figs. 410–411). In the Asiloidea and some Empidoidea, tergite 10 is divided in the midline into two acanthophorites (Hennig, 1976; Irwin, 1976; Griffiths, 1986; Woodley, 1989). The acanthophorites often bear large spines (character



Figs. 424. Female genitalia of the mydid *Mydas clavatus*, tergite 8 removed and vestiture not shown. Scale 0.5 mm.

139). In almost all Asiloidea, these acanthophorites are intimately associated or fused with tergite 9, and this fusion appears to have been achieved independently in many of the families. I divided the apomorphic condition into two states as follows. State 1 occurs in those species in which the tergites were very closely associated, however a line of fusion is still evident. I coded as state 2 those species in which a line of fusion is not evident, and tergites 9 and 10 are completely fused (figs. 412–429, 469–476). Of course, it is possible to interpret state 2 as the complete loss of one or other of the tergites. Within the Bombyliidae, state 2 occurs in all Mythicomyiinae, *Oligodranes*, Usiinae, Toxophorinae, *Myonema*, and *Antonia* (figs. 482, 484). The remainder have state 0, and state 1 occurs in *Aldrichia*, the eclimines (fig. 485) and *Paratoxophora* (fig. 487), *Megapalpus* (fig. 489), *Lomatia* and *Exoprosopa* (fig. 490), and *Villa*. *Rhaphiomidas acton* Coquillett (Apioceridae) appears to have separate tergites 9 and 10 (Peterson, 1981b). [Mühlenberg (1971b) character 19].

135. Tergite 9 shape. The dorsal margin of tergite 9 is most often smoothly rounded, however in the Mydidae and Apioceridae and the eclimines *Thevenetimyia* and *Eclimus* there is a median dorsal spine.

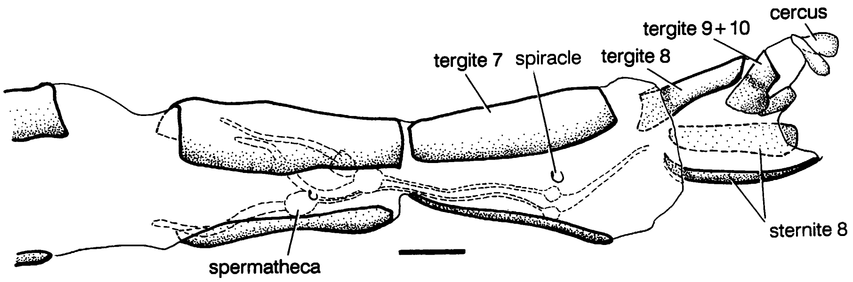
Primitively the furca (sternite 9) is present as one sclerite (genital fork in Nagatomi and Iwata, 1976; McAlpine, 1981). The furca becomes further reduced and divided into two sclerites independently in the Asilidae, Mydidae, and Bombyliidae. Among the Bombyliidae, there appears to be a gradual reduction in the size of the furca and it becomes divided into two sclerotized rods, one each side of the midline (figs. 497–501). While these rods are most often "L" shaped (fig. 497), they can be sinuous or linear (figs. 498–500). I did not use the reduction of the furca as a character because I could not define separate states in its reduction. Additionally, I found it difficult to distinguish between those species in which the furca was separated completely into two rods from those in which the rods were joined by a narrow band of sclerotization anterior to the spermathecal opening.

136. Furca shape. I found that the furca of *Toxophora* had two lateral sclerotized rods joined by a weakly sclerotized band, and was distinguished from all other taxa by a dorsally directed, well sclerotized apodeme (fig. 496) anterior to the spermathecal opening.

137. Furca shape. The furca of *Geron* has two posterior, dorsal apodemes (fig. 495), and this appears to provide an apomorphy for the tribe. [Mühlenberg (1971b) postgenital plate, character 23].

138. Sclerotized strips from T9 and T10. In many Bombyliidae belonging to clade 40, tergites 9 and 10 have long, lateral sclerotized strips which reinforce the dorsal wall of the sand chamber and extend back toward the arms of the furca (figs. 486–489, 491–492). [Mühlenberg (1971b) character 19]. These strips are absent in *Cyrtomyia*, *Mariobezzia*, and the Antoniinae.

139. Acanthophorite spines. In the Rhagionidae examined tergite 10 is undivided and this was considered the plesiomorphic state. In the Asiloidea, tergite 10 divides in the midline to form two lateral sclerites which may fuse with tergite 9 (character 134). These lateral sclerites, termed acanthophorites, may bear large spines (fig. 405). These spines are thought to aid the female when ovipositing in sandy substrates (Irwin, 1976, McAlpine, 1981). Adisoemarto and Wood (1975) were the first to consider acanthophorite spines a



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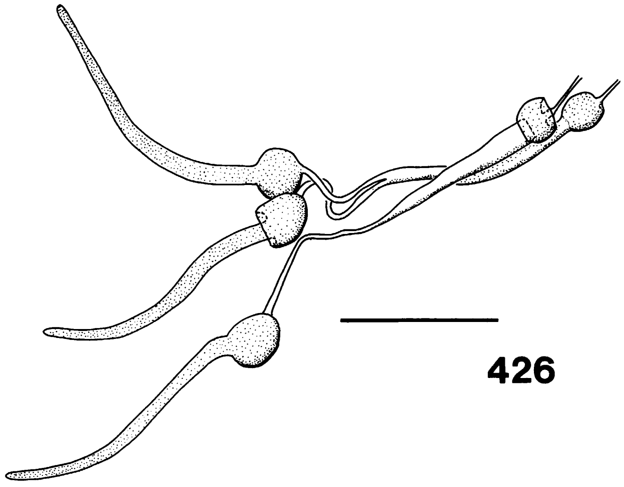

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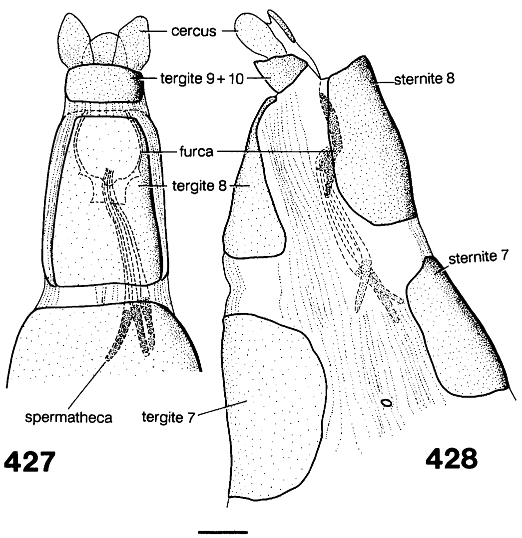
Figs. 425–426. Female genitalia of *Apystomyia elinguis*, vestiture not shown: **425**, lateral view; **426**, detail of spermathecae. Scale 0.1 mm.

groundplan feature of the Asiloidea. Acanthophorites are present in every asiloid family and also in some Empidoidea (Woodley, 1989), however their occurrence in the Empidoidea is probably homoplastic (Hennig, 1976; Chvála, 1983; Griffiths, 1986). Clearly the acanthophorite spines have been lost numerous times independently in different families and their presence or absence is correlated with oviposition behavior. Among the asiloids examined here, acanthophorite spines were absent in the asilids *Leptogaster*, *Leptarthrus* (fig. 422–423), *Dioctria* (fig. 421), *Mydas*, *Apsilocephala* (figs. 414–415), *Scenopinus* (figs. 416–417), the Hilarimorphidae (figs. 427–428, 425), *Oligodranes* (fig. 476), the Mythicomyiinae (figs. 429, 469), the Usiinae (figs. 470, 473), the Toxophorinae (fig. 471–472, 475), the Lordotinae (figs. 430–431) *B. androgynus* (fig. 480), *Cyllenia*, and the Antoniinae (figs. 482, 484). Almost all Bombyliidae lacking acanthophorite spines also lack acanthophorites, the exception being provided by *Cyllenia*, *B. androgynus*, and the Lordotinae. The former two have small but well-separated acanthophorites lacking spines. It is reasonable to assume that the acanthophorites have been lost more recently in these genera than in genera where the acanthophorites have been lost also, such as the Antoniinae. The Lordotinae have large, well differentiated acanthophorites lacking spines (figs. 430–431) which are dorsoventrally flattened and appear to act as blades during oviposition [Mühlenberg, 1971b character 20b].

140. Female cerci. Woodley (1989) considered the reduction in female cerci from two to one segment apomorphic for the Mus-



Figs. 427–428. Female genitalia of *Hilarimorpha mentata*, vestiture not shown: **427**, dorsal view; **428**, lateral view. Scale 0.1 mm.

comorpha. All asiloids examined in this study had one-segmented cerci, as did the Acroceridae and Nemestrinidae (figs. 410–411). Nemestrinids belonging to the subfamilies Tricopsideinae and Atriadopsinae have long, sabre-shaped cerci (Bernardi, 1973), however they are composed of only one segment.

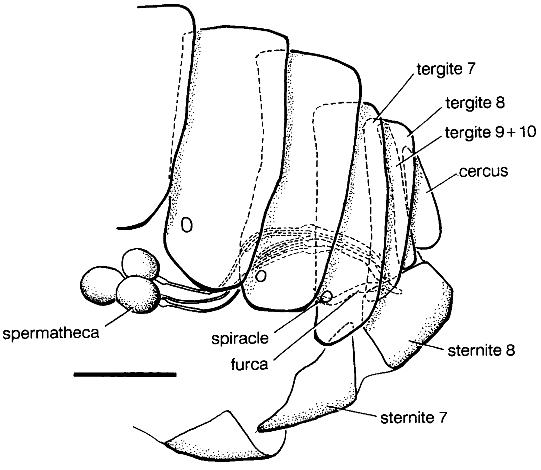
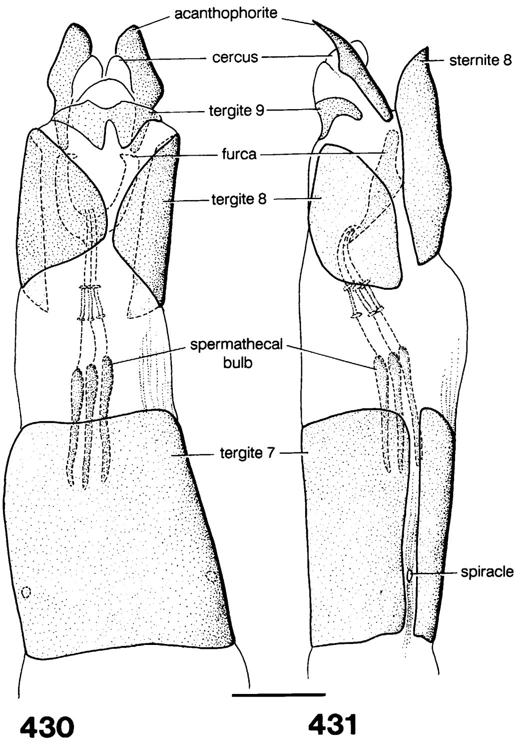


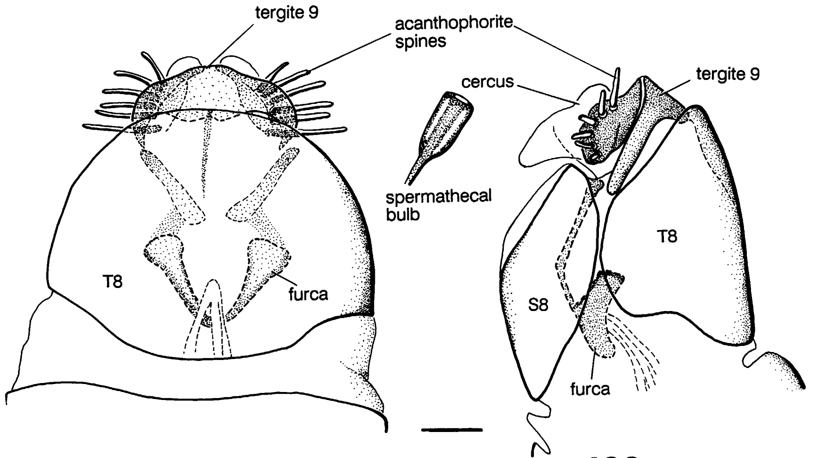
Fig. 429. Female genitalia of *Cephalodromia fusca*, vestiture not shown. Scale 0.2 mm.



Figs. 430–431. Female genitalia of *Lordotus pulchrissimus*, vestiture not shown: **430**, dorsal view; **431**, lateral view. Scale 0.5 mm.

141. Female sternite 10. *Antonia* has a peculiar membranous lobe which emerges beneath the fused 9th and 10th tergites (fig. 482). As female sternite 9 is modified as the furca, I interpret this lobe as a derivative of the next most posterior sclerite, sternite 10. Alternatively, it may be formed from membrane between sternites 9 and 10. Evenhuis (1993) was unable to find this lobe in an undescribed species of *Antonia* from Kenya. This undescribed species had elongate lamellae on tergites 9 and 10, and was similar in this respect to *Antoniaustralia* Becker and *Cyx* Evenhuis. There is obviously a range of variation in female genitalia of species currently placed in *Antonia*.

142. Number of spermathecae. three, 0; two or one, 1. The plesiomorphic number of spermathecae in the Diptera (Sturtevant, 1925; 1926; Downes, 1968) and in the Tabanomorpha is three. Three spermathecae are also found in most asiloids. A reduction to one or no spermathecae is found in all empidoids (Hennig, 1973; Wiegmann et al. 1993). In the Nemestrinidae, *Tricophthalma* has two spermathecae whereas *Hirmoneura*



Figs. 432–433. Female genitalia of *Heterotropus gilvicornis*, vestiture except acanthophorite spines not shown: **432**, dorsal view; **433**, lateral view. Scale 0.1 mm.

(fig. 410) has three. The acrocerids examined had two spermathecae (figs. 412–413). Among the asiloids, a reduction in the number of spermathecae has occurred several times. Theodor (1976) noted that all Asilidae he examined had three spermathecae except the asilines *Proctacanthus* Macquart, *Eccritosia* Schiner, and *Myaptex* Hull, which have two. I assume these are secondary reductions. Two spermathecae are found in the Scenopinidae (figs. 416–420, Yeates, 1992a). Among the Bombyliidae, *Antonia* has one fully developed spermatheca and two vestigial ones (fig. 501). Irwin and Lyneborg (1981b) record three unsclerotized spermathecae in the Therevidae and Peterson (1981b) reports three spermathecae in Apioceridae.

Sturtevant (1925; 1926) surveyed the spermathecae and accessory glands in the Diptera. He found one or two accessory glands to be common in the order, and they lead into the genital chamber adjacent to the spermathecal openings. There are two accessory glands in Tabanomorpha and Asiloidea ex-

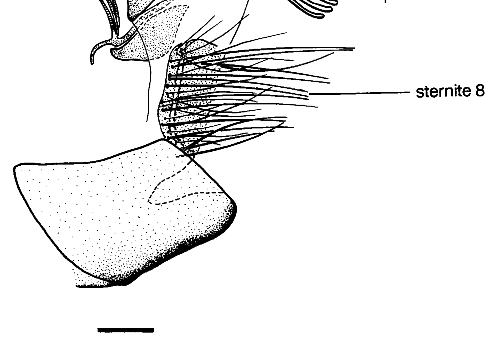


Fig. 434. Female genitalia of *Desmatomyia anomala*, lateral view. Scale 0.1 mm.

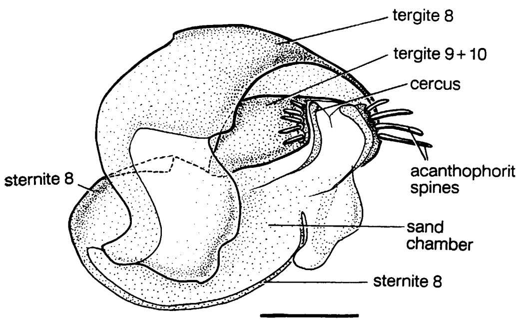
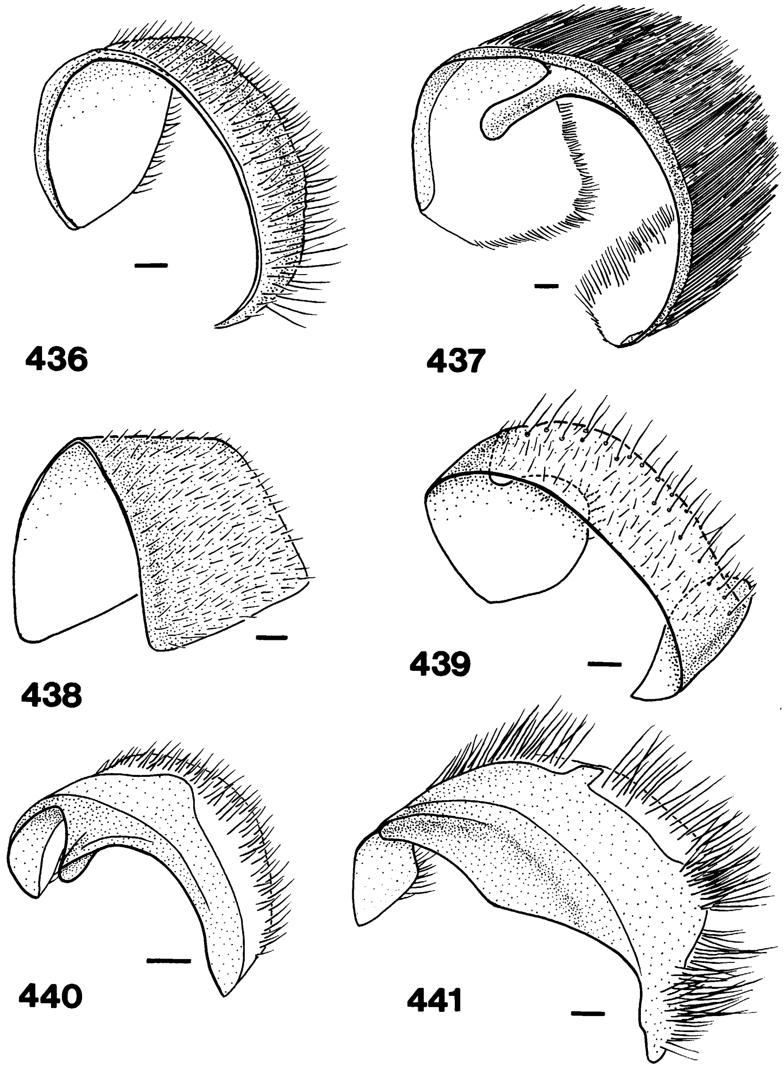


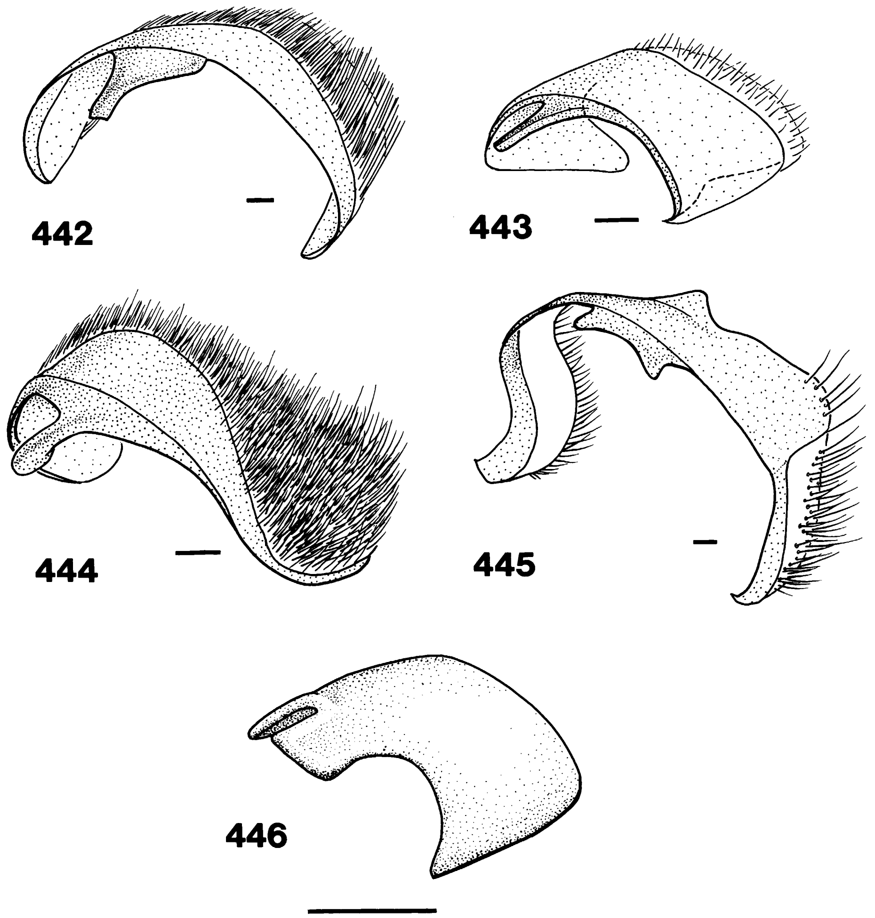
Fig. 435. Female genitalia of *Exoprosopa caliptera*, posterolateral view, vestiture not shown except acanthophorite spines. Scale 0.5 mm.



Figs. 436–441. Anterolateral views of tergite 8 of various female Bombyliidae: **436**, *Usia atrata*; **437**, *Bombylius major*; **438**, *Systropus macer*; **439**, *Geron grandis*; **440**, *Crocidium karooanum*; **441**, *Paratoxophora cuthbertsoni*. Scale 0.1 mm.

cept the Scenopinidae and the Bombyliidae. The Scenopinidae have one accessory gland, however the Bombyliidae exhibit more variation, with one or two additional pairs of accessory glands in Bombyliidae with sand chambers. The bombyliine *Systoechus* has two pairs of accessory glands (Sturtevant, 1925) and Biliotti et al. (1965), working on the anthracine *Villa quinquefasciata* Wiedemann, reported three pairs of glands with ducts leading into the genital chamber, in addition to the spermathecae.

The accessory glands produce secretions which usually function to glue eggs together or to the substrate (McAlpine, 1981) and may function to glue sand particles to the eggs in bombyliids with sand chambers. I was unable to make a survey of the accessory glands in the Bombyliidae because they are not sclerotized and are lost after maceration. How-

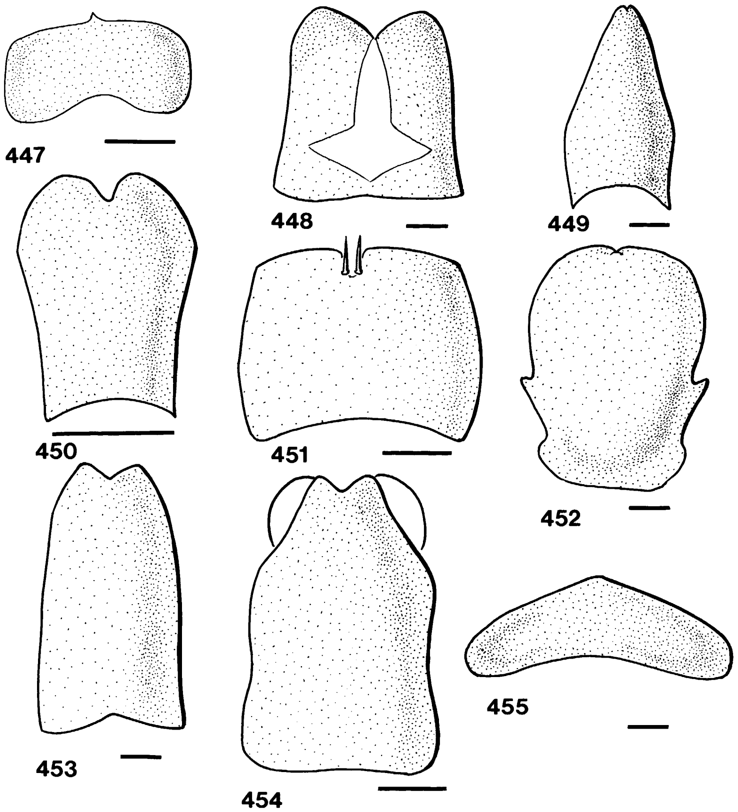


Figs. 442–446. Anterolateral views of tergite 8 of various female Bombyliidae and a therevid: **442**, *Cytherea obscura*; **443**, *Mariobezzia lichtwardti*; **444**, Tomomyza *anthracoides*; **445**, *Exoprosopa caliptera*; **446**, *Thereva fucata*. Scale 0.1 mm except figure 446 0.5 mm.

ever, a survey of the number and structure of accessory glands among Bombyliidae may furnish additional useful characters to distinguish those subfamilies possessing sand chambers from those without.

Mühlenberg (1970) made a detailed study of the microstructure of the spermathecae in *Bombylius medius* Linnaeus. He divided the spermatheca into four sections as follows: (1) a basal sperm duct, (2) muscle apparatus (fig. 409), (3) apical sperm duct (fig. 407), and (4) sperm capsule (fig. 407). I refer to his sperm capsule as the spermathecal bulb, and his muscle apparatus as the sperm pump. Theodor (1983) referred to the spermathecal bulb as the sperm capsule and Hall and Evenhuis (1987) and Evenhuis (1990) referred to the bulb as the spermathecal reservoir. Theodor (1983) and Hall and Evenhuis (1987) and Evenhuis (1990) referred to the sperm pump as the ejection apparatus of the female genitalia.

Both Mühlenberg (1970) and Theodor (1983) reported a gland surrounding the spermathecal bulb and apical region of the duct. The gland cells possess fine, sclerotized tubules which have an apical bulb and exit into the spermatheca. Figures 407–409 are electron micrographs of the spermathecae of *Bombylius major* after maceration, dissec-



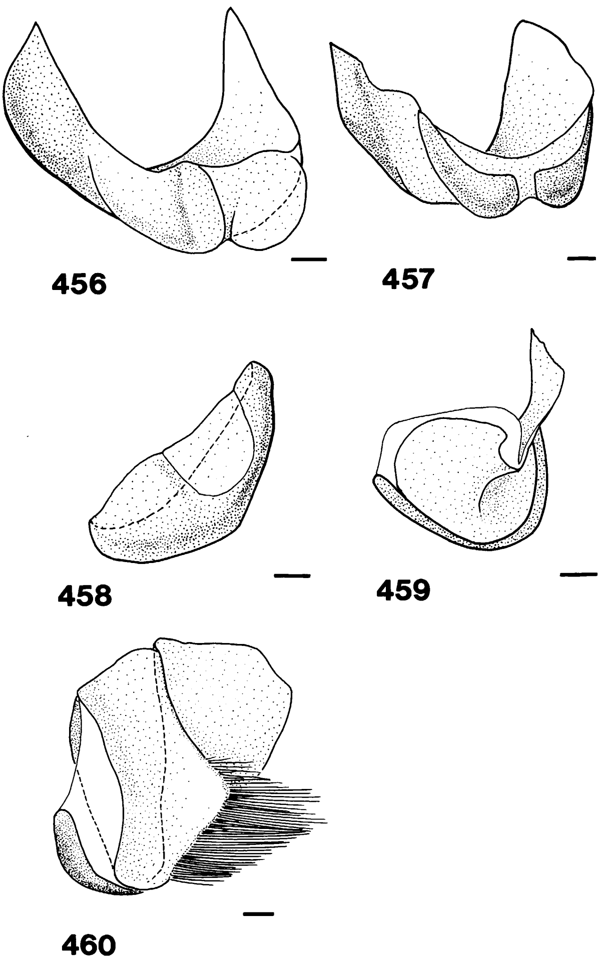
Figs. 447–455. Ventral views of sternite 8 of various Bombyliidae, vestiture not shown: **447**, *Mythicomyia illustris*; **448**, *Geron grandis*; **449**, *Zaclava clavifemorata*; **450**, *Systropus macer*; **451**, *Phthiria gaedei*; **452**, *Usia atrata*; **453**, *Toxophora virgata*; **454**, *Crocidium karooanum*; **455**, *Eclimus gracilis*. Scales 0.1 mm except figure 450 0.5 mm.

tion, and critical point drying. The sclerotized tubules are clearly visible on the surface of the spermathecal bulb and apical duct.

These microtubules appear to be present in many Bombyliidae (Theodor, 1983) and Asilidae (Theodor, 1976), however I was unable to find them in other asiloid families.

143. Form of the spermathecae. Among the Bombyliidae, only the Toxophorinae have a sclerotized, tubular, strongly coiled spermathecal bulb (figs. 406, 495–496) (Greathead, 1988). The spermathecal bulb of *Glabellula* is weakly coiled and gradually widens toward its apex (fig. 494) and I did not consider it homologous with the advanced state described here. Theodor (1976) illustrated the spermathecae of Asilidae in detail, and their form varies widely throughout the family. He found coiled spermathecal bulbs particularly among the Laphriinae (his fig. 34) and Dasypogoninae (his fig. 58), and I found a coiled bulb in *Leptogaster*. I found sinuous or linear bulbs in the other asilids I examined (figs. 421, 423), and the coiled bulbs found in *Leptogaster* and some other asilids are independently derived from those found in the Bombyliidae.

144. Spermathecal sclerotization. Well-sclerotized spermathecal bulbs were found in the rhagionids and nemestrinids (fig. 410) and I consider it the plesiomorphic condition. Among the Asiloidea, only most Bombyliidae, the Mydidae (fig. 424), *Neorhaphiomidas*, *Apystomyia* (fig. 425), *Hilarimorpha* (fig. 427), and the Scenopinidae (fig. 420) except *Scenopinus* (fig. 417) had well-sclerotized spermathecal bulbs. Among Bombyliidae, poorly sclerotized spermathecal bulbs were present in *Acridophagus*, *Desmatomyia*, and *Antonia* (fig. 501). Spermathecal sclerotiza-

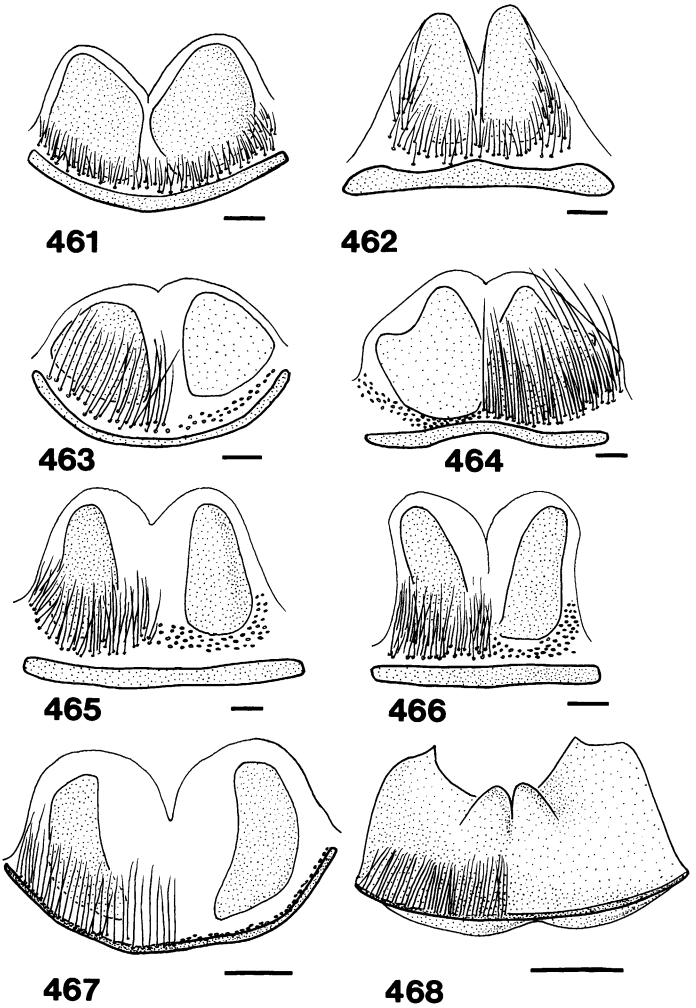


Figs. 456–460. Posterolateral views of sternite 8 of various Bombyliidae, vestiture not shown except median row of hairs on *Marmasoma*: **456**, *Lepidophora lutea*; **457**, *Cyrtomyia chilensis*; **458**, *Eclimus gracilis*; **459**, *Paratoxophora cuthbertsoni*; **460**, *Marmasoma sumptuosum*. Scale lines 0.1 mm.

tion appears to vary considerably in the Asilidae (Theodor, 1976).

145. Sperm pump. The sperm pump is formed by longitudinal muscle limited on either end by sclerotized collars (figs. 409, 430–431, 493–494, 496–497, 500). Between the sclerotized collars the sperm duct is considerably modified, with lateral papillae extending radially into the longitudinal muscle and small spiculae extending into the lumen of the duct. These spiculae are directed toward the basal region of the duct and may function as a valve (Mühlenberg, 1970).

I found a sperm pump of the type described by Mühlenberg (1970) only in the Bombyliidae. The family exhibits much variation in spermathecal structure and I scored the sperm pump absent in *Antonia* (fig. 501), *Sericosoma*, *Heterotropus* (fig. 432–433), *Desmatomyia*, (fig. 434), *Geron* (fig. 495), and the Systropodini. This may be too conservative, however, as Theodor (1983: figs. 103, 201, 213) illustrated an elaboration of the spermathecal duct which may represent the remains of the sperm pump in *Geron*, *Heterotropus*, and *Systropus*, as did Hall and Evenhuis (1987) for *Desmatomyia*. Both collars of the sperm pump may be reduced (figs. 498–499). The Mythicomyiinae appear to have lost at least the basal collar of the sperm



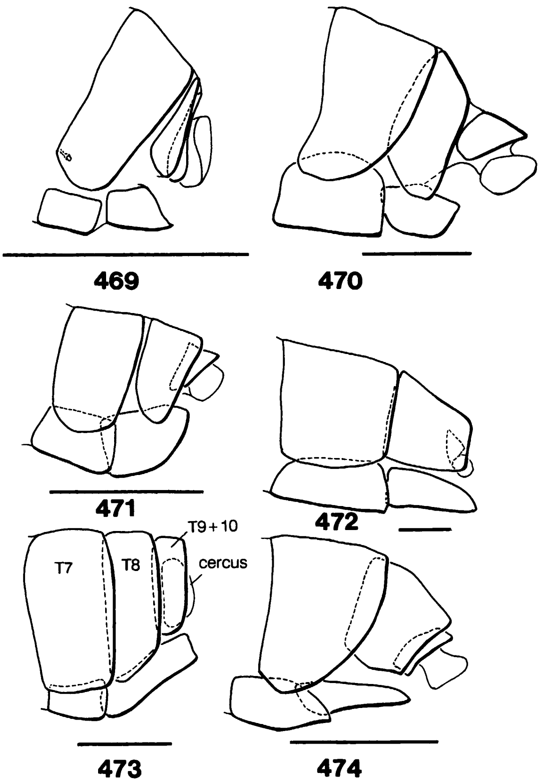
Figs. 461–468. Ventral views of sternite 8 of various Bombyliidae, vestiture shown: **461**, *Conophorus fenestratus;* **462**, *Bombylius major*; **463**, *Desmatomyia anomala*; **464**, *Dischistus mystax*; **465**, *Acrophthalmyda paulseni*; **466**, *Lomatia belzebul*; **467**, *Plesiocera psammophila*; **468**, *Exoprosopa caliptera.* Scales 0.1 mm except figure 468 0.5 mm.

pump, and the apical collar of the pump (figs. 493–494) may be membranous or funnel shaped (Theodor, 1983).

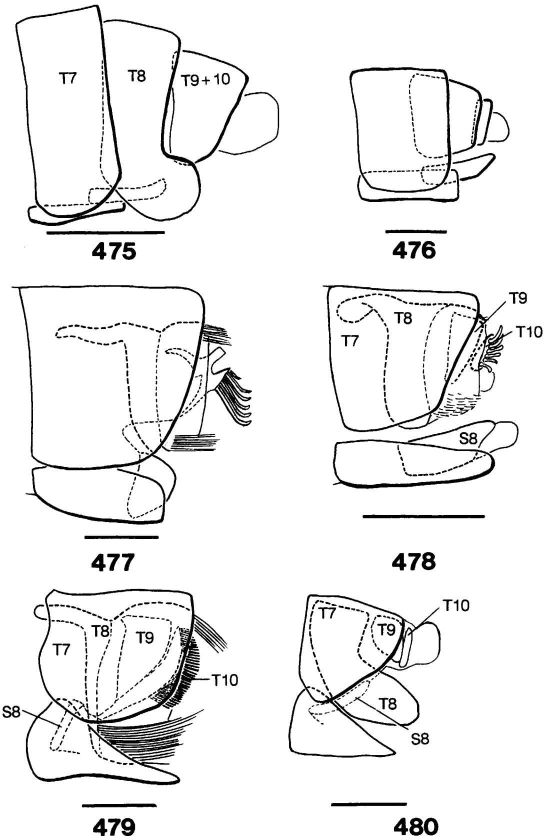
Theodor (1976: fig. 2) described a valve on the spermathecae of some Asilidae which does occasionally possess sclerotized collars (e.g., the Leptogastrinae, his fig. 13; Dasypogoninae, his fig. 66). Further microstructural work will be required to determine whether the valve in Asilidae is homologous or homoplasious relative to the pump of the Bombyliidae.

146. Lateral papillae of sperm pump. Evenhuis (1990) drew attention to the conspicuous lateral papillae on the sperm pumps of the Usiini. I found these conspicuous papillae also on the sperm pumps of *Acrophthalmyda* (fig. 497) and *Exoprosopa*, and they are somewhat enlarged (though coded 0 here) in *Bombylius major* (fig. 409).

147. Common spermathecal duct. Most often the three spermathecal ducts are separate and all three unite shortly before, or at, the spermathecal opening into the genital chamber (figs. 493–498, 500). In a few examples examined here a long common spermathecal duct is evident. Many Asilidae have a short common duct (Theodor, 1976). Irwin (1976)



Figs. 469–474. Lateral views of the female genitalia of various Mythicomyiinae, Usiinae and Toxophorinae, vestiture not shown: **469**, *Mythicomyia illustris*; **470**, *Phthiria gaedei*; **471**, *Apolysis* sp.; **472**, *Systropus macer*; **473**, *Usia atrata*; **474**, *Toxophora virgata*. Scales 0.5 mm



Figs. 475–480. Lateral views of the female genitalia of various Bombyliidae, vestiture not shown: **475**, *Geron grandis*; **476**, *Oligodranes* sp.; **477**, *Thevenetimyia californicus*; **478**, *Crocidium karooanum*; **479**, *Bombylius major*; **480**, *B. androgynus*. Scales 0.5 mm.

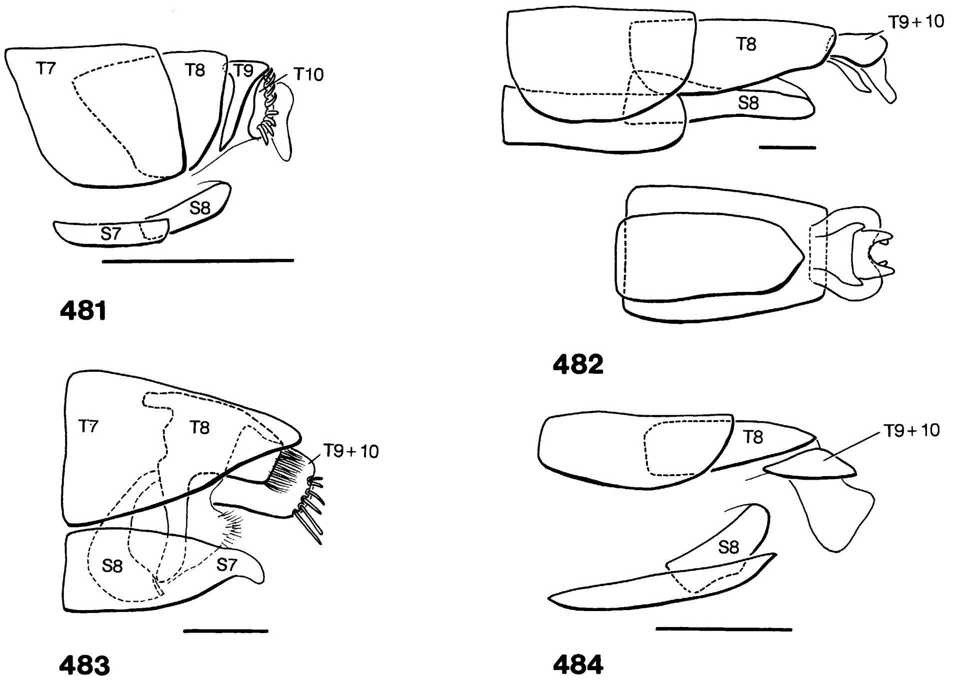
and Yeates (1992) illustrated a long common spermathecal duct in *Prorates*, and one is also evident in *Bonjeania, Paratoxophora* (fig. 499), and *Amictus* (Theodor, 1983).

Two of the three spermathecal ducts found in *Apystomyia* (fig. 426) unite well before the ducts reach the genital chamber. In addition, there is a bulb on each of the two ducts, which continue to the chamber. Wiegmann et al. (1993) reported that two of the three spermathecae share a common duct in many groups of Muscoidea.

LARVAE

148. Larval habits. Most asiloid larvae are free-living predators. The Bombyliidae, Nemestrinidae, and Acroceridae have often been united in one superfamily (e.g., Hennig, 1952, 1954; Rohdendorf, 1974) on account of the larval parasitism and hypermetamorphosis commonly found in the three families. Hypermetamorphosis refers to the change in form of successive instars during larval development. Chapman (1982) preferred the term heteromorphosis for this phenomenon.

Hypermetamorphosis is common in parasitic insects and examples can be found in many orders. In the Bombyliidae, Nemestrinidae, and Acroceridae the first instar larva is well sclerotized and narrow-bodied, with long spines posteriorly, and is termed a "planidium." These larvae are very mobile and search actively for a host. The second and further larval instars are ecto- or endoparasitic and are broad and vermiform, without the long posterior spines of the first instar. Woodley (1989) considered the hypermeta-



Figs. 481–484. Lateral views and one ventral view of the female genitalia of various Bombyliidae, vestiture not shown except acanthophorite spines and long hairs on the apex of tergite 8: **481**, *Heterotropus gilvicornis*; **482**, *Antonia suavissima*, lateral view on top, ventral view on bottom; **483**, *Exoprosopa caliptera*; **484**, *Myonema humile*. Scales 0.5 mm.

morphosis and parasitism of the Bombyliidae to have arisen separately from that of the Nemestrinidae and Acroceridae, and Yeates and Irwin (1992) made this assumption. For the purposes of this analysis, I acted conservatively and coded the hypermetamorphosis and parasitism found in the three families as homologous states. This allows the total evidence (Kluge, 1989) from other characters to decide whether the character is homologous or has been independently derived.

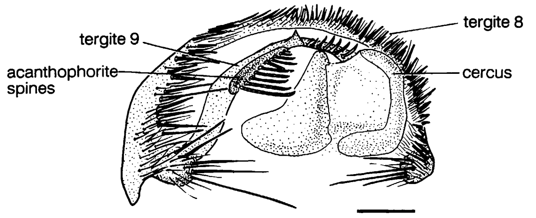
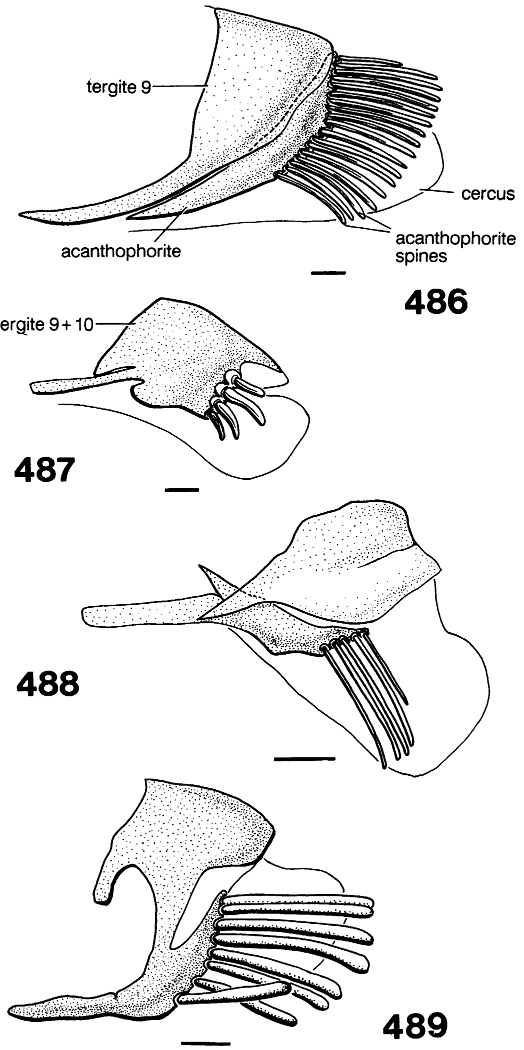


Fig. 485. Posterolateral view of the female genital tergites of *Thevenetimyia gracilis*. Scale 0.5 mm.

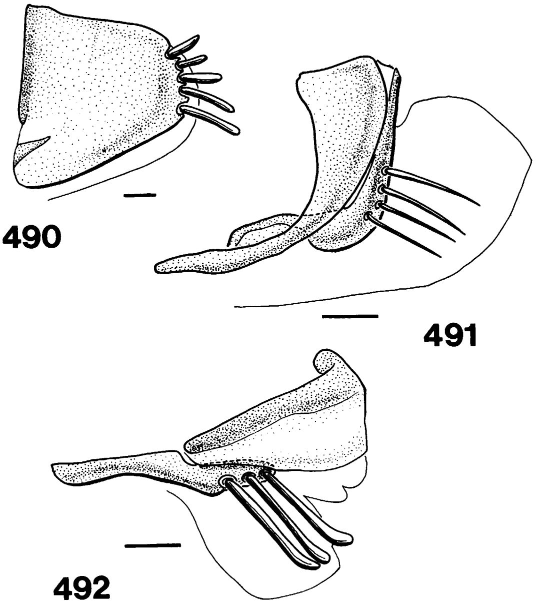
I scored two exceptions to the rule of hypermetamorphosis and parasitism in the Bombyliidae (Du Merle, 1975). Andersson (1974) reported that *Glabellula arctia* (Zetterstedt) was probably a scavenger in ants nests and Yeates and Irwin (1992) found that *Heterotropus* larvae were free living.

149. Larval host. The Acroceridae are parasitic on spiders and this feature is an autapomorphy of the family (Woodley, 1989). Zaytsev and Charykuliev (1981) reported that a species of the anthracine *Petrorossia* was reared from a spider egg sac, however this is quite a different habit from the Acroceridae which have all been reared as internal parasitoids of the spiders themselves.

150. Position of larval posterior spiracle. Larvae of the Tabanomorpha and other more plesiomorphic Diptera have the posterior spiracle located on the ultimate abdominal segment, at or close to the apex of the abdomen. Two advanced states were distinguished here and analyzed additively. Malloch (1917) first noted that the larvae of the



Figs. 486–489. Lateral view of tergites 9 and 10 of various Bombyliidae, vestiture not shown except acanthophorite spines: **486**, *Bombylius major*; **487**, *Paratoxophora cuthbertsoni*; **488**, *Pantarbes capito*; **489**, *Megapalpus capensis*. Scales 0.1 mm.



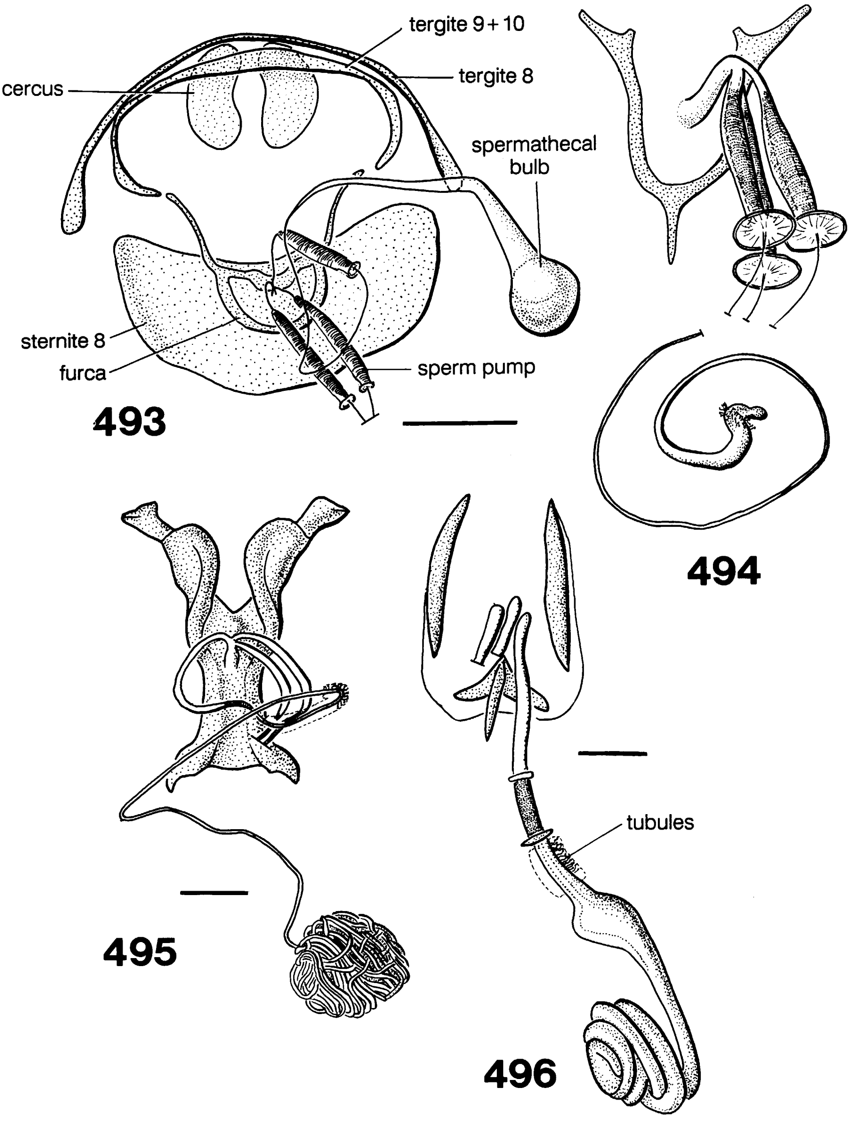
Figs. 490–492. Lateral view of tergites 9 and 10 of various Bombyliidae, vestiture not shown except acanthophorite spines: **490**, *Exoprosopa caliptera*; **491**, *Anthrax analis*; **492**, *Tomomyza anthracoides*. Scales 0.1 mm.

Asiloidea have the last abdominal segment divided so that the posterior spiracles appear to lie dorsally in the penultimate abdominal segment (fig. 502). This character has been suggested and used subsequently (Hennig, 1973; Griffiths, 1986; Woodley, 1989) as an apomorphy of the Asiloidea. The Therevidae and Scenopinidae have the abdominal segments further divided so that the last abdominal spiracle lies in the antepenultimate abdominal segment (see character 154).

Some, but not all (Melin, 1923) larvae of the asilid genus *Laphria* Meigen lack or have poorly developed secondary segmentation on the last abdominal segment (Hennig, 1952: fig. 46; Wood, 1981: fig. 77). I consider this a reversal, not plesiomorphic, as *Laphria* belongs to a relatively advanced subfamily, and other asilids have well-developed secondary segmentation.

Among the Nemestrinidae and Acroceridae an intermediate state occurs in which the posterior spiracles have migrated to an anterodorsal position on the last abdominal segment. This state also occurs in the bombyliid *Heterotropus*, and this led Yeates and Irwin (1992) to suspect that this genus may be the most primitive clade of the Asiloidea.

151. Larval head capsule. Larvae of the Brachycera have at least the posterior third of the head capsule retracted into the thorax (hemicephalic or acephalic condition; Teskey, 1981). Among the Asiloidea, this retraction causes the internalization of the metacephalic rods and much of the remaining

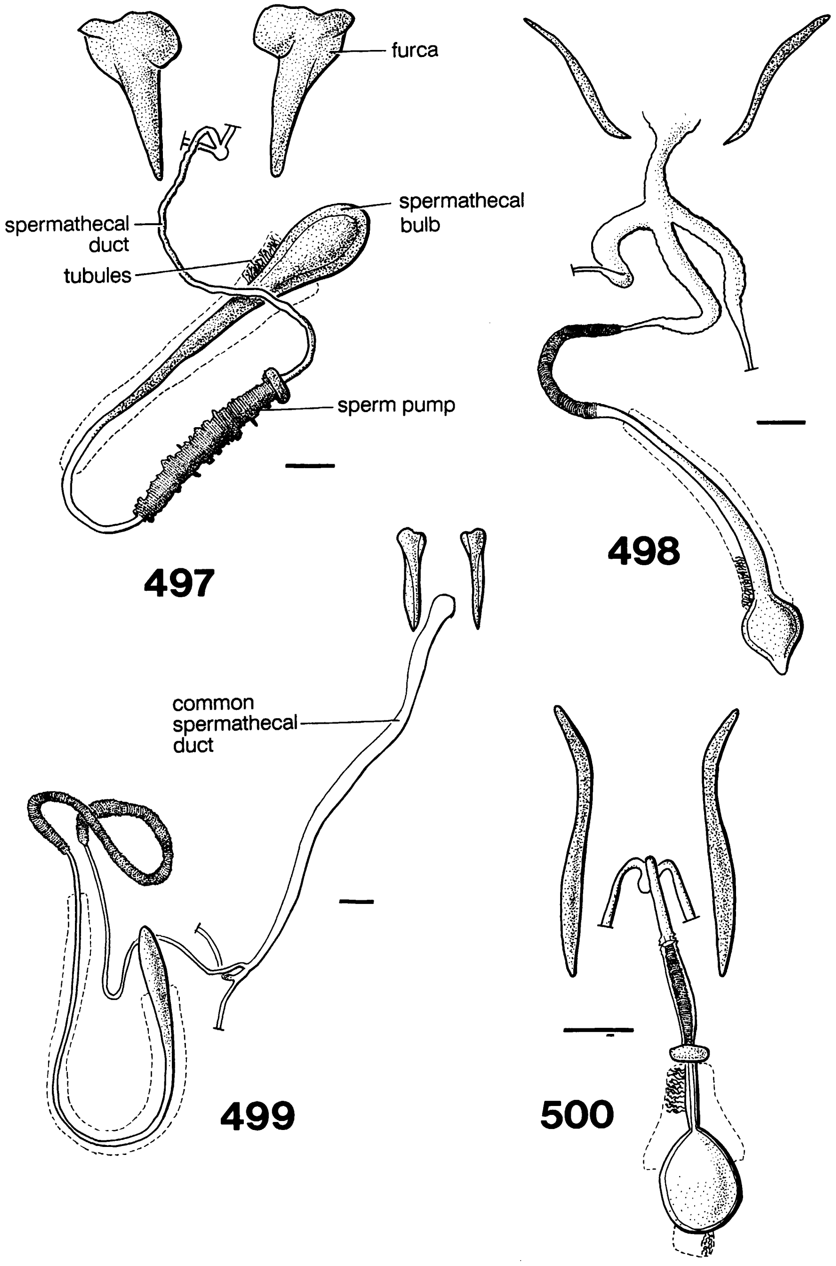


Figs. 493–496. Spermathecae and associated structures of various Bombyliidae: **493**, *Mythicomyia illustris*; **494**, *Glabellula rotundipennis*; **495**, *Geron grandis*; **496**, *Toxophora virgata*. Dotted lines indicate distribution of tubules. Scales 0.1 mm.

dorsal area of the cranium. In the Scenopinidae and Therevidae, however, the advanced state occurs whereby the larval head capsule is well sclerotized and external, with only the metacephalic rods extending into the prothorax (e.g., Irwin, 1972).

152. Metacephalic rod articulation. Among the Asiloidea, only the Bombyliidae have the metacephalic rod solidly joined to the head capsule as is found in more primitive groups. The remaining families possess the apomorphic state in which the metacephalic rod is hinged on the head capsule (Woodley, 1989).

153. Metacephalic rod shape. Malloch (1917) was the first to record the spatulate metacephalic rod of therevids as a characteristic differentiating them from scenopinids which have a parallel-sided metacephalic rod. Woodley (1989) used this character as an autapomorphy for the Therevidae.



Figs. 497–500. Spermathecae and associated structures of various Bombyliidae: **497**, *Acrophthalmyda paulseni*; **498**, *Dischistus mystax*; **499**, *Paratoxophora cuthbertsoni*; **500**, *Oniromyia pachycerata*. Dotted lines indicate distribution of tubules. Scales 0.1 mm.

154. Larval abdominal segmentation. Most asiloid larvae have eight well-defined abdominal segments, however the posterior segment is most often divided so that there appears to be 9 segments (character 150). The larvae of the Scenopinidae and Therevidae are immediately recognizable because they have secondary abdominal segmentation. The abdomen appears to have 17 segments, with the posterior spiracles appearing on the 14th seg-

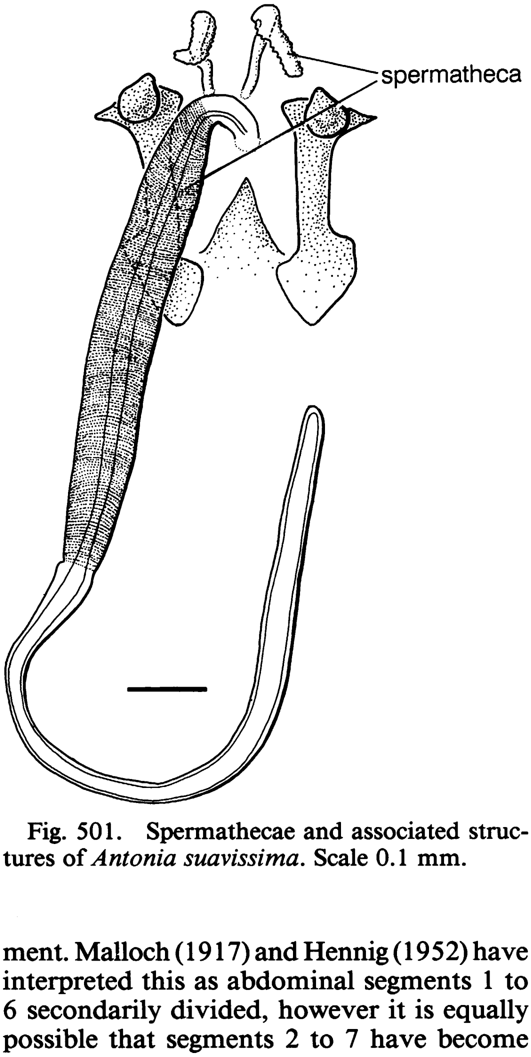


Fig. 501. Spermathecae and associated structures of *Antonia suavissima*. Scale 0.1 mm.

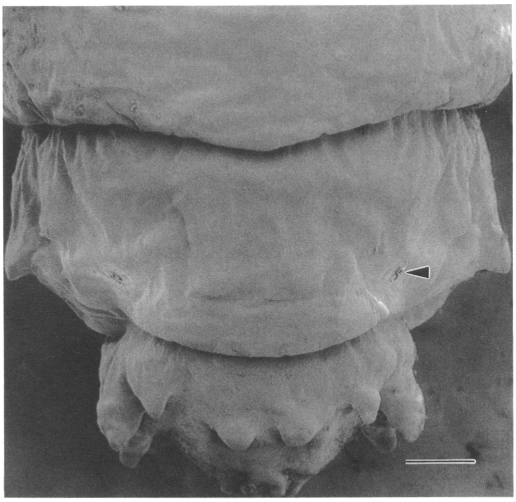


Fig. 502. Scanning electron micrograph of the apex of the abdomen of a mature larva of *Bombylius pulchellus* Loew. Arrow indicates posterior spiracle. Scale 200 μm.

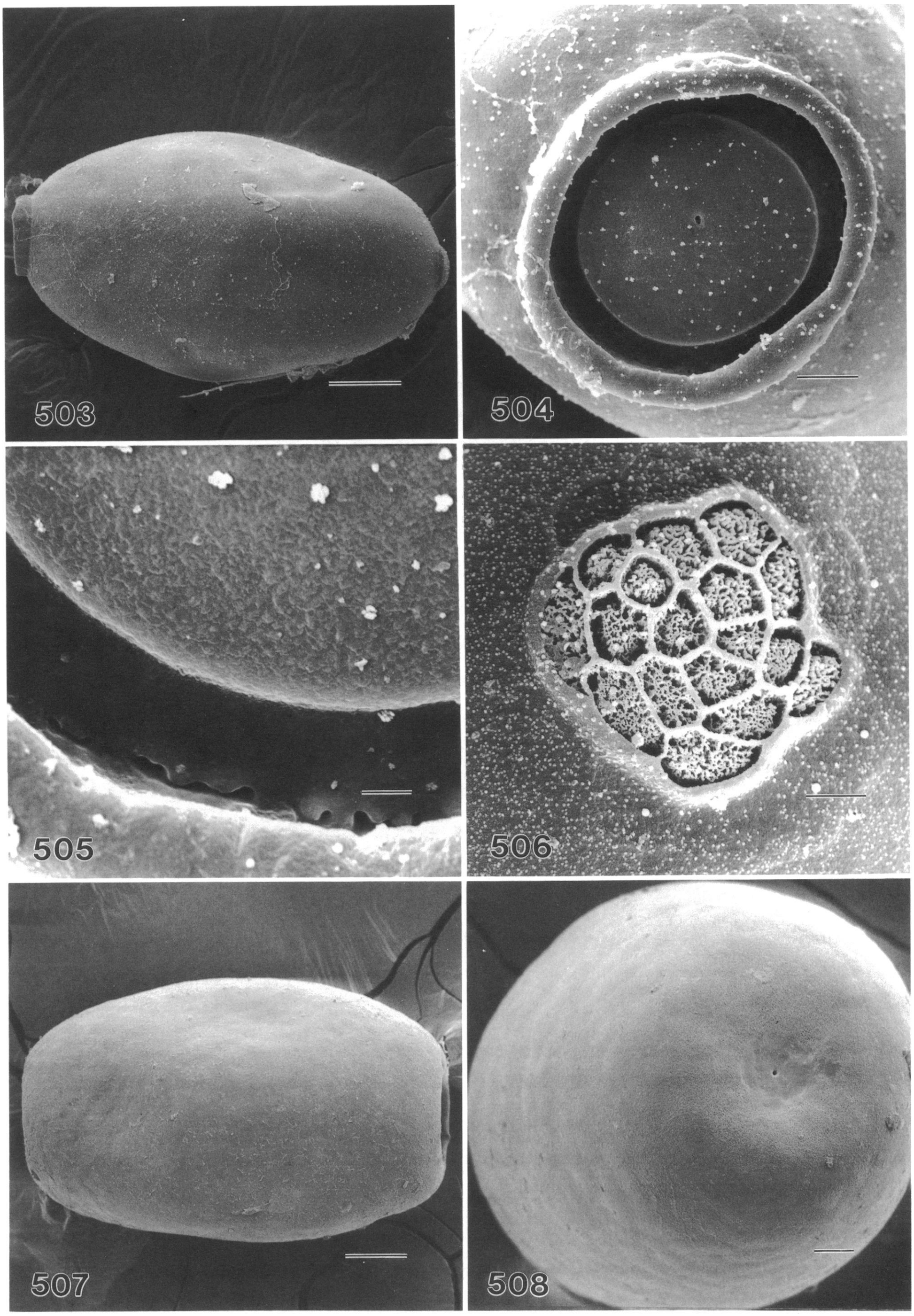
ment. Malloch (1917) and Hennig (1952) have interpreted this as abdominal segments 1 to 6 secondarily divided, however it is equally possible that segments 2 to 7 have become secondarily divided. This character was used by Malloch (1917) and Woodley (1989) to unite the Scenopinidae and Therevidae.

EGGS

Mühlenberg (1971a) first considered egg morphology in the systematics of the Bombyliidae. He found a distinct operculum surrounded by a ridge on eggs of *Toxophora* and *Systropus*, and an operculum lacking a ridge on the eggs of *Geron*, *Phthiria*, and *Oligodranes*. The operculum functions as an exit for the eclosing first instar larva. Noting that Hesse (1956a) reported an operculum and ridge on *Antonia xanthogramma* Bezzi, Greathead (1988) hypothesized that an operculate egg was characteristic of those subfamilies lacking a sand chamber.

I have made observations on all the eggs present in the abdomens of females examined during this study, however there were too few in this condition to include this character in the data matrix. The operculate eggs of *Toxophora compta* are shown in figures 503–506. Figure 504 shows the operculum with surrounding ridge, and figure 505 shows the line of weakness in the chorion just inside the ridge. The opposite pole of *T. virgata* eggs has a sculptured aeropyle (fig. 506). The egg of *Systropus macer* also has a ridged operculum similar to that of *Toxophora*. I was unable to find a ridged operculum on the eggs of any other species examined. The female *Antonia suavissima* examined had well-sclerotized eggs in the abdomen, however these lacked a ridged operculum. Evenhuis (1993) found that the antoniine *Cyx* had an elongate pedicel on the opposite pole to the operculum, and than an unidentified Kenyan *Antonia* had a ridged collar surrounding the operculum.

I found large, well sclerotized eggs in the abdomen of *Bombylius androgynus*, a bombyliine which has secondarily lost a sand chamber. The eggs (figs. 507–508) possess an operculum (right-hand pole of fig. 507), which



Figs. 503–508. Scanning electron micrographs of eggs of two species of Bombyliidae: **503**, *Toxophora virgata*, scale 50 μm; **504**, *T. virgata*, operculum, scale 10 μm; **505**, *T. virgata*, detail of line of weakness inside rim or operculum; **506**, detail of opposite pole to operculum, scale 5 μm; **507**, *Bombylius androgynus*, scale 50 μm; **508**, *B. androgynus*, detail of micropile, scale 20 μm.

can be forced off with gentle pressure, however it lacked a surrounding ridge.

The form of the eggs may indeed furnish useful phylogenetic information; at present it appears that operculate eggs are restricted to some genera which lack sand chambers. It is intriguing to note, however, that the Toxophorinae plesiomophically lack a sand chamber, and *B. androgynus* and the Antoniinae have secondarily lost the sand chamber.

RESULTS

NEMESTRINIDAE AND ACROCERIDAE

Woodley (1989) considered the Bombyliidae to be asiloids, and placed the Acroceridae and Nemestrinidae in the Nemestrinoidea. United only by their larval parasitism and hypermetamorphosis, Woodley (1989) admitted that the sister-group relationship between these flies was questionable. My results indicate that the Nemestrinoidea are paraphyletic, with the Acroceridae being more closely related to the Asiloidea than to the Nemestrinidae (fig. 509). To preserve the structure of the cladogram in the classification derived from it, each of the Nemestrinidae and Acroceridae should be classified in its own superfamily.

Apomorphies that the Nemestrinidae share with the Acroceridae and Asiloidea (and Eremoneura) are the lack of tibial spurs (midtibial spurs reappear in some Bombyliidae); reduction from one- to two-segmented cerci in the female, and larval spiracles migrating to an anterodorsal position on the ultimate or penultimate segment of the abdomen.

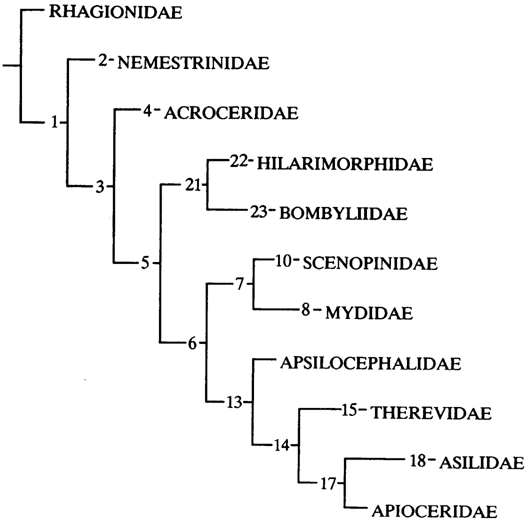


Fig. 509. Summary of relationships between families found in this study. Clade numbers correspond to those in figure 7.

Character 148 (larvae free-living predators or parasitoids) undergoes four steps on the cladogram of figure 7. It makes one forward change along the node leading to Clade 1; reverses on the node leading to clade 5, the Asiloidea; and reverses in *Glabellula* and *Heterotropus* of the Bombyliidae. This character optimization suggests that the plesiomorphic condition of larval habits for the Asiloidea was a parasitoid one, inherited from their ancestors. The Asiloidea excluding the Bombyliidae apomorphically changed to a free-living, predatory habit as larvae. The larval habits of the Hilarimorphidae, at present unknown, are critical to this idea of larval habit evolution. If they are found to be free-living, it would be equally parsimonious to assume that the most plesiomorphic Asiloidea had free-living larvae.

The diagonal vein of the Nemestrinidae (character 61) is a diagnostic apomorphy for the family. The Nemestrinidae share with some apomorphic subfamilies of Bombyliidae a modification of the occipital foramen so that there appears to be two foramina (character 39: fig. 29).

The Acroceridae share with the Asiloidea a number of apomorphies, the most important being the loss of male tergite 10. The male genitalia of the family are highly derived and they may have lost features independently of their loss in the Asiloidea. Acrocerid male genitalia lack the hypandrium, gonostyli (figs. 319–320), and the gonocoxites are fused in the midline without an internal ridge.

Acroceridae share many apomorphies and their monophyly has never been in question. The short hypopharynx (character 23), elongate cibarium (character 33), enlarged lower claypter (character 67), lack of a transverse suture (character 88), features of the male genitalia noted above, two spermathecae with membranous bulb and larval habit as internal parasitoids of spiders all affirm the monophyly of the family.

MONOPHYLY OF THE ASILOIDEA

I was able to find no convincing synapomorphies of the Asiloidea beyond that proposed by Woodley (1989), the larval posterior spiracle placed anterodorsally on the penultimate abdominal segment (character 150, fig. 502). The posterior spiracles of *Heterotropus*, which are anterodorsal on the last abdominal segment (Yeates and Irwin, 1992), represent a reversal to the plesiomorphic condition. An apical antennal style (character 7, fig. 9) appears to be a plesiomorphic feature of the Asiloidea, however it is lost or becomes subapical in a number of families including the Therevidae and Bombyliidae. The anepimeron and laterotergite are plesiomorphically bare in the Asiloidea, but haired in the Nemestrinidae and Acroceridae. The empodium is bristleform or reduced in all Asiloidea, however this feature is shared with all other Muscomorpha except the Nemestrinidae and Acroceridae.

RELATIONSHIPS OF THE ASILOID FAMILIES

The cladogram (fig. 509) of outgroups from all the families of Asiloidea shows family-level relationships similar to those of Woodley (1989, fig. 1) and also some intriguing differences. Like Woodley (1989), I found that the sister group to the remaining asiloids was the Bombyliidae plus Hilarimorphidae. The relationships between the remaining asiloid families that I found are at odds with those proposed by Woodley (1989), as I found the Scenopinidae plus Mydidae to be the sister group to the (Apsilocephalidae + Therevidae + Asilidae + Apioceridae).

The Asiloidea excluding the Bombyliidae and Hilarimorphidae (clade 6) are united by preprocoxal bridges (character 76) present, a feature which reverses in *Apiocera* and many Asilidae, free-living predatory larvae (character 148), and larval metacephalic rod hinged on the head capsule (character 152), and a number of other adult features which have ambiguous optimizations at this node.

SCENOPINIDAE

Yeates (1992) transferred *Caenotus* and *Prorates* to the Scenopinidae, and the relationship of these two genera to the Scenopinidae postulated in that work is identical to the one found here. Apomorphies of the Scenopinidae are: male eyes divided into large dorsal and small ventral facets (character 10, fig. 32); abdominal tergite 2 with a patch of modified setae (character 100, figs. 305–309); phallus bifid or trifid (character 117, fig. 331); two spermathecae (character 142, figs. 417, 420); larval head capsule largely external (character 151, larvae of *Caenotus* and *Prorates* are unknown); and larvae with pseudosegmentation on the abdomen, appearing to have 17 segments (character 154).

Yeates (1992) used Therevidae as the outgroup for the Scenopinidae based on the very similar larvae (character 154), the same feature upon which Woodley (1989) hypothesized a sister-group relationship between the Scenopinidae and Therevidae. Most of the apomorphies of the Scenopinidae postulated by Yeates (1992) remain under the hypothesis that the Mydidae is the sister group to the Scenopinidae, however the longitudinally divided epandrium (character 105) now is an apomorphy of the Mydidae plus Scenopinidae.

APSILOCEPHALIDAE

Nagatomi et al. (1991a, b) recently removed the North American *Apsilocephala* Kröber, and two Tasmanian genera *Clesthentia* White and *Clesthentiella* Nagatomi et al. from the Therevidae to a new family, the Apsilocephalidae. They (1991a) conjectured that the Apsilocephalidae were phylogenetically close to the Jurassic Rhagionempididae and Empidoidea on the basis of the shape of the flagellum (figs. 8–9) and presence of surstyli in the male genitalia (fig. 323).

Apsilocephala has a bulbous first flagellomere, followed by a short cylindrical second flagellomere and a long, cylindrical third flagellomere (about twice as long as the first two combined), and an apical style. *Clesthentia* has a similar flagellum, although it lacks a terminal style and the cylindrical third flagellomere is about as long as the conical first flagellomere. The flagellum of *Clesthentiella* is most similar to that of *Clesthentia*, however, it consists of only two flagellomeres, a basal conical one and short, cylindrical apical one. Nagatomi et al. (1991b) did not discuss whether they consider the flagellum of *Apsilocephala*, *Clesthentia* or *Clesthentiella* to be plesiomorphic within the family. Given the variation in flagellum shape in the Apsilocephalidae, the enormous variation found in more primitive Brachycera, the Asiloidea and plesiomorphic Eremoneura which they document, it is difficult to comprehend how Nagatomi et al. (1991a) are willing to offer this as an indicator of relationships above other characters. Because no Eremoneura were included in this analysis, I was unable to test the suggestions of Nagatomi et al. (1991a) directly. The flagellum of *Opetia nigra* (Platypezidae), belonging the putative sister group of the remaining Cyclorrhapha (Wiegmann et al., 1993), appears to be close to that found in *Apsilocephala*, however the third flagellomere of *Opetia* tapers toward its apex, lacks a terminal style, and is clothed in long hairs.

Only the male genitalia of *Apsilocephala* and *Clesthentia* are known and are similar to each other (Nagatomi et al., 1991c). They appear to be similar in other plesiomorphic asiloids in most respects. There is a separate, well differentiated hypandrium (fig. 324); the gonocoxites are fused and bear articulating gonostyli at their apex. The ejaculatory apodeme is cylindrical and the lateral aedeagal apodemes are small. The phallus of *Apsilocephala* is long and coiled, however that of *Clesthentia* is shorter and directed ventrally, as it is in many Therevidae. The epandrium of both genera have a pair of articulating lobes on the posterior margin termed surstyli (fig. 323), similar to those found in the Asilidae by Adisoemarto and Wood (1975). McAlpine (1989) also found surstyli in Xylomyidae, Stratiomyidae, and primitive Asilidae and Cumming and Sinclair (1990) found surstyli to have evolved within the Eremoneura numerous times. Thus it appears that surstyli, in and of themselves, offer little conclusive phylogenetic evidence.

Woodley (1992, personal commun.) believes that *Apsilocephala* and its relatives are correctly placed in the Asiloidea, and my studies bear this out. They lack tibial spurs, have a bristleform empodium, and 3 flagellomeres with an apical style. The cladogram (fig. 7) places *Apsilocephala* as the sister group to the (Therevidae + Apioceridae + Asilidae) (clade 14), because of the presence of two-segmented palps (character 26), setae on the occiput (character 43), and prealar bristles (character 87).

The Apsilocephalidae possess an intriguing apomorphy with all Therevidae, the presence of a peg on the anterior margin of the hind coxa (fig. 292). Such a peg (character 92), of various forms, is also found in some Tabanomorpha, *Hilarimorpha*, and some plesiomorphic Bombyliidae. Within the Asiloidea, the coxal peg arises on the cladogram (fig. 7) separately twice in the Bombyliidae and once in *Hilarimorpha* and it also arises in the Therevidae and *Apsilocephala*. The Therevidae have not been subject to rigorous cladistic analysis, and convincing apomorphies for the family from adult morphology have not been found. The coxal peg provides one piece of evidence to reunite the Apsilocephalidae and Therevidae in a future analysis.

THEREVIDAE, APIOCERIDAE, MYDIDAE, AND ASILIDAE

The Mydidae plus Scenopinidae share the following synapomorphies: cibarial arms short (character 29, figs. 73–74); epandrium completely divided (character 105, figs. 333, 343) which is also present in *Apiocera* and some Asilidae, and lateral aedeagal apodemes absent (character 119, figs. 331, 342), also found in some Therevidae.

Neorhaphiomidas, an Australian genus placed in the Apioceridae, formed a clade with the Mydidae, and preliminary examination of some other megasceline Apioceridae suggests that they also may be more closely related to Mydidae than Apioceridae, a result presaged by Woodley (1989). The Mydidae share two wing venation characters with *Apiocera*, wing vein R_{2+3} ends in R_1 near the apex of the wing, and R_5 and M_1 end posterior to the wing tip. Mydid gonocoxites are completely fused, lack an internal ridge marking the line of fusion (character 111), and their gonostyli are lacking (character 121, figs. 339, 342).

The Therevidae, *Apiocera*, and the Asilidae are united by the separate gonocoxites (character 111) and poorly sclerotized spermathecal bulb (character 144). *Apiocera* and the Asilidae share a separate probasisternum (character 76), epandrium divided medially (character 105, reverses in some Asilidae), and a laterally compressed ejaculatory apodeme (character 120, also present in the Bombyliidae).

The Asilidae are clearly monophyletic, supported by the apomorphic facial mystax (character 17), long hypopharynx (character 23), reduced labellae (character 25), trapezoidal shape and ventral ridge on the cibarium (fig. 72, characters 32 and 34), and the lateral fusion of the epandrium and hypandrium (fig. 334, character 107). Contrary to the opinion of Martin (1968), *Leptogaster* is nested within the Asilidae and does not deserve separate family status.

The relationships between the Apsilocephalidae, Therevidae, Apioceridae, Asilidae, Mydidae, and Scenopinidae shown in figure 509 are different from traditional views expressed as early as Malloch (1917), and those proposed by Woodley (1989). I believe these differences stem from two problems with the analysis here. A future cladistic analysis should be able to improve on this one by increasing the taxon sampling among the Asilidae and Therevidae in particular. These two families are large; the cladistic relationships of their components are poorly known and are a high priority for future research. Secondly, a future analysis should include additional larval characters. A constant feature of previous analyses was the monophyly of the (Scenopinidae + Therevidae), based on their very similar larvae with secondarily divided abdominal segmentation (character 154) and large external head capsule (character 151). These two features were forced into homoplasy in this analysis by a larger number of adult morphological characters supporting the alternative (Scenopinidae + Mydidae). A detailed study of the larvae of Asiloidea may furnish more supporting larval apomorphies for the (Scenopinidae + Therevidae).

HILARIMORPHIDAE

Traditionally composed of a single genus, *Hilarimorpha* Schiner, with 33 species found in the Nearctic and Palaearctic regions, I here add the Nearctic genus *Apystomyia* Melander, containing a single species, which was originally classified in the Proratinae of the Bombyliidae.

Apomorphies for the family are the head shape (figs. 38–39), with a broad emargination of the inner eye margin at and below the level of the antennae (character 15), and lateral aedeagal apodemes absent (character 119). The flies also lack a swollen basiphallus, and the ejaculatory apodeme continues on at a constant diameter into the aedeagus (figs. 347, 349). These apomorphies are not compelling, and there are some striking differences between the two genera. These include the pattern of setae on the thorax of *Apystomyia* (fig. 280), coxal peg in *Hilarimorpha*, shape of the epandrium, and long gonocoxal apodemes in *Apystomyia*. The discal medial cell is present in *Apystomyia* (fig. 232), however the discal medial and basal medial cells are united in *Hilarimorpha*.

The Hilarimorphidae differ from all other asiloids examined here (except some Therevidae) in the combined loss of the swollen basiphallus and lateral aedeagal apodemes.

DIAGNOSIS

Head. Scape and pedicel small, cylindrical, or conical; flagllum with two flagellomeres plus an apical style; male eye facets divided into two regions, large facets dorsally and small ones ventrally; eye inner margin with broad indentation below the level of the antennal bases (figs. 38–39); face and frons not tumid; mouthparts held within oral cavity, labellae fleshy; palps one-segmented, pits absent (fig. 63); posterior arms of cibarium relatively short, simple; tentorial arms broad; one occipital foramen; occipital pockets absent (*Apystomyia*) or partial (*Hilarimorpha*); occipital apodemes absent.

Thorax. 3 branches of Rs; M_3 absent; M_2 present; crossvein dm-cu present in *Apystomyia* (fig. 232), absent in *Hilarimorpha*, in which cells dm and bm are confluent (crossvein bm-cu is absent); anal cell closed; costal vein not circumambient, extending to R_5; ter-

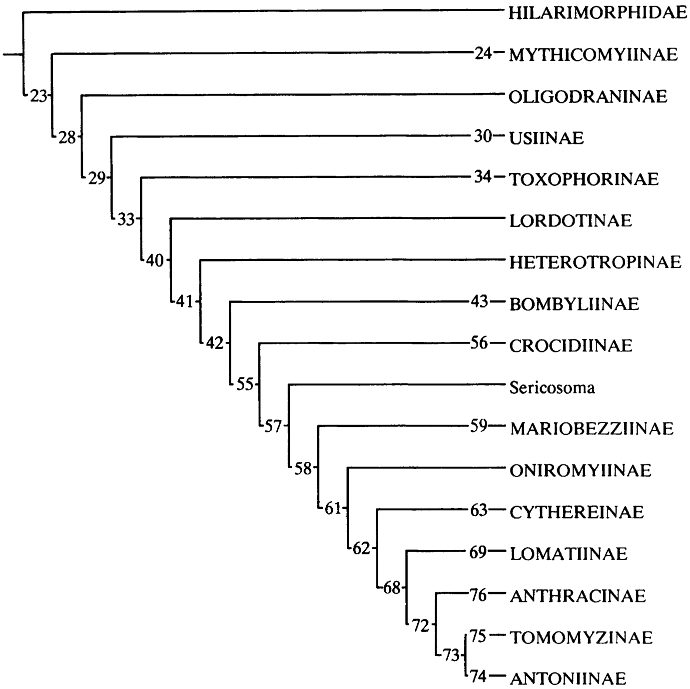


Fig. 510. Summary cladogram of results of Hennig86 analysis shown in figure 7. Terminals are collapsed to subfamily rank in the classification I propose. Node numbers correspond to those in figure 7, *Sericosoma* remains incertae sedis.

gal fulcrum absent; anepimeron, laterotergite, and mediotergite bare; prealar bristles absent (fig. 280); midtibial spurs absent; coxal peg present in *Hilarimorpha*; empodium bristleform or otherwise reduced.

Abdomen. Abdominal spiracles in pleural membrane. *Male.* Genitalia not rotated. Epandrium loosely connected to anterodorsal region of gonocoxites; with convex posterior border in *Hilarimorpha* (fig. 350), with strong lateral arms directed posteriorly in *Apystomyia* (fig. 345); hypandrium absent; gonocoxites fused in midline; gonostyli present; gonocoxal apodemes short in *Hilarimorpha* (fig. 348), long in *Apystomyia* (figs. 344–345); aedeagal sheath extending anteriorly underneath ejaculatory apodeme in *Hilarimorpha*, extending as two rods underneath the ejaculatory apodeme in *Apystomyia*; lateral aedeagal apodemes absent; ejaculatory apodemes rounded, slightly wedge-shaped in *Hilarimorpha*; male tergite 10 absent; swollen basiphallus apparently absent. *Female.* Tergite and sternite 8 simple; sternite 8 external (figs. 425, 428); tergites 9 and 10 fused (alternatively, acanthophorites absent, figs. 425, 428); furca u-shaped in *Hilarimorpha*, absent in *Apystomyia*; cerci one-segmented; three spermathecae; spermathecal bulb sclerotized; sperm pump absent; sperm ducts separate except two join distally to form one duct in *Apystomyia* (fig. 426).

The Hilarimorphidae and Bombyliidae are united by the male eyes divided into larger facets dorsally and smaller facets ventrally, occipital pockets partial or complete (both reverse in many more apomorphic Bombyliidae), and loss of wing vein M_3 (also occurs in the Scenopininae).

FAMILY BOMBYLIIDAE

The apomorphies for the Bombyliidae are occipital apodemes present (not found in any other family but reversing in many apomorphic Bombyliidae), gonocoxal apodemes very short; ejaculatory apodeme laterally compressed (also found in some Asilidae and Mydidae); complex sperm pump present (reversed in some more apomorphic Bombyliidae).

THE DIVISIONS "HOMEOPHTHALMAE" AND TOMOPHTHALMAE

As discussed above, the concepts of the "Homeophthalmae" and Tomophthalmae have changed since they were first introduced to group together some Bombyliidae subfamilies by Bezzi (1924). As currently conceived (Evenhuis, 1991), the Tomophthalmae contains those subfamilies with the apomorphic state of two occipital foramina and the "Homeophthalmae" contain those with the plesiomorphic state of one occipital foramen. This character (number 39) changes once on the cladogram in figures 7 and 510, at clade 57. Thus *Sericosoma,* plus all the subfamilies included in clade 57, Mariobezziinae, Oniromyiinae, Cythereinae, Lomatiinae, Antoniinae, Tomomyzinae, and Anthracinae, form a monophyletic Tomophthalmae. The "Homeophthalmae" are paraphyletic, and consist of all those subfamilies of Bombyliidae between clades 23 and 57. I indicate the paraphyletic nature of this group by placing the name in quotation marks.

PSAMMOPHORIDAE

Mühlenberg (1971b) introduced the term Psammophoridae for those subfamilies which possess a sand chamber. The sand chamber is formed by modifications of the female genitalia, and appears as an apomorphic feature at clade 42. Although the Psammophoridae of Mühlenberg (1971b) are monophyletic, females of the entire clade 42 do not possess a sand chamber; in particular clade 74, the Antoniinae, apomorphically lack such a modification of the female genitalia. Thus the Bombyliinae, *Sericosoma*, Crocidiinae, Mariobezziinae, Oniromyiinae, Cythereinae, Lomatiinae, Tomomyzinae, Antoniinae, and Anthracinae belong in the Psammophoridae. I discourage the use of "Psammophoridae" for this group of subfamilies because the suffix may be confused with a family name. I encourage the term "sand chamber subfamilies" instead, for those subfamilies of Bombyliidae in clade 42.

DIAGNOSIS

Head. Flagellum with one, two, or three flagellomeres with or without a style; inner margin of eye simple or with a small indentation at the level of the antennal bases (some Mythicomyiinae and female *Desmatomyia*); palps absent or with one or two segments, palp pit present or absent; posterior arms of cibarium long except in some Mythicomyiinae; occipital foramen single or divided into two; occipital chambers well developed, partial, or absent; occipital apodemes present or absent; postgena complete behind mouthparts. Proboscis present or absent; when present, labellae may be fleshy or elongate, adapted for nectarophagy.

Thorax. Three branches of Rs except Mythicomyiinae with two; M_3 absent; M_2 present except in the Oligodraninae, Toxophorinae, and some Phthiriini; dm-cu present except in some Mythicomyiinae and *Apolysis*; veins of R and M field reaching wing margin; proprecoxal bridge present or absent; tergal fulcrum present except Mythicomyiinae, Heterotropinae, and Desmatomyiinae; midtibial spurs absent except in the Lordotinae, Crocidiinae, Conophorini, and *Amictus*; coxal peg present in Oligodraninae and Crocidiinae; empodium bristleform or absent.

Abdomen. Tergite 2 simple, lacking the sensory area found in the Scenopinidae; shape varying from elongate to cigar-shaped or rounded. Spiracles in pleural membrane except in the Mythicomyiinae where they have migrated to the tergites. *Male genitalia.* Epandrium consisting of one sclerite with posterior margin concave in some; epandrium loosely connected to anterodorsal region of gonocoxites except in Toxophorini which have a strongly sclerotized posterodorsal connection; surstyli lacking; hypandrium present as a separate sclerite or absent; gonocoxites fused ventrally except in Heterotropinae; if present, gonocoxal apodemes relatively short and often directed ventrally; aedeagal sheath may be produced into one or more epiphallic lobes around the phallus; distiphallus a simple tube in the majority; divided into three apical prongs in the Heterotropinae, some Mythicomyiinae, and *Cyllenia*; lateral aedeagal apodemes present except in *Paraconsors*; ejaculatory apodeme laterally compressed in all except *Antonia* where it has an additional two dorsal vanes; basiphallus (sperm pump) well developed; gonostyli always present, moving in a dorsoventral plane; tergite 10 absent. *Female genitalia*. The tergite and sternite of segment 8 are modified to form a sand chamber in subfamilies including and distal to the Bombyliinae and excluding the Antoniinae; secondarily absent or reduced in a handful of representatives; tergites 9 and 10 (acanthophorites) completely separate or fused; acanthophorite spines present or absent; furca of one or two sclerites surrounding the spermathecal opening; female cerci one-segmented; three spermathecae (one normal and two reduced in *Antonia*); spermathecal bulb sclerotized except *Acridophagus*, *Desmatomyia*, and *Antonia*; sperm pump plesiomorphically present, occasionally reduced, or absent.

KEY TO THE SUBFAMILIES OF BOMBYLIIDAE

I have devised this key for identification rather than to indicate phylogenetic affinity, however plesiomorphic groups tend to key out before the more advanced ones. Wherever possible I have chosen characters which are present externally on both sexes.

1\. Postcranium flat or tumid, without concavity surrounding occipital foramen 2
– Postcranium with deep or shallow concavity surrounding occipital foramen 10
2\. Wing with R_{4+5} unbranched; palps absent or minute; abdominal spiracles located in tergites; very small, 1–5 mm .... Mythicomyiinae
– Wing with R_{4+5} branched; palps present and most often large; abdominal spiracles in pleural membrane 3
3\. Wing with vein M_2 present 6
– Wing with vein M_2 absent 4
4\. Palp 2-segmented .... Oligodraninae
– Palp 1-segmented 5
5\. Antennal flagellum with subapical sulcus containing a style ...... Usiinae (part) Usiini
– Antennal flagellum without a subapical sulcus .... Toxophorinae
6\. Flagellum with an apical sulcus containing a style .... Usiinae (part) Phthiriini
– Flagellum lacking an apical sulcus 7
7\. Anepimeron bare; laterotergite and mediotergite haired; prealar bristles most often absent (if present, scutellum sulcate); female genitalia with differentiated acanthophorites lacking acanthophorite spines ... . Lordotinae New Subfamily
– Either anepimeron haired, or laterotergite bare or mediotergite bare; or prealar bristles present; scutellum not sulcate 8
8\. Hind coxal peg present; tibial spurs present; scape not swollen .... Crocidiinae
– Hind coxal peg absent; if tibial spurs present (Conophorini) then scape swollen 9
9\. Small flies (4–6 mm body length); vestiture sparse; body coloration striking yellow and black or white and black; anal cell closed; prealar bristles absent ... Heterotropinae
– Without this combination of characters .... Bombyliinae
10\. Scape with a short dorsal spine; male eyes broadly dichoptic .... Mariobezziinae
– Scape almost always without dorsal spine; if spine present (*Ylasoia*) then male eyes closely approximated 11
11\. Clypeus reaching base of antennae 12
– Clypeus not reaching base of antennae .. 15
12\. Labrum clothed in scales; scape with ventral, apical bulge .... Oniromyiinae
– Labrum bare or clothed in sparse hairs; scape cylindrical or conical, without ventral, apical bulge 13
13\. Occipital lobes meeting behind ocellar triangle 14
– Occipital lobes separate behind ocellar triangle ...... Antoniinae (part) *Myonema*
14\. Precoxal bridge absent; mediotergite haired .... Lomatiinae
– Precoxal bridge present; mediotergite bare . ...Tomomyzinae (part) *Docidomyia*
15\. Ocellar tubercle placed well forward on frons, at least the length of ocellar tubercle anterior to the posterior eye margin in dorsal view 16
– Ocellar tubercle found on vertex, less than length of ocellar tubercle anterior to the posterior eye margin in dorsal view ... 17
16\. Posterior eye margin with indentation and short bisecting line dividing the facets ... . Antoniinae (part)
– Posterior eye margin simple .. Tomomyzinae
17\. Posterior eye margin with indentation .... Anthracinae (part)
– Posterior eye margin simple 18
18\. Head rounded in anterior view .... Anthracinae (part) Prorostomatini
– Head wider than high in anterior view .... Cythereinae

PROPOSED CLASSIFICATION OF BOMBYLIIDAE

nach welcher Richtung hin sollen oder können die ersten entscheidenden Schnitte behufs Teilung erfolgen? Becker, 1913, p. 425.

Here I present a revised subfamily classification of the Bombyliidae based on the results of this study. My approach is deliberately conservative: I have endeavored to make as little change as possible to the existing classification while reflecting the cladistic relationships of the cladogram in figures 7 and 510. I have restricted each subfamily to a primary branch from the main stem of the cladogram. The cladistic relationships among the 15 subfamilies is shown in figure 510. I propose only one new name at the family level, the Lordotinae, and recognize a total of 15 subfamilies. One of the genera studied, *Sericosoma*, I leave as incertae sedis, as I am not confident of subfamily placement. I expect that further analysis of it and related genera will prove that they belong in the Mariobezziinae.

After providing a diagnosis of each subfamily and a list of apomorphies, I briefly discuss the contents of the subfamily and its geographic distribution. For the purposes of this discussion the Australasian region shall include those species found in the Australasian and Oceanian regions. In the diagnoses I have mentioned exceptions where known and expect that some characters will need to be removed and others added as further genera are examined and fitted to this arrangement.

I found that some groups of traditional subfamilies formed monophyletic groups from the main stem of the cladogram and should be united (e.g., the Usiinae, Toxophorinae), some subfamilies were apomorphic clades of others and should be united (e.g., the Eclimini within the Bombyliinae), some subfamilies were polyphyletic (e.g., the traditional Cythereinae) and should be divided, and that other subfamilies were monophyletic, and should remain unchanged (e.g., the Mythicomyiinae, Oligodraninae, Oniromyiinae, Anthracinae and Tomomyzinae).

1. Mythicomyiinae

Mythicomyiinae Melander, 1902: 336. Type genus *Mythicomyia* Coquillett, 1893.

Platypyginae Verrall, 1909: 478. Type genus *Platypygus* Loew, 1844.

Cyrtosiinae Becker, 1913: 472. Type genus *Cyrtosia* Perris, 1839.

Glabellulinae Cockerell, 1914: 232. Type genus *Glabellula* Bezzi, 1902.

Diagnosis

Head. Scape and pedicel small, flagellum of one or two flagellomeres, with an apical or subapical (fig. 10) style usually present. Mouthparts with palps absent or reduced to small knobs (figs. 34, 71), palpal pit absent; labrum with dorsal, rounded region of membrane at base (figs. 40–41), small microtrichia at apex (figs. 40–41); cibarial arms reduced (fig. 79) except in *Acridophagus*. Postcranium mostly flattened, convex in *Cyrtosia* and its relatives (fig. 153), not tumid anteriorly (figs. 149, 151, 153). Occipital chambers present and complete, partial, or absent.

Thorax. Reduced wing venation in the R field as follows (figs. 234, 236, 238, 240): R_{2+3} present or absent, when present unbranched, either ending independently in costa or in R_1. R_{4+5} unbranched; discal medial cell present or absent; anal vein may be absent, anal cell open; costal vein ending at R_{4+5}. Base of M may be absent or reduced to a trace. Body and legs devoid of setae. Scutum strongly convex dorsally; tergal fulcrum absent. Laterotergite and mediotergite bare.

Abdomen. Spiracles situated in lateral margins of tergites rather than in pleural membrane (figs. 312, 429). Female genitalia with segment 8 very narrow, tergites 9 and 10 fused and very narrow (fig. 329), acanthophorite spines absent; furca joined in midline, three spermathecae, sperm pump present, often with proximal end plate absent (figs. 493–494). Male genitalia with segment 8 very narrow; epandrium large (figs. 351, 384), emarginate at its apex, produced lateroposteriorly. Hypandrium absent; gonocoxites relatively small, fused medially, lacking gonocoxal apodemes. Distiphallus with one or three prongs (fig. 382); lateral aedeagal apodemes absent in *Paraconsors* Hall and Evenhuis; aedeagal sheath with long arms produced posteriorly (fig. 395); gonostyli present, each appearing to be divided into a dorsal and ventral piece (fig. 382).

Synapomorphies

Labrum with a concave region of membrane on the dorsal surface at its base; labrum with small hairs at apex; palps very small or absent; wing with two branches of Rs; abdominal spiracles located in tergites; segment 8 of male abdomen very narrow; phallus sheath of male genitalia produced into two long, anteriorly directed apodemes; gonostyli composed of separate dorsal and ventral components.

Discussion

Almost 300 described species in 21 extant genera of very distinctive small to very small (body length 1.0–5.0 mm) Bombyliidae found in all biogeographic regions. Over half the species currently described in the subfamily are Nearctic *Mythicomyia*, and seven of the genera are endemic to South Africa. The subfamily was originally proposed in the Empididae (Melander, 1902), and was later transferred to the Bombyliidae (Melander, 1928). Some authors (e.g., Hull, 1973) divide this subfamily into two, Mythicomyiinae and Platypyginae (incorrectly referred to as the Cyrtosiinae by authors such as Becker, 1913; Hesse, 1938; 1967; and Hall, 1976), distinguished by the reduced or absent vein R_{2+3} in the former, however Bowden (1975b) synonymized the two. Hull (1973) distinguished five tribes: (1) the Psiloderini, which are orthopteran egg predators and have R_{2+3} present, (2) Cyrtosiini with cell dm-cu absent and vein R_{2+3} present, (3) Platypygini with dm-cu present, (4) Mythicomyiini with R_{2+3} ending in R_1, and (5) the Empidideicini with vein R_{2+3} absent.

Previous authors have concentrated heavily on wing venation in the higher classification of this group. The subfamily is urgently in need of revision using a larger spectrum of characters.

Acridophagus possesses a number of features which indicate that it is plesiomorphic within the subfamily. In particular, *Acridophagus* retains long cibarial arms and occipital apodemes which have been lost in other mythicomyiines. In addition, the tentorial arms are broad and in remaining members of the subfamily they are narrow. These features appear in bee flies belonging to other subfamilies such as the Bombyliinae. It is likely that the most plesiomorphic mythicomyiinae will be found among *Acridophagus* and its relatives, the Psiloderini of Hull (1973).

The Bombyliidae with the exception of the Mythicomyiinae are united by the absence of M_2 absent (character 60, reversing in more apomorphic Bombyliidae), costal vein circumambient (character 69); and tergal fulcrum present (character 79, reverses in Heterotropinae and *Desmatomyia*).

2. Oligodraninae

Oligodraninae Evenhuis, 1990: 66. Type genus Oligodranes Loew, 1844.

Diagnosis

Head. Flagellum of one or two flagellomeres with an apical style. Male eyes dichoptic, divided into large facets above and small below. Face not extending much beyond eye margin in lateral view (fig. 137); two-segmented palps, palp pit present (fig. 65); occipital chambers partially developed (fig. 138); head slightly wider than high.

Thorax. Body and legs with sparse vestiture, one or two small prealar bristles present as is the tergal fulcrum. Hind coxal peg present. Wings hyaline, with R_{4+5} divided, discal medial cell present, M_2 absent and anal cell closed; costa circumambient.

Genitalia. *Male*. Epandrium emarginate, hypandrium present, gonocoxites fused, epiphallus well developed as a rounded lobe above the gonopore. *Female*. Tergites 9 and 10 fused, acanthophorite spines absent (fig. 476), three spermathecae with sperm pump present, bulb sclerotized.

Synapomorphies

Two palpal segments with palp pit present; prealar bristles present; coxal peg present; sternite 9 separate; epiphallus present as a single lobe above the aedeagus.

Discussion

The subfamily contains just one genus with five described species restricted to the Palearctic region. The exemplar used in this study was an undescribed species from Israel. Recently raised to a subfamily (Evenhuis, 1990), *Oligodranes* was previously placed in the Phthiriinae or Usiinae. Evenhuis (1990) noted a similarity in male genitalia between this genus and the Mariobezziinae (as Mariobezzini), and a similarity in the female genitalia to some Bombyliinae. However, female *Oligodranes* lack acanthophorites, acanthophorite spines, or a sand chamber, and thus their genitalia share little with the Bombyliinae.

In some respects this genus possesses more plesiomorphic features than the Mythicomyiinae, for instance the two-segmented palps, divided vein R_{2+3}, and hypandrium present.

The Bombyliidae with the exception of the Mythicomyiinae and Oligodraninae (clade 29) are united by a single apomorphy, occipital pockets present and fully developed (character 41, reverses in more apomorphic Bombyliidae).

3. Usiinae

Usiinae Becker, 1913: 483. Type genus *Usia* Latreille, 1802.

Phthiriinae Becker, 1913: 483. Type genus *Phthiria* Meigen, 1803.

Diagnosis

Head. Flagellum with one or two (*Apolysis* Loew) flagellomeres and an apical (Phthiriini) or subapical (Usiini) sulcus containing a style (figs. 11–12); male eyes dichoptic except in *Usia*, facets smaller ventrally than dorsally except in *Usia*; bases of the antennae at the apex of the tumid face and frons (figs. 139, 141); clypeus reaching bases of antennae; palps one-segmented, palp pit absent; cibarial arms simple; tentorial arms relatively narrow; posterior tentorial pits rounded; postcranial region flattened (fig. 131); one occipital foramen; occipital pockets present and fully developed, often enlarged and extending well above the occipital foramen; occipital apodemes present except in *Phthiria* where they may have been obliterated by the large occipital pockets (fig. 140); posterior eye margin simple; head slightly wider than high.

Thorax. Wing venation simple, three branches of Rs; M_2 present in Phthiriini, absent in Usiini; anal cell closed; costal vein circumambient (*Apolysis*) or ending at or before A_1; propresternum pear-shaped; preprocoxal bridge absent; tergal fulcrum present.

Genitalia. *Male*. Tergite 8 narrow in *Usia* (fig. 314); epandrium with posterior margin concave or convex; hypandrium absent except in some *Apolysis*; gonocoxites fused; gonocoxal apodemes short or absent, directed ventrally in *Apolysis*; epiphallus a lobe above the aedeagus in many *Apolysis*, consisting of more complex lobes in *Poecilognathus* Osten Sacken. *Female*. Tergite 8 simple (fig. 436); tergites 9 and 10 fused; acanthophorite spines absent (figs. 470, 473); sternite 8 simple and external (figs. 451–452), pair of large median hairs in Phthiriini; spermathecal bulb well sclerotized; sperm pump present and well developed, lateral papillae on pump large in Usiini.

Synapomorphies

Flagellum with apical (Pthiriini) or subapical (Usiini) sulcus containing a style; bases of antennae at apex of facial tumidity; clypeus reaching bases of antennae.

Discussion

Evenhuis (1990) recently revised the world genera of these two tribes (as subfamilies), recognizing that they were closely related. I conclude that they form a monophyletic group and should be united in one subfamily, but recognize the tribes of Evenhuis (1990) as subtribes. Using the principle of the first reviser (ICZN, 1985: Art. 24), I choose the Usiinae to have precedence over the Phthiriinae, as the former name has line precedence in Becker (1913). The subfamily contains 13 genera and about 250 species found in all biogeographic regions.

Tribe Usiini, revised status

The Usiini contains three genera: *Apolysis* with almost 100 species found in all biogeographic regions except the Australasian; *Parageron* Paramonov with 7 Palearctic species; and *Usia* with 44 Palearctic species. The monophyly of the tribe is based on the subapical flagellar sulcus containing a style (characters 6 and 7) and well-developed lateral papillae on the sperm pump of the female genitalia (character 146).

Tribe Phthiriini, revised status

The Phthiriini have an interesting distribution pattern, with three genera endemic to Australia, *Phthiria* found in all regions except the Australasian and Nearctic, and the remaining six genera restricted to the New World. The monophyly of the tribe is supported by wing vein M_2 absent (character 60) and a pair of median hairs on female sternite 8 (character 133).

The Bombyliidae excluding the Mythicomyiinae, Oligodraninae, and Usiinae (clade 33) are united by a single character which undergoes much homoplasy, a reversal to the absence of a style on the flagellum (character 7).

4. Toxophorinae

Toxophorinae Schiner, 1868: 116 Type genus *Toxophora* Meigen, 1803.

Systropodinae Brauer, 1880: 115 (as Systropinae). Type genus *Systropus* Wiedemann, 1820.

Gerontinae Hesse, 1938: 866 (as Geroninae). Type genus *Geron* Meigen, 1820.

Diagnosis

Head. Scape and pedicel elongate in Toxophorini and *Systropus* (fig. 24); flagellum with a single flagellomere, flattened in *Systropus*; style absent; male eyes dichoptic, facets smaller ventrally than dorsally in Gerontini; face not tumid (figs. 143, 145, 147); labrum simple except basal third membranous in Toxophorini; one-segmented palp, palp pit absent; cibarium simple (figs. 87–88); posterior tentorial pits rounded (figs. 144, 146, 148); postcranial region flattened; one occipital foramen; occipital pockets present and well developed; occipital apodemes present in Gerontini and *Systropus*; gena with two internal sclerotized ridges in *Zaclava* and *Dolichomyia* (figs. 214, 216); posterior eye margin simple; head rounded (figs. 146, 148) except wider than high in *Toxophora* (fig. 144).

Thorax. Three branches of Rs; M_2 absent; cell r5; dm-cu present (fig. 237); anal vein absent in *Dolichomyia* and *Zaclava*; anal cell closed; costal vein circumambient except ending at A_1 in Gerontini; scales present on wing in Toxophorini; prothorax enlarged in the Toxophorini, with large setae (fig. 250); propresternum pear-shaped; preprocoxal bridge absent; flange above the wing base (fig. 247) except in Gerontini; prealar bristles present in Toxophorini; tergal fulcrum present; anepimeron bare; strigilis present in *Systropus* (fig. 281); laterotergite and mediotergite bare, produced into an angled ridge in Toxophorini; metepisternum and metepimeron enlarged in Systropodini; postmetacoxal bridge present in *Systropus* (fig. 281); sensory area on outer face of forefemora in *Systropus* (fig. 297). Abdomen very elongate in *Systropus*.

Genitalia. *Male*, epandrium with posterior margin concave except for Gerontini; epandrium fused to gonocoxites in *Toxophora* (fig. 367); hypandrium absent; gonocoxites fused, without median internal ridge; gonocoxal apodemes absent; epiphallus well developed as a number of distinct posteriorly directed lobes flanking the phallus (figs. 396, 398). *Female*, tergite 8 simple; tergites 9 and 10 fused (figs. 472, 475), dorsal apodeme present in *Systropus*; acanthophorite spines absent; sternite 8 simple (figs. 449–450, 453), median desclerotized area in Gerontini (fig. 448); furca a single y- or u-shaped sclerite with an anterior projection in Toxophorini (fig. 496), posterior projections present in Gerontini (fig. 495); spermathecal bulb in the form of a well-sclerotized coiled tube (figs. 495–496); sperm pump absent or poorly developed in Geronini and Toxophorini.

Synapomorphy

Spermathecal bulb modified into a well-sclerotized, coiled tube.

Discussion

Bowden (1980) first united the Toxophorinae, Systropodinae, and Gerontinae of previous authors into a single subfamily, however Evenhuis (1990) preferred to retain the Gerontinae as a distinct subfamily. I recognize the subfamily as Bowden (1980) did, and consider that it is composed of three tribes corresponding to the subfamilies of previous authors.

Tribe Toxophorini, revised status

Toxophorini contains one genus, *Toxophora*, with 47 species worldwide. The monophyly of the Toxophorini is supported by their ocellar tubercle with two large, anteriorly directed setae (fig. 35), enlarged prothorax (shared with *Lepidophora* Westwood) with large setae (fig. 250), ridged mediotergite and laterotergite (fig. 284), male epandrium fused to the posterodorsal region of the gonocoxite (fig. 367), and female furca with an anterior spine (fig. 496).

Tribe Gerontini, revised status

Gerontini comprises the genus *Geron* with about 130 species found worldwide. The monophyly of the Geronini is specified by features of the female genitalia; sternite 8 is invaginated and has a large, median, posterior membranous region (fig. 448); the lateral margins of tergite 8 are expanded (fig. 475), and the furca has dorsal flanges on its posterior margin (fig. 495).

A sister-group relationship is weakly supported between the Gerontini and Systropodini, based on their rounded head (character 49) and reduced sperm pump (character 145).

Tribe Systropodini, revised status

Systropodini contains *Systropus* Wiedemann (about 130 species, worldwide), *Dolichomyia* Wiedemann (6 species, New World) and *Zaclava* Hull (4 species, Australia and New Caledonia). The monophyly of the Systropodini is specified by the reduced squama, enlarged metepisternum and metepimeron (fig. 281), and elongate, cylindrical abdomen. *Dolichomyia* and *Zaclava* together form the sister group to *Systropus*; apomorphies they share are the lack of occipital apodemes, internal ridges on the gena (figs. 214, 216), and anal vein absent or reduced. Autapomorphies for *Systropus* include the presence of a postmetacoxal bridge, forefemora with a sensory area (fig. 297), and a small, dorsal apodeme on the anterior margin of the united tergites 9 and 10 of the female.

The Bombyliidae with the exception of the Mythicomyiinae, Oligodraninae, Usiinae, and Toxophorinae (clade 40) are united by the tumid face (character 16); M_2 present (character 60); female tergite 9 and the acanthophorite separate (character 134); and the presence of long strips from tergite 9 and the acanthophorites toward the furca (character 138).

5. Lordotinae, new subfamily

Type genus *Lordotus* Loew, 1863: 303. Type species *Lordotus gibbus* Loew by monotypy.

Diagnosis

Head. Scape longer than pedicel; flagellum with one or two flagellomeres with or without terminal style; male eyes holoptic or almost so, facets often indistinctly divided into small ventral and large dorsal facets; face slightly tumid; proboscis elongate, extending well beyond oral cavity; one-segmented palp, palp pit absent; cibarium simple; postcranium flattened or slightly tumid; occipital pockets well developed; posterior eye margin simple; occipital apodemes present; head wider than high.

Thorax. Costa of many species with modified, enlarged setae in male; three branches of Rs, R_{2+3} sinuous at apex; i-r crossveins present; M_2 present; costal vein circumambient; propresternum pear-shaped; preprocoxal bridge absent; tergal fulcrum present; anepimeron bare; laterotergite and mediotergite haired; one pair of midtibial spurs present; femora with bristles. Scutellum shiny and sulcate in *Geminaria* Coquillett.

Abdomen. Male with 7–8 and female with 6 visible abdominal segments. Female segments and intersegmental membranes 7–9 elongate, folded inside abdomen at rest and forming a long, telescoping ovipositor. *Genitalia*. Male epandrium with concave posterior margin poorly or well developed; hypandrium present in *Geminaria*, absent in *Lordotus*; gonocoxites fused with median ridge; gonocoxal apodemes very short; aedeagal sheath covering aedeagus snugly, epiphallus absent, phallus straight. Female with tergite 8 simple and elongate, divided medially in *Lordotus* (fig. 430); tergites 9 and 10 separate; acanthophorites present, acanthophorite spines absent; acanthophorites modified into elongate plates adapted for penetrating the soil surface (figs. 430, 431), extending anteriorly as far as furca; sternite 8 simple; furca well sclerotized, v-shaped; spermathecal bulb elongate, well sclerotized; sperm pump well developed.

Synapomorphies

Midtibial spurs present (shared with Crocidiinae and Conophorini); female genitalia modified into an elongate tube, acanthophorites present, well developed, lacking spines, produced into digging blades (figs. 430–431).

Discussion

These flies have traditionally been classified in the Bombyliinae. The most striking feature of the Lordotinae is the highly modified female genitalia, first described by Hall and Evenhuis (1982). The dorsal acanthophorites and ventral sternite 8 resemble the dorsal and ventral valves on the ovipositor of an acridid Orthopteran (fig. 431). Segments 7 and 8 and their associated intersegmental membranes are elongate, and telescope out of the abdomen when the fly is ovipositing. This morphology and behavior is unique to the subfamily among the Bombyliidae, and recalls the oviposition behavior and morphology of other asiloid families.

At the outset of this study I assumed that the Lordotinae would form a clade within the Bombyliinae, their peculiar female genitalia merely being autapomorphies or reversals from the complicated sand chamber found in that subfamily. This was not the case, and the most parsimonious hypothesis for the Lordotinae is that they plesiomorphically lack a sand chamber, rather than having apomorphically lost one. The Lordotinae have a simple tergite 8, without anterior apodeme or long brush of hairs on the posterior margin as found in the Bombyliinae, and sternite 8 is simple and its position is external at the time of oviposition, rather than divided into three segments and invaginated as found in the Bombyliinae. In addition, there are no acanthophorite spines. On the cladogram (fig. 7), the Lordotinae are three nodes from the most plesiomorphic Bombyliinae, and most of the apomorphies that separate the two lineages concern the development of the sand chamber.

The Bombyliinae itself is a weak clade supported by two apomorphies replete with homoplasy, and it is possible that additional evidence may favor the traditional placement of *Lordotus* and its relatives within the Bombyliinae. This evidence, if morphological, would be required to suggest that some members of the Lordotinae once possessed a sand chamber, for instance an anterior apodeme on tergite 8, elongate hair brush on the posterior margin of tergite 8, vestigial acanthophorite spines, or sternite 8 divided into three sclerites. The male genitalia and other aspects of the morphology of the Lordotinae are simple and plesiomorphic within the Bombyliidae and do not reveal much phylogenetic information. If the Lordotinae do, in fact, actually belong in the Bombyliinae, their nearest relatives within that subfamily are not obvious. The pattern of pleural vestiture is quite different from that of most other Bombyliinae: prealar bristles are absent, the anepimeron is haired (only found in the Bombyliini), the laterotergite is haired (only found in the Bombyliini and *Marmasoma* of the Eclimini), and the mediotergite is haired, only found in some Eclimini. The costal armature of the males would also suggest an affinitly with the Eclimini. Members of the subfamily also possess one midtibial spur, only present in the Conophorini of the Bombyliinae.

Lordotus contains 29 species and *Geminaria* two. The subfamily is at present limited to the western U.S.A. and northern Mexico. Hull (1973) considered that the South African *Othniomyia* Hesse was related to *Lordotus*, and Hall and Evenhuis (1982) considered that the Chilean *Hallidia* Hull was closely related. *Hallidia* does not have the diagnostic modified female genitalia of *Lordotus* and *Geminaria* and does not belong in the subfamily (Theodor, 1983). The affinities of *Othniomyia* await examination of its female genitalia.

The Bombyliidae except the Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae and Lordotinae (clade 41) are united by male epandrium convex (character 105); gonocoxal apodemes slightly longer (character 113); and female with acanthophorite spines (character 139).

6. Heterotropinae

Heterotropinae Becker, 1913: 481. Type genus *Heterotropus* Loew, 1873.

Diagnosis

Head. Flagellum with apex variable, with a small flagellomere (e.g., *H. gilvicornis* Yeates) without a style or ending with two small flagellomeres and an apical style (e.g., *H. aegyptiacus* Paramonov); male eyes holoptic, facets smaller ventrally than dorsally; face tumid (fig. 155); clypeus not reaching bases of antennae; labellum fleshy (fig. 157), palp one-segmented (fig. 158), palp pit absent; cibarium simple (figs. 81–82); occiput slightly tumid (fig. 155); occipital chambers present and well developed (fig. 156); occipital apodemes absent; posterior eye margin simple (fig. 155); head slightly wider than high.

Thorax. Three branches of Rs; R_{2+3} straight; M_2 present; anal cell closed; costal vein circumambient; propresternum pear-shaped; preprocoxal bridge absent; tergal fulcrum absent; prealar bristles absent; anepimeron bare; laterotergite and mediotergite bare.

Genitalia. *Male*. Epandrium simple, posterior margin convex (fig. 390); hypandrium present, large (fig. 385); gonocoxites separate, not fused in midline (fig. 388); gonocoxal apodemes relatively long, directed ventrally; gonostyli each with a dosal and median arm (fig. 388); distiphallus trifid (fig. 385); aedeagal sheath extending anteriorly underneath and on each side of the base of the ejaculatory apodeme. *Female* (figs. 432–433). Tergite 8 simple; tergites 9 and 10 separate; acanthophorite spines present; sternite 8 simple, not invaginated; furca u-shaped; spermathecal bulbs well sclerotized; sperm pump absent or poorly developed.

Synapomorphies

Tergal fulcrum absent; hypandrium large (figs. 385, 388); gonocoxites separate, only joined through hypandrium; distiphallus trifid; gonostylus composed of a dorsal and lateral arm (fig. 388); larvae free-living, with posterior spiracles anterodorsally placed on ultimate abdominal segment.

Discussion

A small subfamily containing one genus with 44 species confined to the Palearctic and Afrotropical regions. The body has sparse vestiture and is strikingly colored in black and yellow. As traditionally circumscribed, this subfamily contained a polyphyletic assemblage of genera, however this has been recently rectified. Theodor (1983) first suggested that *Prorates* shared characters with the Scenopinidae, and Yeates (1992) moved *Caenotus*, *Prorates* and their relatives to the Caenotinae and Proratinae of the Scenopinidae. I place the enigmatic *Apystomyia* in the Hilarimorphidae above.

Yeates and Irwin (1992) described the immature stages of some South African species and discussed the phylogenetic position of the genus. The larvae are free living predators and their posterior spiracles are on the last abdominal segment rather than the penultimate, thus they lack the synapomorphy of the Asiloidea proposed by Woodley (1989). Because of these features and some plesiomorphic aspects of adult morphology, Yeates and Irwin (1992) entertained the notion that *Heterotropus* may be the sister group to the remaining Asiloidea. The present study does not support that interpretation, and the larval habits and morphology appear as reversals to plesiomorphic character states within the Bombyliidae.

Nevertheless, *Heterotropus* adult and larval morphology presents us with an intriguing juxtaposition of character states and the adult morphology of the genus is conservative for the Asiloidea. The head lacks occipital apodemes but the occipital chambers are fully developed. The thorax lacks the tergal fulcrum, otherwise present in the Bombyliidae except for the Mythicomyiinae and *Desmatomyia*. The hypandrium is better developed than in any other bombyliid, being a large, curved sclerite. It dominates the ventral plane of the genitalia to such an extent that the gonocoxites are separated, arising from the two posterior corners of the hypandrium. The gonocoxites are fused medially in all other Bombyliidae. The female genitalia lack a sand chamber, or any evidence that it has had one in the past. Segment 8 is unmodified, and the acanthophorites are separate and possess large spines. In fact, the female genitalia are similar to what we might expect from the stem asiloid. The larvae are free-living and also possess many plesiomorphic asiloid features, except that they lack the division of the ultimate abdominal segment into two (Yeates and Irwin, 1992). The dorsal surface of the cranium is large and broad in *Heterotropus* larvae, whereas in other asiloid larvae it has been reduced to a smaller rod or rods.

Clade 42 of the Bombyliidae is united by the apodeme on the anterior margin of female tergite 8 (character 125), a long brush of hairs on the posterior margin of female tergite 8 (character 127), invagination of female sternite 8 (character 130) and female sternite 8 modified into three sclerites or with a deep median membranous region (character 132). These apomorphies together constitute the development of the sand chamber, and the subfamilies distal to clade 42 I shall term the sand chamber subfamilies ["Psammophoridae" of Mühlenberg (1971b)].

7. Bombyliinae

Bombyliinae Latreille, 1802: 427 (as Bombylarii). Type genus *Bombylius* Linnaeus, 1758.

Conophorinae Becker, 1913: 479. Type genus *Conophorus* Meigen, 1803.

Ecliminae Hall, 1969: 5. Type genus *Eclimus* Loew, 1844.

Diagnosis

Head. Scape often longer than wide, very long in some Eclimini (fig. 36), very broad in the Conophorini (fig. 25). Pedicel longer than wide in some Eclimini. Flagellum of various forms, composed of three, two, or one flagellomere/s with or without an apical style (figs. 14–17, 19); bases of antennae closely approximated; male eyes almost always holoptic (separated by the width of the median ocellus or less), with facets of similar size dorsally and ventrally; face almost always tumid (figs. 161, 163, 165, 167, 169, 171); clypeus not reaching bases of antennae; labrum simple, dorsal surface sclerotized; labellae fleshy or elongate; palp with one or two segments (figs. 67, 69), apical segment large in the Eclimini (fig. 64), palp pit present or absent; cibarium simple; maxillae joined ventrally or divided (fig. 46); posterior tentorial pits rounded; postcranium flat or slightly tumid (fig. 181); one occipital foramen; occipital chambers present and well developed (figs. 135–136) except in some Eclimini; occipital apodemes present in almost all except *Marmasoma* White (figs. 164, 166, 168, 170, 172); posterior eye margin simple or sinuous, when sinuous (*Heterostylum* Macquart, *Eurycarenus* Loew, *Triploechus* Edwards, *Efflatounia* Bezzi, and *Karakumia* Paramonov) it is simple (figs. 171, 218) and is not associated with a short bisecting line between the eye facets as found in the Anthracinae; gena with a single internal ridge in some Eclimini (figs. 213, 215), head wider than high.

Thorax. Basicosta produced into an elongate spine in some Bombyliini (fig. 227); costa of some male eclimines with modified, enlarged setae (fig. 222); three branches of Rs; R_{2+3} arises at an acute angle and in a proximal position; M_2 present; cell r5 open or closed; dm-cu present; costal vein circumambient, except in some eclimines where it ends at vein A_1; propresternum pear-shaped (fig. 263); preprocoxal bridge present in *Eurycarenus*; tergal fulcrum present (fig. 277); prealar bristles present; anepimeron, laterotergite and mediotergite bare or haired; one or two pairs of midtibial spurs, only present in Conophorini (fig. 287).

Genitalia. *Male*. Epandrium with posterior margin convex (fig. 357) or concave (fig. 358), small median notch in Conophorini (fig. 356); hypandrium present or absent; gonocoxites fused, most with a median ridge present (absent in *Marmasoma*); gonostyli present; aedeagal sheath fitting closely over the aedeagus or modified into a lobe or lobes (epiphallus) above the aedeagus; single gonopore. *Female*. Tergite 8 with an anterior apodeme (fig. 437) except in forms with reduced sand chambers (e.g., *B. androgynus*, *Lepidophora*, and *Cyrtomyia* Bigot); tergite 8 with long hairs on posterior margin (except *B. androgynus*, and modified into spines in *Eclimus*); tergites 9 and 10 separate or fused but line of fusion evident (figs. 486–487); acanthophorite spines present except in *B. androgynus*; straps extending anteriorly from tergites 9 and 10 to the furca; sternite 8 invaginated, consisting of three sclerites (figs. 461–462, 464–465) except in some Eclimini (figs. 456–460); furca u-shaped or two separate sclerites (fig. 497–499); spermathecal bulb well sclerotized; sperm pump present, well developed.

Synapomorphies

Male eyes with facets of similar size above and below; prealar bristles present.

Discussion

The large, typical subfamily of the Bombyliidae is a heterogeneous assemblage of 63 genera and almost 1000 species found in all biogeographic regions. Hull (1973) enlarged the concept of the subfamily and proposed ten tribes, the two largest being the Bombyliini and the "Dischistini." Three of Hull's subfamilies (Eclimini, Cythereini, and Mariobezzini) had been traditionally, and were subsequently (Bowden, 1985) recognized in different subfamilies. Five tribes have been recently recognized (Evenhuis, 1991); Hull's Heterostylini and Paratoxophorini were synonymized with the "Dischistini." Bowden (1985) reevaluated the characters used to distinguish the tribes "Dischistini" and Bombyliini. He restricted the Bombyliini to those genera having a hair tuft on the laterotergite and wing cell r5 closed, and the "Dischistini" to those genera having a bare laterotergite, or, if haired, cell r5 open. This analysis shows that Bowden's (1985) characters are useful for defining a monophyletic Bombyliini, but his characters for the "Dischistini" are plesiomorphies.

Members of all five recently recognized tribes were included in this analysis. The Ecliminae of previous authors form the most distal members of the Bombyliinae clade (fig. 7, clade 43), and I have relegated them to tribal level within the Bombyliinae. The Conophorini are monophyletic and form the sister to the remaining Bombyliinae. The "Dischistini" are paraphyletic, with the Acrophthalmydini, Bombyliini, and the Eclimini nested within them. I have raised the Crocidiini to subfamily status below. The tribe "Dischistini" contains over half the genera in the subfamily. It should be recognized as a paraphyletic assemblage and only used for taxonomic convenience. A more detailed study of the relationships of the "Dischistini" genera to the Bombyliini and Eclimini is required to elucidate its monophyletic components.

Tribe Conophorini

The Conophorini presently contains eight genera (Evenhuis, 1991; Greathead personal commun. indicates that *Conophorina* Becker belongs in the Dischistini), four of which contain one species each and are restricted to southern Africa. Theodor (1983) reported that one of these genera, *Legnotomyia* Bezzi, lacked a sand chamber. This absence would jeopardize the classification of this genus in the Conophorini. The monophyly of Conophorini is supported by the swollen and enlarged scape (character 2, figs. 25, 163), midtibial spurs present (character 90, fig. 287), and median notch on the epandrium (character 106, fig. 356).

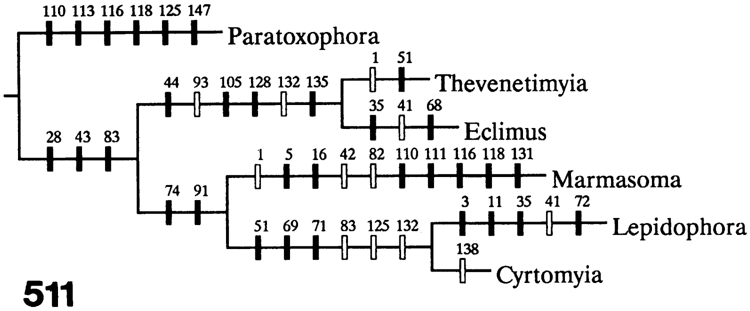
Tribes Acrophthalmydini and Bombyliini

Acrophthalmyda Bigot and the Bombyliini form clade 48, with maxillae fused ventrally (character 24, also present in *Dischistus* Loew) and one palpal segment (character 26). The three Bombyliini form clade 49, united by their closed cell r5 (character 62), haired anepimeron (character 80), and laterotergite (character 82). The tribe Acrophthalmydini is undoubtedly monophyletic, containing just one genus with two species from South America. There appears to be little justification for its recognition as a tribe separate from the Bombyliini if future analyses corroborate its sister-group relationship with the Bombyliini. The Bombyliini contains four genera and almost 500 described species, and members can be found in all except the Australasian biogeographic regions (Bowden, 1985). The two coded members of *Bombylius* Linnaeus form a paraphyletic group with respect to *Eurycarenus*. *Bombylius* itself contains over 350 species found in all biogeographic regions except the Australasian. Due to the very small percentage of *Bombylius* species coded, I do not have much confidence in the precise topology of clade 49.

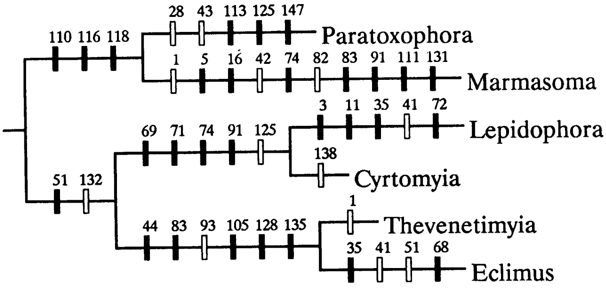
Tribe Eclimini, revised status

The Eclimini form clade 52, including *Paratoxophora* Engel which has been traditionally placed in the "Dischistini." The Eclimini are united by female sternite 8 (character 132) either being simple, or forming a small, concave sclerite with a median ridge (figs. 456–460), and female tergites 9 and 10 fused, but the line of fusion between them is evident (character 134, fig. 485).

In comparison to other members of the subfamily the Eclimini have a modified sand chamber with a simple female sternite 8. It is possible that the eclimine sternite 8 represents a stage in the development of the sand



511



512

Figs. 511–512. The two most parsimonious arrangements of the genera of Eclimini found among the eight most parsimonious trees. The clade detailed here corresponds to clade 52 in figure 7. Characters are numbered and closed hash marks represent forward character state changes: open hash marks represent reverse character state changes. ACCTRAN optimization.

chamber, rather than a reversal. Another conspicuous feature of the Eclimini is the modified, enlarged setae found in *Lepidophora*, *Cyrtomyia*, and *Thevenetimyia* Bigot on the costa of males. The tribe contains seven genera and approximately 50 species; many of the genera have restricted distributions: *Tillyardomyia* Tonnoir in New Zealand, *Marmasoma* White in Australia, *Palinotus* François in central Africa, and *Cyrtomyia* Bigot in Chile. Greathead (1988) conducted a phenetic analysis of members of the subfamily and this supported a Gondwanaland origin for the subfamily except for the relict *Thevenetimyia* restricted to Australia and North America. My cladistic analysis reveals a sister-group relationship between the New World genera *Lepidophora* and *Cyrtomyia*, and the Palearctic *Eclimus* and a Nearctic *Thevenetimyia*.

The eight most parsimonious trees contain two different resolutions of the Eclimine clade, shown in figures 511–512, which differ primarily in their placement of *Marmasoma*. In figure 511 *Marmasoma* is the sister of *Lepidophora* and *Cyrtomyia*, based on the presence of large bristles on the proantepronotum and at the apex of the coxa in these three genera. In figure 512 *Marmasoma* is the sister of *Paratoxophora*, united by the apomorphic loss of a separate hypandrium, shape of the epiphallus, and curvature of the male genitalia. I prefer the resolution in figure 512 because of its reliance on male genitalic characters to unite *Marmasoma* and *Paratoxophora*, rather than the resolution of figure 511, which relies on two features of vestiture in its placement of *Marmasoma*. Further analyses using *Palinotus*, *Tillyardomyia* Tonnoir, and a greater taxonomic and geographic sampling of *Thevenetimyia* may further resolve the relationships of the genera of the Eclimini.

Lepidophora has been classified in the Toxophorini by some authors (e.g., Zaytsev, 1992), largely due to the wing scales and enlarged prothorax. On the cladogram (fig. 7) these features are independently derived in *Lepidophora* and *Toxophora*.

The Crocidinae and other subfamilies more distal on the cladogram (clade 55) share the following apomorphy: occipital chambers reduced to partial or absent (character 41).

8. Crocidiinae

Crocidiinae Hull, 1973: 70, new status. Type species *Crocidium* Loew, 1860.

Desmatomyiinae Hall and Evenhuis, 1987: 629. Type species *Desmatomyia* Williston, 1895.

Diagnosis

Head. Flagellum with two or three flagellomeres and an apical or subapical style (figs. 22–23); male eyes holoptic, eye facets smaller ventrally than dorsally; face tumid (figs. 159, 161); clypeus not reaching antennae; two-segmented palp (fig. 66), palp pit present; cibarium simple (figs. 85–86); posterior tentorial pits rounded; postcranium flattened or slightly tumid; one occipital foramen; occipital chambers absent (*Desmatomyia*, fig. 160) or partial (*Crocidium*, fig. 162); posterior eye margin simple; head wider than high.

Thorax. Three branches of Rs; R_{2+3} arising proximally and at an acute angle; M_2 present; cell r5 open; dm-cu present; anal cell open; costal vein circumambient; propresternum pear-shaped; preprocoxal bridge absent; tergal fulcrum present in *Crocidium*, absent in *Desmatomyia*; anepimeron, laterotergite, and mediotergite bare; midtibial spurs present (figs. 285, 288); coxal peg present (fig. 296).

Genitalia. *Male*. Epandrium with posterior margin convex (fig. 393), simple; hypandrium absent; gonocoxites fused (fig. 372), with or without median ridge; aedeagal sheath fitting snugly over the aedeagus (*Crocidium*), or forming a complex epiphallus (*Desmatomyia*, figs. 391–392). *Female*. Tergite 8 with anterior apodeme (figs. 434, 440) and posterior margin with dense brush of hairs; tergites 9 and 10 separate (fig. 454); acanthophorite spines present; sclerotized strips extending from tergites 9 and 10 to the furca; sternite 8 invaginated, simple in *Crocidium* (fig 454), divided into three sclerites in *Desmatomyia* (fig. 434); furca u-shaped; spermathecal bulb well sclerotized in *Crocidium*, membranous in *Desmatomyia*; sperm pump present in *Crocidium*, absent in *Desmatomyia*.

Synapomorphies

Midtibial spurs present (figs. 285, 288); coxal peg present.

Discussion

The limits of this subfamily remain to be determined, however I assume here it includes genera formerly classified in the tribe Crocidiini of the Bombyliinae and the subfamily Desmatomyiinae. Under this assumption the subfamily contains nine genera and about 34 species; the Nearctic genera *Desmatomyia* and *Inyo* Hall and Evenhuis, and seven genera found in the Neotropical, Afrotropical, and Palearctic regions; *Crocidium, Adelogenys* Hesse, *Apatomyza* Wiedemann, *Megaphthiria* Hall, *Mallophthiria* Edwards, *Semiramis* Becker, and *Timiomyia* Evenhuis. *Apatomyza* and *Mallophthiria* are represented in collections by one specimen each. Hull (1973) evidently considered that the genera of this subfamily were related, and placed *Desmatomyia* in the tribe Crocidiini of the Bombyliinae. The structure of the female genitalia of the genera placed in the Crocidiini should be examined before their affinities are ascertained.

Desmatomyia and *Inyo* possess a large flagellum of three flagellomeres with a subapical style (figs. 22-23). The other genera have elongate flagella consisting of one or three flagellomeres with an apical style. Female *Crocidium* have a simple sternite 8 (fig. 454), not divided into three sclerites as found in *Desmatomyia* (fig. 463) and most of the other members of the sand chamber subfamilies. This is treated as a reversal on the cladogram, and the morphology of female sternite 8 in closely related genera may shed further light on the evolution of the sand chamber.

Sericosoma Macquart and other subfamilies in clade 57 have a moderately or deeply concave postcranium (states 1 and 2 of character 37); two occipital foramina (character 39); occipital windows present (character 40, reverses in Mariobezziinae); and occipital pockets completely absent (character 41, reverses in Mariobezziinae).

Sericosoma Macquart

Sericosoma falls between the Crocidiinae and Mariobezziinae on the cladogram (fig. 7), and I am unsure of its correct subfamily placement so leave the genus incertae sedis at present. The occiput of *Sericosoma* is similar to that of the Mariobezziinae, with a shallow concavity; the male eyes are dichoptic and the bases of the antennae are well separated, however the pedicel lacks a short dorsal spine characteristic of Crocidiinae. The posterior arms of the cibarium are simple in *Sericosoma*, whereas they have small knees in Mariobezziinae except in *Corsomyza*. All Mariobezziinae are known only from Africa and the Southern Palearctic and *Sericosoma* and its sister genus *Sericothrix* Hall are restricted to South America. I expect future phylogenetic studies on *Sericosoma* and *Sericothrix* will ally them with the Mariobezziinae.

The subfamilies including and more distal to the Mariobezziinae on figure 7 share the following synapomorphy; posterior arms of cibarium with median projections or fused together (character 30).

9. Mariobezziinae

Mariobezziinae Becker, 1913: 470. Types species *Mariobezzia* Becker, 1913.

Corsomyzinae Theodor, 1983: 17. Type genus *Corsomyza* Wiedemann, 1820.

Diagnosis

Head. Pedicel usually with dorsal process or spine (figs. 173, 175, 177); flagellum clavate or elongate, with one flagellomere; if style present then apical; male eyes broadly dichoptic, facets smaller ventrally than dorsally in some genera; face tumid; clypeus not reaching bases of antennae; palps one-segmented (fig. 70), palp pit absent; cibarium with posterior arms long, simple or with knee (figs. 91–92, 95–96, 99–100), ventral ridge in *Mariobezzia* (fig. 99); posterior tentorial pits rounded (figs. 174, 176, 178); postcranium concave (fig. 209), but more shallow than found in the Lomatiinae, Antoniinae, Tomomyzinae, and Anthracinae; occipital lobes separate; two occipital foramina (figs. 174, 176, 178), however cervical condyles not as closely approximated as in Cythereinae, Lomatiinae, Tomomyzinae, Antoniinae, and Anthracinae; occipital chambers present or absent; occipital windows absent; occipital apodemes present; posterior eye margin simple; head wider than high.

Thorax. 3 branches of Rs; R_{2+3} arises proximally and at an acute angle; i-r crossvein present or absent; M_2 present; anal cell usually closed. Propresternum pear-shaped (fig. 269); anepimeron bare; laterotergite and mediotergite bare. Prealar bristles absent except a few present in *Megapalpus* Macquart.

Genitalia. *Male*. Epandrium with posterior margin convex, with complex median notch (fig. 359); hypandrium absent; gonocoxites fused with median ridge; aedeagal sheath fitting snugly over aedeagus, thus no epiphallus. *Female*. Tergite 8 with apodeme on anterior margin (fig. 443), dorsoventrally flattened in *Corsomyza* Wiedemann and *Megapalpus*; dense brush of hairs on posterior margin, reduced in *Mariobezzia*; tergites 9 and 10 separate or fused but line of fusion evident (fig. 489); acanthophorite spines present; sternite 8 invaginated; composed of a single u-shaped sclerite; furca fused in midline or separate; spermathecal bulb sclerotized; sperm pump present.

Synapomorphies

Pedicel with small dorsal spine (figs. 173, 175, 177); posterior margin of epandrium with complex notch (fig. 359, also found in Lomatiinae).

Discussion

Bowden (1975a) discussed the classification of this subfamily (as the tribe Corsomyzini of the subfamily Cythereinae), and included eight genera. Evenhuis (1991) added the Australian *Neosardus* Roberts, which has been transferred to the Cythereinae here. As currently conceived the subfamily contains seven genera restricted to southern Africa, and *Mariobezzia* from Africa (Sudan) and the southern Palearctic region. Bowden (1975a) referred to the latter distribution as Afro-Iranian, and found it common in the Bombyliidae.

Except for *Sericosoma*, the Mariobezziinae are the most plesiomorphic Tomophthalmae. A characteristic feature of the subfamily is the dorsal projection on the pedicel, found in all but *Hyperusia muscoides* Hesse. The relationship of this species to the others is in need of clarification. The postocciput of members of the subfamily possesses a depression, however it is more shallow than in more distal Tomophthalmae. There are two occipital foramina, however these are less distinctly separated than in other Tomophthalmae. This is the most apomorphic subfamily in which the occipital chambers are fully developed. The females have a well-developed sand chamber, and the epandrium of the males have a distinct median notch on the posterior margin not found elsewhere except the Lomatiinae. Female sternite 8 is modified into a u-shaped sclerite, rather than being divided into three, which may provide an additional synapomorphy for the subfamily.

The Oniromyiinae, Cythereinae, Lomatiinae, Antoniinae, Tomomyzinae, and Anthracinae (clade 61) are united by the following synapomorphies; occipital apodemes absent (character 42, reverses in Lomatiinae and some Cythereinae) and prealar bristles present (character 87, reverses in Tomomyzinae).

10. Oniromyiinae

Oniromyiinae Greathead, 1972: 27. Type genus *Oniromyia* Bezzi, 1921.

Diagnosis

Head. Scape with a characteristic ventral bulge (fig. 183); flagellum with two flagellomeres and an apical style; male eyes dichoptic; median ocellus reduced; face not tumid (fig. 183); clypeus reaching antennae; labrum with scales on dorsal surface; proboscis and labellae elongate (fig. 56); one-segmented palp, palp pit absent; posterior arms of cibarium with knees (figs. 93–94); posterior tentorial pits rounded (fig. 184); postcranium concave, but more shallow than found in the Lomatiinae, Antoniinae, Tomomyzinae, and Anthracinae; occipital lobes separate; two occipital foramina (fig. 184), however cervical condyles not as closely approximated as in Cythereinae, Lomatiinae, Tomomyzinae, Antoniinae, and Anthracinae; occipital lobes separate; occipital windows present; occipital chambers absent; occipital apodemes absent; posterior eye margin simple; head wider than high (fig. 184), and wider than thorax.

Thorax. Wings small; three branches of Rs; R_{2+3} arises proximally and at an acute angle; M_2 present; cell r5 closed; anal cell open. Propresternum pear-shaped (fig. 264); anepimeron haired; laterotergite haired; mediotergite bare; prealar bristles present.

Genitalia. *Male*. Epandrium with posterior margin simple and convex; hypandrium absent; gonocoxites fused with median ridge; gonostyli with apical strong hairs; phallus curved dorsally then ventrally on apical half. *Female*. Tergite 8 with apodeme on anterior margin and brush of long hairs on posterior margin; tergites 9 and 10 separate; acanthophorite spines present; sternite 8 invaginated, divided into three sclerites; furca composed of two slightly sinuous sclerites (fig. 500); spermathecal bulb well sclerotized; sperm pump present, proximal end-plate reduced.

Synapomorphies

Scape with ventral bulge (fig. 183); clypeus reaching bases of antennae; dorsal surface of labrum with scales.

Discussion

This small subfamily of one genus and two species is restricted to South Africa. Greathead (1972) discussed the classification of the genus and proposed a new subfamily for it, suggesting that it belonged between the Cythereinae and Cylleniinae. The results of this study largely confirm Greathead's (1972) conclusions, the genus occupying a position between the Mariobezziinae, previously classified as a tribe of the Cythereinae, and the Cythereinae, which now includes genera of both Cythereinae and Cylleninae of previous authors.

The distinct bulge on the ventrally surface of the scape and scales on the labrum provide synapomorphies for the subfamily.

The Xenoprosopinae, known only from a single female *Xenoprosopa paradoxa* Hesse 1956b collected in South Africa, is the only subfamily not represented in this analysis. It has reduced mouthparts, lobed palps, and a large bulge on the ventral surface of the scape, recalling the scape shape found in *Oniromyia*. In addition, both *Oniromyia* and *Xen-*

oprosopa Hesse have relatively short wings. These features suggest a relationship between the two genera (N. Evenhuis, personal commun.). If this relationship is substantiated, Xenoprosopinae Hesse, 1956b, is prior to Oniromyiinae Greathead (1972).

The Cythereinae, Lomatiinae, Antoniinae, Tomomyzinae, and Anthracinae (clade 62) are united by the labrum with basal third membranous (character 20), and femora with bristles (character 93, reverses in Tomomyzinae).

11. Cythereinae

Cythereinae Becker, 1913: 455. Type genus *Cytherea* Fabricius, 1794.

Cylleniinae Becker, 1913: 472. Type genus *Cyllenia* Latreille, 1802.

Enicinae Hall, 1969: 3 (as Henicinae). Type genus *Enica* Macquart, 1834.

Diagnosis

Head. Antennal bases widely separated in *Cytherea*, *Pantarbes*, Osten Sacken and *Callostoma* Macquart (fig. 26); flagellum of one, two, or three flagellomeres with an apical style; male eyes dichoptic except in *Enica*, facets smaller ventrally than dorsally in *Neosardus* and *Pantarbes*; face tumid (figs. 185, 187, 189, 191, 193); clypeus not reaching antennae; palp of one or two segments, palp pit present; posterior arms of cibarium with knee (figs. 97, 101, 103), joined apically in *Pantarbes* (fig. 105), median ventral ridge in *Cyllenia*; posterior tentorial pits rounded; postcranium concave, but more shallow than found in the Lomatiinae, Antoniinae, Tomomyzinae, and Anthracinae (figs. 210–211); occipital lobes separate, except meeting in *Cyllenia*; two occipital foramina (figs. 186, 188, 190, 192, 194), distinctly separated; occipital windows present; occipital chambers absent except partial in *Pantarbes*; posterior eye margin simple (figs. 185, 187, 189, 191, 193); head wider than high.

Thorax. Three branches of Rs; R_{2+3} arises proximally and at an acute angle; M_2 present; cell r5 open or closed; i-r crossvein present in most; anal cell open; wing scales present in *Enica*. Propresternum (fig. 267) rounded, however poorly defined posteriorly; anepimeron bare or haired; laterotergite bare except *Cytherea*, and Hull (1973) records a few hairs on the laterotergite of *Gyrocraspedum* Becker; mediotergite bare; midtibial spurs present in *Amictus* Wiedemann (fig. 289); pulvilli reduced in size in *Cytherea*, *Enica*, and *Neosardus*.

Genitalia. *Male*. Genital capsule rotated; segment 8 narrow in *Amictus* and *Cyllenia* (figs. 315–316); posterior margin of tergite 9 convex in *Cytherea* and *Enica*, concave in the remaining genera examined (figs. 360–361), margin simple; hypandrium present except in *Enica* (figs. 376–377); gonocoxites fused with ridge absent in *Enica*; gonocoxal apodemes relatively long (fig. 399); epiphallus present as a single lobe (fig. 399); distiphallus with one gonopore except divided into three tubes near apex in *Cyllenia* (figs. 403–404); phallus curved anteriorly then posteriorly in *Amictus* (fig. 399) and *Cyllenia*. *Female*. Tergite 8 with apodeme on anterior margin (fig. 442), brush of long hairs on posterior margin; tergites 9 and 10 separate (fig. 488); acanthophorites with spines except in *Cyllenia*; sternite 8 invaginated, composed of three sclerites; furca a u- or y- shaped sclerite; spermathecal bulb well sclerotized; sperm pump present.

Synapomorphies

Inter-radial crossvein present; hypandrium present and separate (except in *Enica*); epiphallus present as a single lobe above the phallus (fig. 397).

Discussion

As here conceived, the Cythereinae comprises the Cythereini of traditional classifications (excluding *Sericosoma*), in addition to the Cylleniinae excluding *Peringueyimyia* which I have transferred to the Lomatiinae. Using the principle of the first revisor (ICZN, 1985; Art. 24), I choose the Cythereinae to have priority over the Cylleniinae, as the former has page precedence in Becker (1913).

The subfamily is rather disparate, does not have a compelling suite of synapomorphies, and may well prove paraphyletic on further study. In particular, one of the synapomorphies, the presence of an inter-radial crossvein, does not occur in all members of the subfamily. The male genitalia (except in *En-*

ica) possess a hypandrium, a reversal to a plesiomorphic condition not seen since the Bombyliinae (clade 43). Except in *Cyllenia*, the females have a fully functional sand chamber. *Cyllenia* lacks acanthophorite spines, however, the remaining features of the sand chamber such as a modified tergite and sternite 8, are still evident, suggesting that *Cyllenia* has only recently lost a functional sand chamber. A study of the oviposition behavior of this genus would no doubt be revealing.

The subfamily Cylleninae has traditionally been distinguished from the Lomatiinae by the form of the posterior eye margin, it being simple in the former, and indented in the latter. The cladogram (fig. 7) interprets the posterior eye indentation of the Tomophthalmae evolving independently three times, once each within the Lomatiinae, Antoniinae, and Anthracinae. The genus *Peringueyimyia* possesses the apomorphies of the Lomatiinae, and thus is the only member of that subfamily lacking an indentation on the posterior eye margin.

As characterized here, the Cythereinae contains members of three tribes of traditional classifications, the Cythereini, Cylleniini, Enicini. Of these, the Cylleniini appear monophyletic, based on apomorphies of the male terminalia (characters 103, 104, and 118). Only one member of the Enicini was examined, thus its monophyly was not tested. The traditional subfamily Cythereini is broadly polyphyletic on the cladogram, with *Sericosoma* appearing more basal than the Mariobezziinae, and the remaining members not forming a monophyletic group within the Cythereinae. A reexamination of the tribal divisions of this subfamily is in order.

The Cythereinae is found in all biogeographic regions except the Oriental, the Cyllenini being found in the Palearctic and Neotropical regions, Enicini in the Afrotropical, *Neosardus* in the Australasian region, and the remaining Cythereini in the Palearctic, Nearctic, and Neotropical regions. The relationships of the four Neotropical *Cytherea* species, and *Gyrocraspedum* Becker, are worthwhile goals for future researchers.

The Lomatiinae, Tomomyzinae, Antoniinae, and Anthracinae (clade 68) are united by the following apomorphies, all associated with the deeply concave postcranium found in these subfamilies: posterior tentorial pits elongate (character 36); postcranium deeply concave (character 37); occipital lobes meeting behing ocellar tubercle (character 38); head rounded (character 49); and propresternum arrow-shaped (character 75).

12. Lomatiinae

Lomatiinae Schiner, 1868: 115 (as Lomatinae). Type genus *Lomatia* Meigen, 1822.

Diagnosis

Head. Flagellum of one flagellomere, style absent; male eyes holoptic, facets of similar size; face not tumid (figs. 195, 197); clypeus reaching antennae; palp one-segmented, palp pit present except absent in *Comptosia* and its other Australian relatives (Yeates, 1989); posterior arms of cibarium united (figs. 107, 109), arms bent ventrally in lateral view in all except *Peringueyimyia*; posterior tentorial pits elongate (fig. 196, 198); occiput deeply concave (figs. 196, 198); occipital lobes meeting behind ocellar triangle; two occipital foramina; occipital windows present; occipital chambers absent; occipital apodemes present; posterior eye margin with a simple indentation in all but *Peringueyimyia*; head rounded, as wide as high.

Thorax. Three branches of Rs; R_{2+3} arises at an acute angle, and proximally, often with a pronounced sinuosity at its apex; M_2 present. Postcervical sclerite fused to proepisternum; propresternum arrow-shaped (fig. 265); preprocoxal bridge absent; anepimeron and laterotergite bare or haired; mediotergite haired.

Genitalia. *Male*. Genitalia not rotated; tergite 9 convex and with a complex median notch (figs. 363–364); hypandrium absent (fig. 379); gonocoxites fused with median ridge; aedeagal sheath fitting snugly over aedeagus, no epiphallus. *Female*. Tergite 8 with apodeme on anterior margin, brush of long hairs on posterior margin; tergites 9 and 10 separate, or fused but line of fusion evident; acanthophorite spines present; sternite 8 invaginated, consisting of three sclerites (fig. 466); furca composed of two sclerites; spermathecal bulb well sclerotized; sperm pump present.

Synapomorphies

Face flat, not tumid (figs. 195, 197); clypeus reaching antennae; cibarium arms joined (figs. 107, 109); occipital apodemes present; mediotergite haired; male epandrium with complex median notch on posterior margin (fig. 363–364).

Discussion

Since Hull's study (1973) the scope of the Lomatiinae has been gradually reduced (Bowden, 1980), and it is now putatively monophyletic. Containing 15 genera and almost 300 species, there are two tribes recognized in traditional classifications, the Comptosiini, in the Australasian, Oriental, and Neotropical biogeographic regions, and the Lomatiini, found in the Nearctic, Neotropical, Afrotropical, and Palearctic regions.

Peringueyimyia Bigot is the only genus in the subfamily to have a simple posterior eye margin. It forms the sister group to the remaining genera, and should be recognized in its own tribe, the Peringueyimyiini Hull. The two traditional lomatiine tribes have been separated because of the deep radial loop in some Comptosiini. I was unable to find apomorphies for the Lomatiini alone, and *Comptosia* Macquart forms a trichotomy with the genera of the Lomatiini, a result which echoes my previous findings (Yeates, 1989). Thus, the Lomatiini is paraphyletic, and should be united with the Comptosiini.

The Comptosiini have been considered an example of a group showing a transantarctic, or Gondwanan, biogeographic relationship (Hennig, 1966a). The cladistic relationships of the subfamily are consistent with an origin on Gondwana, with genera and species found in Laurasian regions being derived from them.

The Antoniinae, Tomomyzinae, and Anthracinae (clade 72) are united by the following synapomorphies: cibarium elongate (character 33); postcervical sclerite separate from proepisternum (character 73); and the male epandrium with a concave posterior margin (character 105, reverses within the Anthracinae).

The Antoniinae and Tomomyzinae are united by the following synapomorphies: ocellar tubercle placed well forward, anterior to posterior margin of eyes (character 12); laterotergite haired (character 82).

13. Antoniinae

Antoniinae Hull, 1973: 303 (as tribe). Type genus *Antonia* Loew, 1856.

Diagnosis

Head. Flagellum with one or three flagellomeres and an apical style; male eyes dichoptic, facets of similar size; ocellar triangle displaced anteriorly so that it is on the face, anterior to the posterior margin of the eyes; face tumid (fig. 201); clypeus reaching antennae in *Myonema* Roberts; palp with two segments in *Myonema*, one in *Antonia*, palp pit absent; cibarium elongate, posterior arms with knees, bent ventrally in lateral view (fig. 118), median ventral ridge in *Antonia* (fig. 117); posterior tentorial pits elongate; occiput deeply concave; occipital lobes joining behind ocellar tubercle (except in *Myonema*); two well-separated occipital foramina; occipital windows present; occipital chambers absent; occipital apodemes; posterior eye margin simple in *Myonema*, indented and bisected in *Antonia* (fig. 201); head rounded.

Thorax. Three branches of Rs; R_{2+3} arises at an acute angle, and proximally; M_2 present; cell r5 closed in *Antonia*; anal cell open. Postcervical sclerite fused to proepisternum in *Myonema*, separate in *Antonia*; proprosternum arrow-shaped; preprocoxal bridge present in *Antonia*, absent in *Myonema*; prealar bristles present; anepimeron bare; laterotergite haired.

Genitalia. *Male*. Epandrium with posterior margin concave, simple; hypandrium absent; gonocoxites fused with median ridge; epiphallus well developed in *Antonia* (fig. 401), present as a large, dorsal blind lobe; ejaculatory apodeme with three vanes (fig. 401), *Myonema* laterally compressed. *Female*. with tergite 8 simple, without apodeme on anterior margin or brush of dense hairs on posterior margin (figs. 482, 484); tergites 9 and 10 completely fused, acanthophorite spines absent; sternite 8 simple, composed of one sclerite, external in *Antonia*, invaginated in *Myonema*; ventral lobe in the region of sternite 10, arising beneath the fused sternites 9 and 10; furca divided into two separate sclerites (fig. 501); three spermathecae except in *Antonia* with one large and two small vestigial spermathecae (fig. 501); *Antonia* with membranous spermathecal bulb; lacking sperm pump; *Myonema* with sclerotized bulb, pump present; cerci elongate in *Antonia* and *Antoniaustralia*.

Synapomorphies

Female tergite and sternite 8 simple; acanthophorite spines absent; acanthophorites absent or completely fused with tergite 9 (figs. 482, 484).

Discussion

The Antoniinae was first raised to a subfamily by Bowden (1980) and presently consists of three genera, *Antonia*, *Antoniaustralia* Becker and *Cyx* Evenhuis 1993. The female genitalia of *Cyx* and *Antoniaustralia* have the plesiomorphic condition of three spermathecae. With the addition of *Myonema* there are a total of 17 species occurring in the Palearctic, Afrotropical, and Australasian biogeographic regions.

The genera are united chiefly by the absence of a sand chamber, and some other aspects of their morphology suggest that *Myonema* may have lost the sand chamber independently from *Antonia* and *Antoniaustralia* rather than through a common ancestor. The occipital lobes are separate behind the ocellar triangle in *Myonema* but meet in *Antonia* and *Antoniaustralia*, the posterior eye margin is simple in *Myonema* but has an identation and a short dividing line between the facets in *Antonia* and *Antoniaustralia* and the postcervical sclerite is fused to the proepisternum in *Myonema*, but free in the other genera. These characters indicate a more apomorphic position in Bombyliidae phylogeny for *Antonia* and *Antoniaustralia* than *Myonema* if the sand chamber was lost independently in the two groups.

As I have remarked when referring to other members of the sand chamber subfamilies which have secondarily lost the sand chamber, knowledge of the oviposition behavior which these flies have adopted may provide further evidence on their phylogenetic relationships. *Antonia* has been reported following closely behind *Bembix* and *Sceliphron* (Hymenoptera: Sphecidae) wasps in Africa (Hesse, 1956a; Greathead, 1967), and probably parasitizes them.

Evenhuis (1993) illustrates the female genitalia of an unidentified *Antonia* species from Kenya which differs markedly from the type species examined here. The unidentified species has tergite 9 + 10 produced into elongate lateral lobes, as found in *Antoniaustralia* and *Cyx*, but unlike the type of *Antonia*. Clearly the female genitalia of the Antoniinae have been modified in various ways since losing the sand chamber, and a revision of the type genus is now due.

14. Tomomyzinae

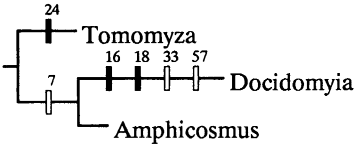
Tomomyzinae Becker, 1913: 457. Type genus *Tomomyza* Wiedemann, 1820.

Diagnosis

Head. Flagellum of one flagellomere; style apical if present; male eyes dichoptic, facets of similar size; ocellar tubercle displaced onto frons, anterior to posterior margin of eyes; face flat in *Docidomyia* White, tumid in remainder (fig. 199); clypeus reaching antennae only in *Docidomyia*; labrum with basal third of dorsal surface membranous; one-segmented palp, palp pit present; posterior arms of cibarium straight (fig. 112), united (fig. 111), elongate except in *Docidomyia*; posterior tentorial pits elongate (fig. 200); postcranium deeply concave; occipital lobes meeting behind ocellar tubercle; two distinct occipital foramina (fig. 200); occipital windows present; occipital chambers absent; occipital apodemes absent; posterior eye margin simple; head rounded.

Thorax. Three branches of Rs; R_{2+3} arises at an acute angle, proximally; M_2 present; anal cell open; squama reduced. Postcervical sclerite separate from proepisternum; propresternum arrow-shaped; preprocoxal bridge present (fig. 253); anepimeron bare; laterotergite haired; mediotergite bare; prealar bristles absent.

Genitalia. *Male*. Genital capsule not rotated; tergite 9 with concave posterior margin (fig. 365); hypandrium absent (fig. 378); gonocoxites fused, median ridge absent; aedeagal sheath fitting snugly over aedeagus, no epiphallus. *Female*. Tergite 8 with apodeme on



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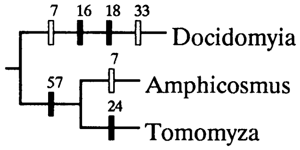

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Figs. 513–514. The two most parsimonious arrangements of the genera of Tomomyzinae found among the eight most parsimonious trees. The clade detailed here corresponds to clade 75 in figure 7. Characters are numbered and closed hash marks represent forward character state changes; open hash marks represent reverse character state changes. ACCTRAN optimization.

anterior margin (fig. 444), brush of long hairs on posterior margin; tergites 9 and 10 separate; acanthophorite spines present (fig. 492); sternite 8 invaginated, composed of three sclerites; furca composed of two separate sclerites; spermathecal bulb sclerotized; sperm pump present.

Synapomorphies

Squama reduced; prealar bristles absent; gonocoxites fused without a median ridge.

Discussion

The Tomomyzinae is a small subfamily containing 6 genera and 39 species. At various times the subfamily has been synonymized with the Cylleniinae (Bezzi, 1924; Hull, 1973; Hall, 1976; Theodor, 1983).

The monophyly of the Tomomyzinae is supported by a number of characters, all which exhibit some homoplasy on the cladogram. The advanced state of character 111, gonocoxites fused together without a median ridge, and the femora without bristles (character 93) occur in the Cylleniinae, and prealar bristles (character 87) are also absent in *Ogcodocera* Macquart of the Lomatiinae. *Docidomyia* exhibits a number of features which suggest it may have closer affinities with the Lomatiinae than with the other tomophthalmine genera. Members of the subfamily characteristically have bare bodies and legs. The Tomomyzinae have traditionally been recognized because of the very tumid frons and face, however *Docidomyia* lacks this feature. In addition, *Docidomyia* lacks the elongate cibarium found in all other Antoniinae, Tomomyzinae, and Anthracinae, but absent in the Lomatiiane. The clypeus of *Docidomyia* reaches the base of the antennae, a feature shared with the Lomatiinae, and absent in other Tomomyzinae. This feature, among others, led me to believe that *Docidomyia* belonged in the Lomatiinae (Yeates, 1990).

The eight most parsimonious trees include two distinct resolutions of the genera in the Tomomyzinae, shown in figures 513–514. In figure 513, *Docidomyia* and *Amphicosmus* Coquillett are united by the absence of a flagellar style (character 7) and in figure 514, *Amphicosmus* and *Tomomyza* are united by the presence of an inter-radial crossvein (character 57). I do not consider either arrangement well supported, as both characters undergo much homoplasy.

The distribution of the 6 genera is disjunct as follows: *Amphicosmus*, *Metacosmus* Coquillett, and *Paracosmus* Osten Sacken are Nearctic and extend into Mexico, *Docidomyia* is restricted to southern Australia, and *Tomomyza* and *Pantostomus* Bezzi are found in southern Africa.

15. Anthracinae

Anthracinae Latreille, 1804: 189 (as Anthracii). Type genus *Anthrax* Scopoli, 1763.

Spogostylinae Sack, 1909: 505 (as Spongostylinae). Type genus *Spogostylum* Macquart, 1840.

Exoprosopinae Becker, 1913: 449. Type genus *Exoprosopa* Macquart, 1840.

Aphoebantinae Becker, 1913: 467. Type genus *Aphoebantus* Loew, 1872.

Diagnosis

Head. Flagellum with three, two, or one flagellomere (figs. 20–21); style present, apical; circlet of hairs around apex of second flagellomere in Anthracini (fig. 21); male eyes dichoptic except in Aphoebantini; face tumid (figs. 203, 205) or flat; clypeus not reaching antennae; labrum with basal third of dorsal surface membranous; palp one-segmented except in Aphoebantini with two, palp pit present in Aphoebantini; cibarium elongate, posterior arms straight in lateral view (figs. 114, 116), with knees or joined medially, median ridge except in *Plesiocera* Macquart (figs. 113, 115); posterior tentorial pits elongate (figs. 204, 206); postcranium deeply concave (figs. 133, 212, 217) ; occipital lobes meeting behind ocellar tubercle (figs. 133, 204, 206, 217); two occipital foramina; occipital windows present; occipital chambers absent; occipital apodemes absent; subgena with troughs extending from posterior tentorial pits in Exoprosopini and Villini (fig. 217); posterior eye margin indented with short bisecting line dividing facets except in Prorostomatini; head rounded.

Thorax. Basicosta produced or spinelike in all but Prorostomatini (fig. 228); Three branches of Rs; R_{2+3} arises at 90° in all but Aphoebantini and Xeramoebini; R_{2+3} arising distally in Anthracini, Exoprosopini, and Villini; M_2 present. Postcervical sclerite separate from proepimeron in all but Aphoebantini; propresternum arrow-shaped; preprocoxal bridge in Xeramoebini and Aphoebantini; pleural vestiture various; prealar bristles present; pulvilli modified into spinelike lobes below tarsal claws (figs. 303–304) in Exoprosopini; foretarsal claws small in comparison to others in Exoprosopini and Villini (fig. 302–303).

Genitalia. *Male*. Genitalia rotated; male epandrium with posterior margin convex or concave, margin simple (fig. 366); hypandrium absent except in Prorostomatini and Aphoebantini (figs. 380–381); gonocoxites fused with median ridge; epiphallus a simple blind lobe above the aedeagus (fig. 402). *Female*. Tergite 8 with apodeme on anterior margin (figs. 444-445) except in *Anthrax*, brush of long hairs on posterior margin; tergites 9 and 10 separate or fused but line of fusion evident (figs. 490–491); acanthophorite spines present; sternite 8 invaginated, consisting of three separate sclerites except in the Exoprosopini and Villini where sternite 8 is modified into a large, concave sclerotized sheet (figs. 468, 483); furca of one or two sclerites; spermathecal bulb sclerotized; sperm pump present.

Synapomorphies

Epiphallus a large lobe above the aedeagus (fig. 402).

Discussion

I found three apomorphies for the subfamily (Appendix 6); only one is unreversed within it, the presence of a large, blind epiphallus above the aedeagus (fig. 402). As discussed in the methods section, my taxon sampling was deliberately biased against this subfamily, which contains almost half the described Bombyliidae species. I have coded one member of each of the traditional tribes, except the bizarre Villoestrini Hull, found in all biogeographic regions except the Australasian. This tribe contains 4 genera and 19 species united by their reduced mouthparts. The degree of reduction of the mouthparts varies and the monophyly of the Villoestrini is in need of clarification.

The Anthracini, Exoprosopini, and Villini form a well-established monophyletic group which will be discussed further below. The boundaries and relationships of the plesiomorphic anthracine tribes are less certain. In addition to Aphoebantini Becker, Bowden (1980) and Evenhuis (1991) used tribal names based on the genera *Plesiocera* and *Petrorossia* Bezzi, however these are nomen nuda (Sabrosky, personal commun., 1992). Here I use the tribal names made available by Hull (1973) for these generic groupings.

Tribe Prorostomatini Hull

This group of genera comprises *Plesiocera* Macquart, *Conomyza* Hesse, *Coryprosopa* Hesse, *Epacmoides* Hesse, *Prorostoma* Hesse, and *Stomylomyia* Bigot. The tribe is only found in the Afrotropical and Palearctic regions.

Hull (1973: 303) proposed the tribe in the Lomatiinae and incorrectly considered that they had an indented posterior eye margin with divided facets. The tribe is characterized by a tumid face, simple posterior eye margin (see *Plesiocera psammophila*, fig. 203) which may have a shallow indentation (e.g., *Epacmoides* Hesse) but no line dividing the facets, vein R_{2+3} arising at a right angle proximal to the r-m crossvein, and a pilose mediotergite.

Plesiocera is a disparate genus, the Palearctic type species *P. algira* Macquart being the only member possessing a indentation on the posterior eye margin and a line bisecting the facets. All the remaining *Plesiocera* species, which are confined to southern Africa, have simple hind eye margins. Hull proposed the name *Calledax* for them, however Bowden (1980) and Evenhuis (1991) consider it a synonym of *Plesiocera*. *P. psammophila*, the type species of *Calledax*, was examined and coded here. When the tribe is revised *Calledax* will be removed from synonymy under *Plesiocera*, and *Plesiocera* itself, containing only the type species, will be removed to another tribe. *P. psammophila* lacks a median ventral ridge on the cibarium and has a rounded basicosta, both plesiomorphic states relative to the remaining Anthracinae.

The Anthracinae except Prorostomatini (clade 77) are united by the following synapomorphies: cibarium with ventral ridge (fig. 113); posterior eye margin with indentation and dividing line between the facets (fig. 220); and basicosta produced or spinelike (fig. 228).

Tribe Aphoebantini Becker

Originally proposed as a subfamily by Becker (1913), this group of genera was placed in the Lomatiinae by Bezzi (1924) and subsequent authors until Bowden (1980) transferred them to his expanded Anthracinae. As currently conceived (Evenhuis, 1991), the tribe contains 7 genera and a little over 100 species; *Aphoebantus* Loew, *Epacmus* Osten Sacken, *Eucessia* Coquillett, *Exepacmus* Coquillett, *Cononedys* Hermann, *Pteraulax* Bezzi, and *Pteraulacodes* Hesse. The tribe is found all over the world except in the Oriental and Australasian biogeographic regions, and about half the included species are Nearctic *Aphoebantus*.

Hull characterized the tribe as having a smoothly curving face (not tumid), posterior margin of eyes with an indentation, R_{2+3} arising proximally and at an acute angle (unlike that in other members of the Anthracinae), and mediotergite bare. The Aphoebantini share a number of plesiomorphic features relative to the remaining Anthracinae including the Prorostomatini: two-segmented palps with palp pit, some members have three flagellomeres, the male eyes are holoptic, and the postcervical sclerite is fused to the proepisternum. The classification of *Exepacmus* is worthy of review because R_{2+3} arises at a right angle (Hull, 1973: fig. 293), unlike that in other members of the tribe.

Tribe Xeramoebini Hull

The tribe contains about 90 species in 5 genera; *Xeramoeba* Hesse, *Petrorossia* Bezzi, *Desmatoneura* Williston, *Pipunculopsis*, Bezzi and *Prothaplocnemis* Bezzi. The distribution is strongly biased toward the Old World, with only one species of *Desmatoneura* in the New World. Hull characterized the tribe as having the face smoothly curved, (not tumid as in the Prorostomatini), vein R_{2+3} arising at a right angle just proximal to or opposite the r-m crossvein, and metepisternum and mediotergite bare. The Xeramoebini form a clade with the remaining tribes (clade 78) on the basis of a number of features which reverse in more distal clades, and one which does not, the convex posterior margin of the epandrium.

Most of the diversity within the subfamily Anthracinae is contained in the three most apomorphic tribes, the Anthracini, Exoprosopini, and Villini, found worldwide. These three tribes comprize a well-established monophyletic group characterized by wing venation (fig. 243), with R_{2+3} arising at 90° and distally, close to the r-m crossvein.

Tribe Anthracini Latreille

A tribe of 9 genera and just over 330 species, almost three-quarters (240 spp.) belong to the genus *Anthrax* Scopoli, which is found in all biogeographic regions. The remaining smaller genera are more restricted and occur in only one or two biogeographic region(s). The diagnostic feature of the tribe is the circlet of hairs surrounding the apex of the antennal flagellum (fig. 21). This apomorphy is present in all genera except *Walkeromyia* Paramonov (Hull, 1973), and the relationships of this genus are in need of clarification. Other features of the tribe include: flagellum of two flagellomeres with apical style, face not produced anteriorly, palps one-segmented, median, ventral ridge on cibarium, posterior eye margin with indentation and bisecting line, preprocoxal bridge present, basicosta produced, but not spinelike as found in Exoprosopini and Villini, wing vein R_{2+3} arising at 90° near the r-m crossvein, laterotergite and mediotergite bare, pulvilli and fore tarsal claws not reduced in size, male hypandrium fused or absent, female with sand chamber, tergite 8 with anterior apodeme reduced or absent, female sternite 8 small, consisting of two or three sclerotized regions.

The Exoprosopini and Villini form a compelling clade, supported by the following features: subgena with two troughs exending posteriorly from posterior tentorial pits (fig. 217); cibarial arms joined, basicosta spinelike; laterotergite and mediotergite haired; pulvilli short, resembling teeth of the tarsal claw (figs. 303–304) in Exoprosopini; foreclaws reduced in size (figs. 302–303), and female sternite 8 a large concave sheet (figs. 435, 468).

Tribe Exoprosopini Becker

A speciose tribe of relatively large flies belonging to 9 genera with a total of almost 650 species. Over half the species belong to *Exoprosopa* Macquart, which is found in all biogeographic regions, and of the remaining species over 100 belong to *Ligyra* Newman, which is also found in all biogeographic regions. These two large genera are separated by a rather superficial character, the presence or absence of an inter-radial crossvein.

This tribe is closely related to the Villini with a characteristic of the tarsal claws distinguishing the two. The Exoprosopini have reduced pulvilli which are conical in shape (fig. 304), and have been mistaken for a tooth on the tarsal claw in the past. Most often the Exoprosopini have a two flagellomeres with an apical style (fig. 20) and most often the Villini have one flagellomere with apical style (Hull, 1973). Both tribes lack a proprecoxal bridge which is present in the Anthracini. The exoprosopine genera *Atrichochira* Hesse and *Micomitra* Bowden have one flagellomere with apical style and some members of the the villine genus *Thyridanthrax* Osten Sacken have two flagellomeres with an apical style.

Separating the Exoprosopini as a subfamily, as has been the practice until recently (for example, see Hull, 1973, and Zaytsev, 1992) renders the remainder of the Anthracinae paraphyletic.

Tribe Villini Hull

A large tribe containing 27 extant genera and over 750 species, with almost one-third belonging to *Villa* Lioy which is found in all biogeographic regions. Twenty of the genera of the Villini are found in the New World. Characters distinguishing this tribe from the Exoprosopini are listed above, in particular they have reduced but rounded pulvilli. Clearly there is a pressing need to test the monophyly of each of the two tribes using as many characters as possible.

Laminanthrax Greathead has a single flagellomere characteristic of this tribe, but large, padlike pulvilli and bare laterotergite, and its tribal position requires clarification.

DISCUSSION

I have used the cladogram of figure 7 to formulate a revised, phylogenetic classification of the Bombyliidae, however the cladogram may also be used to trace the evolution of features within the Bombyliidae. In future works I plan to trace such characteristics as host preference and oviposition behavior in the evolution of the Bombyliidae. Here I wish to discuss the evolution of two complex morphological features in the Bombyliidae as indicated by the cladogram. I urge caution in interpreting the evolution of these structures from the cladogram; the form of the cladogram is dependent, in part, on these characters as they were part of the evidence used in its construction.

FOSSIL HISTORY

The cladogram generated here was based on extant species only: no fossils were included. There are over 50 species of fossil Bombyliidae known, recently reviewed by Zaytsev (1987). Many are rock fossils from the Florrisant shales of Colorado, largely consisting of body smudges and wing imprints, however there are better preserved specimens from amber deposits in the Baltic and the Dominican Republic (Hennig, 1966b; Schlüter, 1976).

There has been a recent debate over the importance of fossils in phylogenetic inference. Some authors (Nelson, 1978; Patterson, 1981) have relegated fossils to a secondary status in comparison to extant forms in phylogenetic analysis, others (paleontologists) consider that fossils are important, and their inclusion can alter hypotheses derived from data on extant animals (Gauthier et al., 1988; Donoghue et al., 1989). As De Pinna (1992) has argued, the inclusion of fossils in a phylogenetifc hypothesis can influence tree topology just as the inclusion of living groups can. The arguments for including fossils in a phylogenetic analysis are not restricted to fossils, but could be applied to any taxon, extinct or extant. The addition of a taxon to a data matrix can affect its topology by presenting novel character combinations. In addition, the inclusion of additional taxa can change our hypotheses of character evolution by presenting new intermediate states. Fossils were not considered in this analysis because of the small percentage of characters for which they could be scored, a problem which is particularly acute in the rock fossils. They were not excluded because I subscribe to the view that their cladistic information is inferior.

The age of appearance of the subfamilies of Bombyliidae as fossils does lend weak support to the phylogenetic scheme proposed here. I emphasize the term "weak" support because there is no reason to expect that taxa should be first fossilized in the order in which they are generated in phylogeny. We should expect, due to the stochastic nature of the fossilization process, that some relatively early taxa may not be fossilized until after some of their descendants. However, there is some empirical support for a positive correlation between cladistic rank of fossil taxa and their age (MacFadden, 1992; Norell and Novacek, 1992). Given a phylogenetic hypothesis then, it is possible to predict that some taxa existed during a particular geological age, but no trace of them has yet appeared in the fossil record (Norell, 1992).

Given the cladogram of Bombyliidae presented here, I would predict that the Mythicomyiinae should be the first Bombyliidae found in the fossil record, being the most plesiomorphic subfamily. This is in fact the case; the oldest Bombyliidae is the Jurassic mythicomyiine *Palaeoplatypygus zaitsevi* from Siberia (Kovalev, 1985). From the Cretaceous, only fossil Usiinae and Mythicomyiinae, two of the most plesiomorphic subfamilies, are known (Zaytsev, 1987). The next oldest Bombyliidae are from the Eocene, where both Mythicomyiinae and Cythereinae are known (Hennig, 1966b). By the Oligocene, many subfamilies are known (Zaytsev, 1987), including members of the most advanced subfamily Anthracinae (Cockerell, 1916).

The age of first appearance of particular Bombyliidae subfamilies in the fossil record allows us to make some rather imprecise inferences regarding the absolute timing of cladogenetic events. It appears that the Bombyliidae, and therefore the Asiloidea, probably arose in the Jurassic, and most of the cladogenesis of Bombyliidae subfamilies occurred prior to the Oligocene. This is in accordance with Woodley's (1989) conclusion that the Brachycera probably arose during the Triassic. Because Bombyliidae with sand chambers and concave occiputs were present in the Eocene, it is likely that much of this cladogenesis occurred in the Mesozoic, and that many of the basal clades in the family had their genesis during the Cretaceous. The Cretaceous is the time of origin and diversification of the Angiosperms (Pellmyr, 1992). These common ages of diversification are consistent with the idea that the Bombyliidae diversified along with the main adult food source, pollen and nectar from the flowering plants. The other Endopterygote orders also underwent major diversification beginning in the Cretaceous, thus larval food sources for the Bombyliidae also became more plentiful and diverse at this time (Kukalova-Peck, 1991).

EVOLUTION OF THE SAND CHAMBER

The sand chamber is a unique, complex adaptation for oviposition found only in some derived subfamilies of Bombyliidae (Schremmer, 1964; Muhlenberg, 1971b;

Theodor, 1983). Females of the subfamilies Bombyliinae, Mariobezziinae, Oniromyiinae, Cythereinae, Lomatiinae, Tomomyzinae, and Anthracinae which possess a sand chamber (here denoted the sand chamber subfamilies) have a complex mode of oviposition in which they first alight and charge the sand chamber with small particles of the substrate, using vigorous movements of tergites 8, 9, and 10. The particles are used to individually coat the eggs in sand as they are discharged from the common oviduct into the sand chamber. The females fly to a suitable oviposition site and oviposit by flicking coated eggs with vigorous motions of the abdomen while hovering.

The sand chamber has evolved once, in the common ancestor of clade 42, but has been lost a number of times. Theodor (1983) considered the sand chamber to be absent in the Eclimini and Mariobezziinae, however I found a modified sand chamber in these groups, as discussed below. The sand chamber is formed primarily by a extension of the lateral margins of tergite 8, in concert with the invagination and movement of sternite 8 into a more vertical position. Although this position of tergite 8 allowed the sand chamber to increase in volume, it is probably possible for a sand chamber to function with tergite 8 merely invaginated, and not turned vertically. The features of the sand chamber all appear at clade 42, and I wish to discuss the reduction and modification of the various components of this feature in more highly derived subfamilies.

Tergite 8 forms the dorsal and lateral walls of the sand chamber (Mühlenberg, 1971a). In plesiomorphic Bombyliinae it appears fully modified, extending laterally around the pleural regions of the abdomen, a rounded median apodeme on the anterior margin, and a brush of long hairs on the posterior margin (fig. 437). In some Eclimini the anterior apodeme becomes shorter and dorsoventrally flattened (fig 441), and this also occurs independently in the Anthracinae (fig. 445), and other subfamilies. The anterior brush of hairs becomes reduced in *Mariobezzia* (fig. 443), but otherwise these flies have a well-developed sand chamber.

I found sternite 8 to be invaginated in all sand chamber subfamilies. It is usually composed of three separate sclerites (figs. 461–467), and forms the anterior and ventral walls of the sand chamber. The common oviduct opens just above sternite 8, between the two anterior lobes. The Eclimini possess a variety of shapes of sternite 8 (figs. 456–460), and this led Mühlenberg (1971b) to the conclusion that they had an independently derived sand chamber and Theodor (1983) to the conclusion that they had no sand chamber at all. Sternite 8 of *Eclimus*, *Lepidophora*, and *Cyrtomyia* has reversed to a plesiomorphic shape, and sternite 8 of *Paratoxophora* and *Marmasoma* has been modified into a small, concave sheet with a median ridge and a long brush of hairs on the anterior margin. Sternite 8 in the Exoprosopini and Villini has been modified into an enlarged, rather evenly sclerotized concave sheet with a long brush of hairs on the anterior margin (figs. 435, 468, 483). This form is superficially similar to that found in *Paratoxophora* and *Marmasoma*.

The acanthophorite spines are an important feature of the sand chamber, and the acanthophorites become closely associated or fused with tergite 9 in species with a sand chamber. Adisoemarto and Wood (1975) first considered acanthophorite spines a groundplan feature of the Asiloidea, and they do occur in some members of every family of Asiloidea. The idea that acanthophorites were present in the most plesiomorphic Asiloidea is not in accordance with the phylogeny presented here, in which acanthophorite spines do not appear until clade 41 in Bombyliidae (Heterotropinae and more highly derived subfamilies). More plesiomorphic subfamilies lack these spines, as do the Hilarimorphidae. Thus the cladogram supports the interpretation that the acanthophorites have evolved at least twice in the Asiloidea, once within the Bombyliidae, and once in the other families. The acanthophorites are not distinguishable in the Mythicomyiinae, Oligodraninae, Usiinae, and Toxophorinae, and have either been lost entirely or fused indistinguishably with tergite 9. In the Lordotinae the acanthophorites are separate from tergite 9, however they lack acanthophorite spines. The Heterotropinae have well-developed acanthophorites separate from tergite 9 and acanthophorite spines are present. Among the sand chamber subfamilies I examined, the acanthophorite spines have only been lost in the Antoniinae, *B. androgynus* and *Cyllenia maculata*.

Evolution of the Postcranium

The most striking feature of the apomorphic subfamilies of Bombyliidae is the modified, deeply concave postcranium (fig. 133). This feature is just one aspect of the evolution of the postcranium I wish to discuss.

The concave postcranium initially occurs at clade 57, and becomes fully developed at clade 68, to include the subfamilies Lomatiinae, Anthracinae, Tomomyzinae, and Antoniinae. The subfamilies Mariobezziinae, Oniromyinae, and Cythereinae have postcrania with intermediate levels of concavity, illustrated in figures 207–212. A number of other structures become modified in association with the changing shape of the bombyliid postcranium. As the postcranium becomes more deeply concave, the tentorial arms become broader in lateral view (cf. figs. 163 and 201). Initially found at clade 57 also, the occipital foramen becomes divided into a dorsal and ventral orifice, and this apomorphy defines the Tomophthalmae.

Most plesiomorphic Bombyliidae with flattened or slightly tumid occiputs have paired internal occipital apodemes extending dorsolaterally from the occipital foramen. These apodemes become lost in most highly derived forms with concave occiputs, however are present in *Pantarbes* and the Lomatiinae. As the postcranium becomes more concave, the dorsal occiput becomes lobed, and these lobes eventually abut behind the ocellar tubercle in the Lomatiinae, Tomomyzinae, Anthracinae, and Antoniinae except in *Myonema*. The posterior tentorial pits also become modified from a simple rounded form to elongate in the Lomatiinae, Tomomyzinae, Anthracinae, and Antoniinae. The occipital pockets, often well developed in plesiomorphic Bombyliidae, are only seen above clade 57 in the Mariobezziinae and *Pantarbes*.

Associated with the development of a concave postcranium are modifications of the prothorax to maintain the articulation between head and thorax. The elongation of the cephalingers of the second laterocervical sclerites begins at clade 57 and they become fully elongate at clade 68. The tips of the cephalingers articulate with the occipital condyles between the dorsal and ventral occipital foramina. I did not score this feature as a separate character because I believe it is fully dependent on the form of the postcranium. The propresternum also becomes elongate and arrow-shaped at clade 68. The postcervical sclerite disassociates from the proepisternum and aligns with the posterior margin of the second laterocervical sclerite.

The indentation of the posterior eye margin has arisen independently at least five times in bee fly evolution. It has appeared twice in the Bombyliinae (*Eurycarenus* and *Heterostylum*), and occurs in other members of that subfamily such as *Triploechus* and *Efflatounia*. An indented posterior eye margin has also appeared a number of times in the Tomophthalmae; in the Lomatiine clade 70 and in all Lomatiinae, except *Peringueyimyia*; in *Antonia* of the Antoniinae and in all tribes of Anthracinae except the Prorostomatini (clade 77). Within the Antoniinae and Anthracinae the indentation of the posterior eye margin is associated with a short line dividing the compound eye facets.

CONCLUSIONS

I emphasize that this study represents a framework for the phylogenetic classification of the Bombyliidae and it is my hope that it will provide a basis for further studies. It is important that future researchers test my hypotheses with additional taxa and characters. The family contains over 230 valid genera and over 4500 species; thus there are many interesting and rewarding avenues to be explored.

It is essential that we learn as much as we can about the most plesiomorphic Mythicomyiinae, which will probably be found among the Psiloderini, as these are the most plesiomorphic Bombyliidae. Most mythicomyiines are highly modified, at least partly due to their small size, however the most primitive ones may provide further insights about the relationship of the entire subfamily to the other Bombyliidae. The curious larvae, larval habit, and male genitalia of the Heterotropinae are puzzling to me, and their relationship to the remaining Bombyliidae would benefit from additional scrutiny. Further analysis of the limits of the Lordotinae and Crocidinae and placement of *Sericosoma* are required, and further evidence on the monophyly of the Bombyliinae and Cythereinae is needed. A more detailed scrutiny of the relationships between the most plesiomorphic anthracine tribes is also a priority for future work.

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APPENDIX 1

Reanalysis of Data Presented in Woodley (1989)

Data matrix used in the reanalysis of data presented by Woodley (1989). The data comprise characters 24–3.13 of Woodley, in the same order as he presented them, except that 27 and 3.1 are united here in character 4.

	1	1111111112	22
Character no.	1234567890	1234567890	12
Rhagionidae	0000000000	0000000000	00
Acroceridae	1111011100	0000000000	01
Nemestrinidae	1111100000	0000000000	00
Asilidae	1110000011	1000011100	00
Scenopinidae	1110010011	1101100000	01
Therevidae	1110000011	1110000000	00
Apioceridae	1110000011	1000000011	00
Mydidae	1110000011	1000000011	11
Bombyliidae	1111000011	0000000000	00
Empididae	1110000010	0000000000	01

APPENDIX 2

Musculature of the Male Genitalia: Reanalysis of Ovchinnikova (1989)

Here I provide the details of my reanalysis of the data from male genital musculature presented by Ovchinnikova (1989). My nomenclature for the muscles follows hers and autapomorphies at the family level have been retained (Yeates, 1992b). These data comprise the gain, loss, and division of muscles and the modification of their points of attachment. I have scored the family Rhagionidae as an outgroup. Ovchinnikova also examined a number of stratiomyids, however these are inappropriate as outgroups because they have diverged considerably from the type of male genital musculature found in rhagionids, nemestrinoids and asiloids. In particular they have lost muscles M30, M31, amd M32 and have a single muscle M5. I have scored the families Asilidae (Dasypogoninae), Apioceridae, Therevidae, Mydidae, Bombyliidae (Bombyliinae), Nemestrinidae, and Acroceridae. Ovchinnikova did not include scenopinids in her study and their examination is a worthwhile goal for future research. Future research into the comparative morphology of the male genitalia of the Bombyliidae should include subfamilies more plesiomorphic than the Bombyliinae.

Character analysis

1. Protractor of aedeagal sheath (M1). Primitively present, acrocerids and mydids have lost M1.

2. Muscles M1 and M2 of the aedeagal sheath. Plesiomorphically M1 functions as the retractor and M2 the protractor but in the Bombyliidae these roles are reversed; M1 becomes the protractor and M2 the retractor. In addition, the origin of M2 moves from distal to basal on the gonocoxae and the insertion moves from the ventrobasal region to the outer ventral region of the aedeagal sheath. The origin of M1 moves to a more distal position.

3. Retractor of ejaculatory apodeme (M30). Only the Mydidae lack M30.

4. Protractor of ejaculatory apodeme (M32). Only the Mydidae lack M32.

5. Flexor of hypandrium (M33). This muscle is apomorphically absent in the Nemestrinidae, Acroceridae, Bombyliidae and Therevidae that Ovchinnikova examined. This character is at least partially dependent on the presence or absence of the hypandrium.

6. Flexor of hypandrium (M33). Muscle M33 is usually present as a single pair, however in the Mydidae and Apioceridae two pairs are present.

7. Adductor of lateral process of gonocoxa (M38). Present in asilids, apiocerids and mydids. These muscles attach to distal lobes of gonocoxae which are not homologous with gonostyli.

The following two characters concern muscles plesiomorphically inserted on the gonostyli. Two families scored here, Acroceridae and Mydidae, consistently lack gonostyli, hence their lack of one or both of these muscles.

8. Adductor of gonostyli (M27). Apomorphically absent in the Mydidae only.

9. Abductor of gonostyli (M28). Apomorphically absent in the Acroceridae and Mydidae.

10. Tergosternals (M5). Plesiomorphically there are two pairs of tergosternals, $M5^1$ and $M5^2$. In asilids, apiocerids, and therevids there are three pairs, $M5^1$, $M5^2$, and $M5^3$, the additional pair inserted on aedeagus. From its position, M5 appears homologous to $M5^1$. Ovchinnikova considered this an indicator of relationship between the three families. The point of insertion of $M5^3$ on the aedeagus differs slightly in the three families where it occurs. In therevids it inserts on the ejaculatory apodeme, in asilids and apiocerids its insertion is distal to the basiphallus. The Mydidae have only one pair of tergosternals and this appears to be an additional apomorphy for the family.

11. Retractors of cerci (M29). One pair of muscles M29 is plesiomorphic, the Bombyliidae have two pairs.

12. Retractor of epandrium (M19). The Therevidae and Nemestrinidae have two pairs of muscles M19, double the usual complement.

13. Retractor of epandrium (M36). The muscle M36 is present only in the Acroceridae and Bom-

byliidae. A single muscle is present in Bombyliidae whereas a symmetrical pair is present in Acroceridae. The single muscle in Bombyliidae has its origin on the left-hand side of sternite 8 and its insertion on the right hand side of the epandrium.

14. Retractor of epandrium (M19). These muscles are usually symmetrical but were found to be assymetrical in the Bombyliidae. This muscle is paired in *Hemipenthes* and *Anastoechus* but fused into one bundle in *Villa*. In *Hemipenthes* the left bundle is larger than the right and in *Anastoechus* the right bundle is larger than the left.

This asymmetry was only found in the Bombyliidae, and the muscles function to rotate the genitalia about the long axis of the body. *Hemipenthes* and *Villa* also have asymmetrical retractors of the hypandrium (M18). In this muscle pair the left is broad and short in *Villa* and the right is broad and short in *Hemipenthes*. The asymmetrical nature of M18 may be considered an apomorphy of *Villa* + *Hemipenthes*. It is unfortunate that Ovchinnikova did not examine Bombyliidae with symmetrically disposed male genitalia.

15. Retractor of hypandrium (M18). Only the Therevidae possess retractors of the hypandrium, and two pairs are present.

16. Retractor of hypandrium (M20). M20 is plesiomorphically absent, but present in the Asilidae, Apioceridae, and Mydidae.

Analysis of this data set with Hennig86 (Farris, 1988) produces two cladograms. Their consensus is shown in figure 2a, and the characters are mapped onto one of the most parsimonious cladograms in figure 2b. The other most parsimonious cladogram differs only in that it unites the Asilidae and Apioceridae, supported by character 10. See text for further discussion of these results.

Data matrix

	1	111111
Character no.	1234567890	123456
Rhagionidae	0000000000	000000
Nemestrinidae	0000100000	010000
Acroceridae	1000100010	001000
Bombyliidae (Bombyliinae)	0100100000	101100
Asilidae (Dasypogoninae)	0000001001	000001
Apioceridae	0000011001	000001
Therevidae	0000100001	010010
Mydidae	1011011110	000001

APPENDIX 3

Female Genitalia: Reanalysis of Mühlenberg (1971b)

Here I present a reanalysis of the data presented in Mühlenberg (1971b). A few comments are in order concerning my interpretation of the characters and their states. Fifty-six numbered characters appeared in the original data matrix; most were binary, however some were divided into multiple states, for example character 15 has five (15a–e). I have assumed that Mühlenberg considered states of a character to be additive when two subcategories of a numbered character are joined by a hatched bar in his data matrix (e.g., 16a and b). When lettered character states are completely separate in the data matrix (e.g., character states 11a and b), I assume that Mühlenberg considered them nonadditive (characters 2, 11, 15, 20, 37). Only character 26 poses a problem to this interpretation, where 26b and c are additive and 26a forms a separate apomorphic state. This was coded in two columns of the matrix with 26a in one column as a binary character and 26b and c in another column treated as a three-state additive character.

Two inconsistencies were found in Mühlenberg's character matrix as I rescored the data: (1) he scored *Eclimus* as having the advanced states b and c of character 20, I have coded it as 20c; (2) character 26a is missing from the matrix but present in the accompanying cladogram. Advanced states observed by Mühlenberg were indicated by a black dot or bar in the taxon column in his figure 4, and those assumed but not observed were indicated by vertical hatching. These "assumed" apomorphies appear to be muscles scored as present because of the structure of sclerotized parts, however not directly observed due to inadequate preservation of the material. I have scored Mühlenberg's assumed character states as actually present. Mühlenberg's original matrix includes data from 25 species belonging to 25 genera from 13 currently recognized subfamilies. *Heterotropus*, tentatively included in the original data matrix with many missing entries, was excluded from this reanalysis.

The rescored data matrix was analyzed by Hennig86 using the implicit enumeration (ie) command, which outputs all most parsimonious trees, using an all zero outgroup. This returned 48 trees of length 87 steps, ci 0.85 and ri 0.94. Mühlenberg's published tree was among those found (tree # 34). The consensus of the 48 trees is shown in figure 4. See text for further discussion.

Data Matrix

Character no.	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555 1234567
Outgroup	0000000000	0000000000	0000000000	0000000000	0000000000	0000000
Platypygus	0001010110	0000000000	0000000000	000000000?	0?0?000000	00000?0
Usia	0001100000	0000000000	0000000011	0000000000	0000000000	0000000
Systropus	0001100001	0000100000	0000010000	000000000?	0?0?000000	00000?0
Toxophora	0001100000	0000000000	0000010000	1000000000	0101000000	0001011
Phthiria	0001000000	0000000000	0000001000	0000100001	0101000000	0000010
Oligodranes	0001100000	0000000000	0000001000	1000100001	0101000000	0000010
Geron	0001100000	0100010000	0010001000	0000000001	0101000001	0000010
Eclimus	0001010001	1101210003	0000002000	0000000001	01?10?0001	1001?1?
Bombylius	0001011001	1110220011	1000002000	0001000001	0111010001	1001111
Systoechus	0001011001	1110220011	1000002000	0001000001	0111010001	1001111
Anastoechus	0001011001	1110221011	1100002000	0001000001	0111010001	1001111
Amictus	1001010001	1110220011	0000002000	0100000011	0111010001	1001111
Cyllenia	1001010001	1110220012	0000002000	0100000011	0111010001	1001111
Cytherea	1001010001	1110320011	0000002000	0100010001	0111010001	1001111
Callistoma	1001011001	1110320011	0000002000	0100000001	0111010001	1001111
Conophorus	?011010001	1110220001	0000002000	0001010001	0111110001	1001111
Prorachthes	?011010001	1110220004	0000002000	0000000001	0111010001	1001111
Lomatia	2101010001	1110220101	0000002000	0000000001	0111010001	1001111
Petrorossia	2201010001	1110220001	0001002100	0010000001	0111010111	1101111
Spongostylum	2201010001	1110220001	0001002100	0000000101	0111010111	1101111
Anthrax	2201010001	1110220001	0001002100	0000000101	0111010111	1101111
Villa	2201010001	2120220001	0000102100	0000001001	0121121001	2011111
Hemipenthes	2201010001	2120420001	0000102100	0000002001	0121121001	2011111
Thyridanthrax	2201010001	2120420001	0000102100	0000002001	0121121001	2011111
Exoprosopa	2201010001	2120520001	0000102100	0010001001	1121121001	2011111

APPENDIX 4

Data Matrix for the 87 Taxa and 154 Characters

Character no.

1	10	20	30
31	40	50	60
61	70	80	90
91	100	110	120
121	130	140	150

Rhagio

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0

Arthroceras

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0

APPENDIX 4—(*Continued*)

Hirmoneura
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1
0 0 0 0

Trichophthalma
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 1 0 1
0 0 0 0

Lasia
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 0 2 - - 0 0
0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 1 0 0 0 0 1 1 1
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 1 0 0 0
1 - - 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 1 0 1 0 0 0 1 1 1
0 0 0 0

Eulonchus
0 0 0 0 3 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 1 1 - 0 0
0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 1 0 0 0 0 1 1 1
1 - - 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 1 0 1 0 0 0 1 1 1
0 0 0 0

Leptogaster
0 0 0 0 2 0 1 0 0 0 1 1 0 0 0 0 1 0 0 0 0 0 1 1 1 1 0 - 1 0
0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 1 1 0 1 1
0 0 1 0 0 1 1 0 0 0 1 0 0 0 2 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 1 0 1 0 0 0 0 2
0 1 0 0

Dioctria
0 0 0 0 2 0 2 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 1 1 1 - 0 0
0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 2
0 1 0 0

Stenopogon
0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 2 1 0 0 0 0 0 1 0 1 0 0 0 0 0
0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 2 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 1 1 0 0 0 1 0 0 0 ? ? ?
? ? ? ?

Leptarthrus
0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0
0 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1

APPENDIX 4—(*Continued*)

0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 1 0 0 0 ? ? ?
? ? ? ?

Caenotus
0 0 0 0 2 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 - 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 1 0 1 3
0 1 0 1 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 1 0 1 0 0 0 0 0 ? ? ?
? ? ? ?

Prorates
0 0 0 0 2 0 1 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 1 0 - 1 0
0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 2 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 1 0 0 0 0 2 0 0 0 0 1 2 0 0 0 0 2 1 0 1 0
0 1 0 1 0 0 0 0 1 0 0 0 0 2 0 0 0 0 1 1 0 1 0 0 0 0 1 ? ? ?
? ? ? ?

Scenopinus
0 0 0 0 3 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 - 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1
0 0 1 0 0 1 0 0 2 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 1 0 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 2 0 1 0
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 1 0 1 0 0 0 0 0 2
1 1 0 1

Propebrevitrichia
0 0 0 0 3 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 - 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1
0 1 1 0 0 1 0 0 2 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 1 0 0 1 1 2 0 0 0 0 1 1 0 0 0 0 0 1 0 1 0
0 1 0 1 0 0 0 0 1 0 0 0 0 2 0 0 0 0 1 1 0 1 0 0 0 0 0 ? ? ?
? ? ? ?

Thereva
0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 - 0 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 1
1 1 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0
0 1 0 1 2 0 0 0 1 0 0 0 0 2 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 2
1 1 1 1

Phycus
0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 1
1 1 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0
0 1 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 1 0 0 0 0 0 2
1 1 1 1

Bonjeania
0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 1
1 1 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 3
0 1 1 1 1 0 0 0 1 0 0 0 0 2 0 0 0 0 1 1 0 0 0 1 0 0 1 0 0 2
1 1 1 1

Apsilocephala
0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0

APPENDIX 4—(*Continued*)

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0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 1 1
0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 0 0 0 0 0 0 0
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 0 0 1 ? ? ?
? ? ? ?
```

Apiocera

```
0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 1 0 0 0 1 1 0 0 0 1 0 0 0 0 0 2
0 1 0 0
```

Neorhaphiomidas

```
0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0
0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 1 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0
1 - - 1 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 0 0 0 ? ? ?
? ? ? ?
```

Apiophora

```
0 0 0 0 2 0 1 0 0 0 1 1 1 0 0 2 0 0 0 1 0 0 0 0 0 1 1 - 1 0
0 0 0 0 0 0 1 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0
0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 1 1
0 0 0 0 1 0 1 0 0 0 0 0 0 0 2 0 0 0 0 1 2 0 0 0 0 1 0 0 1 1
1 - - 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 0 0 0 0 0 ? ? ?
? ? ? ?
```

Mydas

```
0 0 0 0 2 0 1 0 0 0 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 1 1 - 1 0
0 0 0 0 0 0 1 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 1 0 0 0 0 0 0 1 1
0 0 0 0 1 0 1 0 0 0 0 0 0 0 2 0 0 0 0 1 2 0 0 0 0 2 0 0 1 1
1 - - 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 2
0 1 0 0
```

Hilarimorpha

```
0 0 0 0 2 0 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 - 1 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0
0 0 0 1 0 1 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 0 0 0 ? ? ?
? ? ? ?
```

Apystomyia

```
0 0 0 0 2 0 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 2 0 0 0 0 0 0 0 1 0
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 0 0 0 ? ? ?
? ? ? ?
```

Mythicomyia

```
0 0 0 0 2 0 2 0 0 1 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 2 1 - 1 0
0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 1 0
0 0 0 0 1 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 1 1 1 1 0 0 0 0 1 1 1 1 1 0 0 0 0 0 1
```

APPENDIX 4—(*Continued*)

0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Glabellula
0 0 0 0 2 0 1 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 0 2 1 - 1 0
0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 0
0 0 0 1 1 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 1 1 1 1 0 0 0 0 1 2 0 1 1 0 0 0 0 0 1
0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 2
0 0 0 0

Acridophagus
0 0 0 0 2 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 2 1 - 0 0
0 0 1 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 1 0
0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 1 1 1 1 0 0 0 0 1 1 1 1 1 0 0 2 0 0 1
0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 1 1 0 0 ? ? ?
? ? ? ?

Paraconsors
0 0 0 0 2 0 2 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 0 2 1 - 1 0
0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 1 1 0 1 0 0 0 1 0
0 0 0 1 1 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 1 1 1 1 0 0 0 0 1 2 0 1 1 0 0 2 0 1 1
0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Cephalodromia
0 0 0 0 2 0 1 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0 0 0 0 2 1 - 1 0
0 1 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 1 0
0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 1 1 1 1 0 0 0 0 1 1 1 1 1 0 0 0 0 0 1
0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Geron grandis
0 0 0 0 3 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 1 0 0 1 0 0 0 1
0 1 0 1 0 0 0 0 0 1 0 0 0 2 0 0 1 0 0 1 0 0 1 0 0 0 0 1 0 ?
? ? ? ?

Geron albaria
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 1 0 0 1 0 0 0 1
0 1 0 1 0 0 0 0 0 1 0 0 0 2 0 0 1 0 0 1 0 0 1 0 0 0 0 1 0 ?
? ? ? ?

Phthiria
0 0 0 0 3 1 1 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 1 2 0 0 0 0 0 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Poecilognathus
0 0 0 0 3 1 1 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 1 - 0 0

APPENDIX 4—(*Continued*)

0 0 0 0 1 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 2 0 1 0 0 2 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 1 2 0 0 0 0 0 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Apolysis
0 0 0 0 2 2 2 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 1 0 ? ? ?
? ? ? ?

Usia
0 0 0 0 3 2 2 0 0 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 1 0 1 0 ?
? ? ? ?

Oligodranes
0 0 0 0 3 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 1 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Systropus
1 0 1 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 1 0 1 1 0 0 1 1 0 0 1 1
0 0 0 1 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 2 0 1 0 0 2 0 0 0 1
0 1 0 1 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 ?
? ? ? ?

Dolichomyia
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 1 - 0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 2 0 1 0 0 2 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 1 0 0 0 0 ? ? ?
? ? ? ?

Zaclava
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 1 0 0 0 0 0 2 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 1 - 0 1 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 1 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 2 0 1 0 0 2 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 0 0 1 0 0 0 0 ? ? ?
? ? ? ?

Toxophora virgata
1 0 1 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 1 1
0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 1 0 1 2 0 1 0 0 2 0 0 0
1 0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 1 0 0 0 1 0 0 1 0 1 0 0 1 0
? ? ? ? ?

APPENDIX 4—(*Continued*)

Toxophora compta
1 0 1 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 1 1
0 0 0 0 0 1 0 0 0 0 1 1 0 1 0 0 0 1 1 0 0 1 0 1 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 1 0 1 2 0 1 0 0 2 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 1 0 0 0 1 0 0 1 0 1 0 0 1 0 ?
? ? ? ?

Heterotropus
0 0 0 0 3 0 0 0 0 1 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 1
0 0 0 0

Desmatomyia
0 0 0 0 1 0 2 0 0 1 0 0 0 0 0 2 0 0 1 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0
0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 1 0 0 2 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 1 0 0 0 ? ? ?
? ? ? ?

Crocidium
0 0 0 0 2 0 1 0 0 1 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0
0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Lordotus
0 0 0 0 3 0 0 0 0 1 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 1 0
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Acrophthalmyda
0 0 0 1 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 1 0 ? ? ?
? ? ? ?

Bombylius major
0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 2
0 0 0 0

Bombylius androgynus
0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 1 0 1 1

APPENDIX 4—(*Continued*)

0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 0 0 0 0 0 1 0 2 0 0 0 0 0 1 0 1 0 0 0 0 1 0 0 1 0 2
0 0 0 0

Eurycarenus
0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 1 0 0 2 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Conophorus
0 1 0 0 2 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Aldrichia
0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Dischistus
0 0 0 1 2 0 0 0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 1 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Paratoxophora
1 0 0 0 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 1 0 1
0 1 0 1 2 0 1 0 0 1 0 1 0 1 0 0 0 1 1 1 0 0 0 0 1 0 1 ? ? ?
? ? ? ?

Eusurbus
0 0 0 0 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 1 0 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Heterostylum
0 0 0 0 2 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 2
? ? ? 0

APPENDIX 4—(*Continued*)

Marmasoma
0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 0 0 0 2 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1 0 0 0 1 0 1 1
1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 0 0 0 0 0 1 0 1
0 1 0 1 1 0 1 0 0 1 1 1 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Lepidophora
1 0 1 0 3 0 1 0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 0 0 1 0 0 1 0 0 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 ? 0 ?
? ? ? ?

Thevenetimyia
0 0 0 0 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 0 0 0 2 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 1 0 1 0 0 0 1 1 0 0 1 1 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Eclimus
1 0 0 0 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 1 0 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 1 0 1 0 0 0 1 1 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Cyrtomyia
1 0 0 0 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 1 0 0
0 0 0 0 0 0 0 0 0 0 2 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 1 0 1 0 0 1 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 0 0 1 0 0 1 0 0 0 1 0 0 0 0 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Cytherea
0 0 0 0 3 0 1 0 1 0 1 0 0 0 0 2 0 0 0 1 0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 1 0 1 1
0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 2 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 2
0 0 0 0

Sericosoma
0 0 0 0 2 0 1 0 1 1 1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 1 1 - 0 0
0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 0 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 ? ? ?
? ? ? ?

Corsomyza
0 0 0 1 3 0 0 0 0 1 1 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 0
0 0 0 0 0 0 1 0 1 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 1 0 0 0 0 0 0 1 1

APPENDIX 4—(*Continued*)

0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 2 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Mariobezzia
0 0 0 1 3 0 0 0 0 1 1 0 0 0 0 2 0 0 0 1 0 0 0 0 0 1 1 - 0 1
0 1 0 0 0 0 1 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 0 0 0 1 0 2 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Megapalpus
0 0 0 1 3 0 1 0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 1 0 1 1 - 0 1
0 0 0 0 0 0 1 0 1 0 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 2 0 1 0 0 1 0 2 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Neosardus
0 0 0 0 1 0 1 0 0 1 1 0 0 0 0 2 0 0 0 1 0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Pantarbes
0 0 0 0 1 0 1 0 1 1 1 0 0 0 0 2 0 0 0 1 0 0 0 0 0 1 0 - 0 2
0 0 0 0 0 0 1 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 2 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Oniromyia
0 0 0 0 2 0 1 0 0 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 1 - 0 1
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Amictus
0 0 0 0 1 0 1 0 0 0 1 0 0 0 0 2 0 0 0 0 0 0 0 0 0 1 0 - 0 1
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 0
0 0 1 0 0 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 0 1 0 1 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 1 1 0 ?
? ? ? ?

Cyllenia
0 0 0 0 2 0 1 0 0 0 1 0 0 0 0 2 0 0 0 1 0 0 0 0 0 0 0 0 0 1
0 1 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 1 0 0 1 2 1 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 0 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

APPENDIX 4—(*Continued*)

Enica
0 0 0 0 3 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 0 0 0 0 0 1 0 - 0 1
0 0 0 0 0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Peringueyimyia
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 0 1 0 - 0 2
0 0 0 0 0 1 2 1 1 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 1 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Docidomyia
0 0 0 0 3 0 0 0 0 0 1 1 0 0 0 0 0 1 0 1 0 0 0 0 0 1 0 - 0 2
0 0 0 0 0 1 2 1 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 2 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Myonema
0 0 0 0 0 3 0 1 0 0 0 1 1 0 0 0 2 0 1 0 0 0 0 0 0 0 0 1 0 0
1 1 0 1 0 0 1 2 0 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 1
1 0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 1 0 0 0 0 0 0
1 0 1 0 1 0 0 0 0 0 1 0 0 0 2 0 0 0 0 0 1 0 0 0 0 1 0 0 ? ?
? ? ? ? ?

Amphicosmus
0 0 0 0 3 0 0 0 0 0 1 1 0 0 0 2 0 0 0 1 0 0 0 0 0 1 0 - 0 2
0 0 1 0 0 1 2 1 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 2 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Tomomyza
0 0 0 0 3 0 1 0 0 0 1 1 0 0 0 2 0 0 0 1 0 0 0 1 0 1 0 - 0 2
0 0 1 0 0 1 2 1 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 1 0 0 0 0 1 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 1 1
0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 2 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Antonia
0 0 0 0 1 0 1 0 0 0 1 1 0 0 0 2 0 0 0 0 0 0 0 0 0 1 1 - 0 1
1 1 1 0 0 1 2 1 1 1 0 0 0 0 0 0 2 0 1 0 0 0 0 0 0 0 1 0 1 0
0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 1 0 0 0 1 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 0 1 0 0 0 2
0 1 0 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0 0 1 1 1 0 1 0 0 0 ? ? ?
? ? ? ?

Comptosia
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 1 1 - 0 2
1 0 0 0 0 1 2 1 1 1 0 1 0 0 0 0 1 0 1 0 1 0 0 0 0 0 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1

APPENDIX 4—(*Continued*)

0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Lomatia
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 1 0 - 0 2
1 0 0 0 0 1 2 1 1 1 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Ylasoia
0 0 0 1 3 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 - 0 2
1 0 0 0 0 1 2 1 1 1 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 1 1 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Ogcodocera
0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 - 0 2
1 0 0 0 0 1 2 1 1 1 0 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 1 1 0 0 1 0 0 0 0 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 1 0 1 0 0 0 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Anthrax
0 0 0 0 2 0 1 1 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 - 0 1
0 1 1 0 0 1 2 1 1 1 0 0 0 0 0 0 2 0 1 1 0 0 0 1 0 1 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 1 1 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0 0 1
0 1 0 1 0 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 2
0 0 0 0

Aphoebantus
0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 2 0 0 0 1 0 0 0 0 0 0 0 0 0 1
0 1 1 0 0 1 2 1 1 1 0 0 0 0 0 0 2 0 1 1 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 2 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

Exoprosopa
0 0 0 0 2 0 1 0 0 0 1 1 0 0 0 2 0 0 0 1 0 0 0 0 0 1 1 - 0 2
1 1 1 0 0 1 2 1 1 1 0 0 0 0 0 1 2 0 1 2 0 0 0 1 0 1 1 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 1 0 0 1 0 0 0 1 0 1 1
0 0 1 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1 1 0 0 0 1
0 1 0 1 2 0 1 0 0 1 0 3 0 1 0 0 0 1 1 1 0 0 0 0 1 1 0 1 0 ?
? ? ? ?

Petrorossia
0 0 0 0 2 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 - 0 2
0 1 1 0 0 1 2 1 1 1 0 0 0 0 0 0 2 0 1 1 0 0 0 0 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 1 0 0 1 0 0 1 0 0 0 0 1 0 1 1
0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 ?
? ? ? ?

APPENDIX 4—(*Continued*)

Plesiocera

0 0 0 0 2 0 1 0 0 0 1 0 0 0 0 2 0 0 0 1 0 0 0 0 0 1 1 - 0 1
1 0 1 0 0 1 2 1 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 0 0 1 1 0 0 0 1 0 1 1
0 0 1 0 0 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 1 0 0 ? ? ?
? ? ? ?

Villa

0 0 0 0 3 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 1 - 0 2
0 1 1 0 0 1 2 1 1 1 0 0 0 0 0 1 2 0 1 2 0 0 0 1 0 1 0 0 1 0
0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 1 0 0 1 0 0 0 1 0 1 1
0 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 1 0 0 0 1
0 1 0 1 1 0 1 0 0 1 0 3 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 1 0 2
0 0 0 0

APPENDIX 5

Character Fits for the Cladogram in figure 7

Format is as follows:
Character no.
steps on cladogram
consistency index × 100
retention index × 100

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
5	1	3	4	25	2	19	1	3	11	12	4	1	3	1
20	100	33	25	12	100	10	100	33	9	8	25	100	33	100
33	100	33	40	51	100	52	100	0	50	70	62	100	60	100
16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
12	1	7	4	7	1	1	2	10	1	15	15	3	5	7
16	100	14	25	14	100	100	100	10	100	13	6	33	20	28
75	100	53	57	71	100	100	100	35	100	58	58	60	63	85
31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
4	6	4	1	7	2	3	3	3	4	18	11	6	2	2
25	16	25	100	14	50	66	33	33	25	11	9	16	50	50
57	58	75	100	57	93	97	86	93	88	76	70	68	50	50
46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
1	7	1	5	6	4	3	1	2	3	1	11	2	2	4
100	28	100	20	33	25	33	100	50	33	100	9	50	50	25
100	68	100	82	55	25	33	100	66	66	100	33	66	94	72
61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
1	9	1	3	2	9	1	5	7	1	3	2	3	5	1
100	11	100	33	50	11	100	20	28	100	33	50	33	20	100
100	20	100	50	75	75	100	50	66	100	50	50	75	33	100
76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
9	5	2	3	10	1	13	9	1	2	2	12	2	1	5
11	20	50	33	10	100	7	11	100	50	50	8	50	100	20
52	33	75	93	50	100	57	46	100	66	0	70	50	100	42

APPENDIX 5—(*Continued*)

91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
3	5	10	1	1	5	1	2	1	1	2	2	4	3	17
33	20	10	100	100	20	100	50	100	100	50	50	25	33	11
60	42	72	100	100	33	100	50	100	100	66	80	66	75	65
106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
5	1	1	1	16	15	2	15	1	1	16	7	4	5	6
40	100	100	100	6	13	50	6	100	100	12	28	25	20	50
70	100	100	100	55	61	50	63	100	100	60	28	25	63	80
121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
2	1	2	1	13	1	4	1	3	3	1	10	1	15	4
50	100	50	100	15	100	25	100	33	33	100	30	100	13	25
75	100	80	100	76	100	92	100	50	95	100	90	100	81	25
136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
1	1	4	9	1	1	4	2	8	7	3	5	4	1	3
100	100	25	11	100	100	25	50	12	14	33	20	25	100	66
100	100	92	77	100	100	57	85	46	80	33	0	72	100	85
151	152	153	154											
2	1	1	2											
50	100	100	50											
66	100	100	66											

APPENDIX 6
Character Diagnoses for Clades in Figure 7

All character state changes are given in ACCTRAN optimization. Clade numbers correspond to those in figure 7. The format is as follows: x:y>z, where character number x changes from state y to state z on the node leading to the clade in bold.

Clade 1 (Nemestrinidae, Acroceridae + Asiloidea): 77:0>1, 80:0>1, 89:0>1, 90:0>1, 140: 0>1, 148:0>1, 150:0>1.

Clade 2 (Nemestrinidae): 27:1>0, 39:0>1, 61: 0>1, 105:0>1.

Clade 3 (Acroceridae + Asiloidea): 5:0>3, 26:0>1, 66:0>1, 110:0>1, 111:0>1, 122:0>1, 124:0>1, 134:0>2.

Clade 4 (Acroceridae): 23:0>2, 33:0>1, 67:0>1, 83:0>1, 88:0>1, 121:0>1, 142:0>1, 144:0>1, 149:0>1.

Clade 5 (Asiloidea): 5:3>2, 7:0>1, 77:1>0, 80: 1>0, 82:0>1, 97:0>1, 150:1>2.

Clade 6 (Asiloidea except Bombyliidae and Hilarimorphidae): 11:0>1, 76:0>1, 110:1>0, 139: 0>1, 148:1>0, 152:0>1.

Clade 7 (Mydidae + Scenopinidae): 29:0>1, 105: 0>2, 119:0>1.

Clade 8 (Mydidae): 55:0>1, 58:0>1, 111:1>2, 121:0>1, 134:2>1, 135:0>1.

Clade 9 (Mydidae except *Neorhaphiomidas*): 12: 0>1, 13:0>1, 20:0>1, 37:0>1, 39:0>1, 40: 0>1, 41:0>1, 80:0>1, 95:0>1, 110:0>1, 116: 0>2, 120:0>1.

Clade 10 (Scenopinidae): 10:0>1, 11:1>0, 100: 0>1, 117:0>1, 129:0>1, 142:0>1, 151:0>1, 154:0>1.

Clade 11 (Proratinae + Scenopininae): 59:0>1, 69:0>2, 70:0>1, 110:0>1.

Clade 12 (Scenopininae): 5:2>3, 60:0>1, 63:0>1, 103:0>1, 104:0>1.

Clade 13 (Apsilocephalidae + Therevidae + Apioceridae + Asilidae): 5:2>1, 7:1>0, 26:1>0, 43:0>1, 87:0>1, 92:0>1.

Clade 14 (Therevidae + Apioceridae + Asilidae): 27:1>0, 111:1>0, 144:0>1.

Clade 15 (Therevidae): 82:1>0, 91:0>1, 119:0>1, 151:0>1, 153:0>1, 154:0>1.

Clade 16 (Therevidae except *Phycus*): 105:0>1, 125:0>1, 129:0>1.

Clade 17: (Apioceridae + Asilidae) 76:1>0, 92: 1>0, 93:0>1, 105:0>2, 120:0>1.

Clade 18 (Asilidae): 7:0>1, 17:0>1, 23:0>1, 25: 0>1, 32:0>1, 34:0>1, 107:0>1.

Clade 19 (Asilidae except *Stenopogon*): 24:0>1, 82:1>0, 139:1>0.

Clade 20 (*Leptogaster* + *Dioctria*): 5:1>2, 26:0>1, 66:1>0.

Clade 21 (Hilarimorphidae + Bombyliidae): 10: 0>1, 41:0>1, 59:0>1, 69:0>2, 105:0>1.

Clade 22 (Hilarimorphidae): 15:0>2, 119:0>1.

Clade 23 (Bombyliidae): 42:0>1, 113:0>1, 120: 0>1, 145:0>1.

Clade 24 (Mythicomyiinae): 10:1>0, 11:0>1, 19: 0>1, 21:0>1, 26:1>2, 49:0>1, 53:0>1, 64: 0>1, 66:1>0, 102:0>1, 103:0>1, 104:0>1, 112:0>1, 114:0>1, 123:0>1.

Clade 25 (Mythicomyiinae except *Acridophagus*): 14:0>1, 29:0>1, 35:0>1, 42:1>0, 52:0>1.

Clade 26 (Mythicomyiinae except *Acridophagus* and *Cephalodromia*): 7:1>2, 49:1>0, 55:0>1, 148:1>0.

Clade 27 (*Glabellula*, *Paraconsors*): 65:0>1, 111: 1>2, 112:1>0.

Clade 28 (Bombyliidae except Mythicomyiinae): 5:2>3, 60:0>1, 69:2>0, 79:0>1.

Clade 29 (Bombyliidae except Mythicomyiinae and Oligodraninae): 41:1>2.

Clade 30 (Usiinae): 6:0>1, 16:0>1, 18:0>1, 35: 0>1, 69:0>1.

Clade 31 (Usiini): 6:2>1, 7:1>2, 146:0>1.

Clade 32 (Phthiriini): 60:1>0, 133:0>1.

Clade 33 (Bombyliidae except Mythicomyiinae, Oligodraninae and Usiinae): 7:1>0.

Clade 34 (Toxophorinae): 10:1>0, 78:0>1, 111: 1>2, 116:0>2, 143:0>1

Clade 35 (Toxophorini): 1:0>1, 3:0>1, 20:0>1, 42:1>0, 48:0>1, 57:0>1, 71:0>1, 72:0>1, 74: 0>1, 84:0>1, 87:0>1, 108:0>1, 136:0>1.

Clade 36 (Gerontini + Systropodini): 35:0>1, 49: 0>1, 145:1>0.

Clade 37 (Gerontini): 24:0>1, 69:0>1, 78:1>0, 105:1>0, 116:2>1, 130:0>1, 132:0>1, 137: 0>1.

Clade 38 (Systropodini): 68:0>1, 81:0>1, 85:0>1, 101:0>1.

Clade 39 (*Dolichomyia* + *Zaclava*): 42:1>0, 45: 0>1, 65:0>1.

Clade 40 (Bombyliidae except Mythicomyiinae, Oligodraninae, Usiinae and Toxophorinae): 16: 0>2, 60:1>0, 134:2>0, 138:0>1.

Clade 41 (Bombyliidae except Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae and Lordotinae): 105:1>0, 113:1>0, 139:0>1.

Clade 42 (Bombyliidae except Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae, Lordotinae and Heterotropinae): 5:3>2 , 7:0>1, 66:1>0, 125:0>1, 127:0>1, 130:0>1, 132:0>2.

Clade 43 (Bombyliinae): 10:1>0, 87:0>1.

Clade 44 (Conophorini): 2:0>1, 57:0>1, 90:1>0, 106:0>1, 110:1>0.

Clade 45 (Bombyliinae except Conophorini): 26: 1>0, 116:0>1.

Clade 46 (Bombyliinae except Conophorini and *Dischistus*): 5:2>3.

Clade 47 (Bombyliinae except Conophorini, *Dischistus* and *Eusurbus*): 93:0>1, 110:1>0.

Clade 48 (Acrophthalmydini and Bombyliini): 24: 0>1, 26:0>1.

Clade 49 (Bombyliini): 5:3>1, 50:0>1, 62:0>1, 80:0>1, 82:1>0.

Clade 50 (Bombyliini except *B. androgynus*): 7: 1>0, 113:0>1.

Clade 51 (*Paratoxophora*, *Heterostylum* and Ecliminae: 27:1>0.

Clade 52 (*Paratoxophora* + Ecliminae): 1:0>1, 28:0>1, 43:0>1, 132:2>1, 134:0>1.

Clade 53 (*Lepidophora* + *Cyrtomyia*): 51:0>1, 69: 0>1, 71:0>1, 74:0>1, 91:0>1, 125:1>0, 132: 1>0.

Clade 54 (*Thevenetimyia* + *Eclimus*): 44:0>1, 83: 0>1, 93:1>0; 105:0>1; 128:0.1, 132:1>0; 135: 0>1.

Clade 55 (Bombyliidae except Mythicomyiinae, Oligodraninae, Usiinae, Toxophorinae, Lordotinae, Heterotropinae and Bombyliinae): 41: 2>1.

Clade 56 (Crocidiinae): 26:1>0, 27:1>0, 90:1>0, 92:0>1.

Clade 57 (*Sericosoma* + Mariobezziinae + Oniromyiinae + Cythereinae + Lomatiinae + Antoniinae + Tomomyzinae + Anthracinae): 11: 0>1, 37:0>1, 39:0>1, 40:0>1, 41:1>0.

Clade 58 (Mariobezziinae + Oniromyiinae + Cythereinae + Lomatiinae + Antoniinae + Tomomyzinae + Anthracinae) : 5:2>3, 30:0>1, 113:0>1.

Clade 59 (Mariobezziinae): 4:0>1, 40:1>0, 66: 0>1, 106:0>2.

Clade 60 (*Corsomyza* + *Megapalpus*): 24:0>1, 41: 0>2, 125:1>2.

Clade 61 (Oniromyiinae + Cythereinae + Lomatiinae + Antoniinae + Tomomyzinae + Anthracinae): 10:1>0, 42:1>0, 87:0>1.

Clade 62 (Cythereinae + Lomatiinae + Antoniinae + Tomomyzinae + Anthracinae): 20:0>1, 93:0>1.

Clade 63 (Cythereinae): 27:1>0, 57:0>1, 113:1>0, 116:0>1.

Clade 64 (*Cytherea* + *Enica*) : 80:0>1, 96:0>1.

Clade 65 (*Neosardus* + *Pantarbes* + *Amictus* + *Cyllenia*): 5:3>1, 105:0>1, 110:1>0.

Clade 66 (*Amictus* + *Cyllenia*): 103:0>1, 104:0>1, 118:0>1.

Clade 67 (*Neosardus* + *Pantarbes*): 10:0>1, 42: 0>1.

Clade 68 (Lomatiinae + Antoniinae + Tomomyzinae + Anthracinae): 36:0>1, 37:1>2, 38: 0>1, 49:0>1, 75:0>1.

Clade 69 (Lomatiinae): 7:1>0, 11:1>0, 16:2>0, 18:0>1, 27:1>0, 30:1>2, 42:0>1, 83:0>1, 106:0>2.

Clade 70 (Lomatiinae except *Peringueyimyia*): 31:0>1, 47:0>1.

Clade 71 (*Ylasoia* + *Ogcodocera*): 20:1>0, 80:0>1.

Clade 72 (Antoniinae + Tomomyzinae + Anthracinae): 33:0>1, 73:0>1, 105:0>1.

Clade 73 (Tomomyzinae + Antoniinae): 12:0>1, 57:0>1, 76:0>1, 82:1>0.

Clade 74 (Antoniinae): 20:1>0, 31:0>1, 125:1>0, 127:1>0, 132:2>0, 134:0>2, 138:1>0, 139:1>0.

Clade 75 (Tomomyzinae): 27:1>0, 30:1>2, 68:0>1, 87:1>0, 93:1>0, 111:1>2.

Clade 76 (Anthracinae): 5:3>2, 113:1>0, 116:0>1.

Clade 77 (Anthracinae except Prorostomatini): 32:0>1, 47:0>2, 50:0>1.

Clade 78 (Anthracinae except Prorostomatini and Aphoebantini): 16:2>0, 30:1>2, 76:0>1, 105:1>0.

Clade 79 (Anthracini + Exoprosopini + Villini): 54:0>1, 56:0>1, 80:0>1, 113:0>1.

Clade 80 (Exoprosopini + Villini): 46:0>1, 50:1>2, 76:1>0, 82:1>0, 83:0>1, 96:0>1, 98:0>1, 132:2>3, 134:0>1.

Villa: 5:2>3.

Plesiocera: 31:0>1, 54:0>1, 83:0>1, 98:0>1, 110:1>0.

Petrorossia: no autapomorphies.

Exoprosopa: 12:0>1, 16:0>2, 31:0>1, 57:0>1, 99:0>1, 115:0>1, 125:1>2, 146:0>1.

Aphoebantus: 5:2>1, 11:1>0, 26:1>0, 27:1>0, 73:1>0, 110:1>0, 125:1>2.

Anthrax: 8:0>1, 30:2>1, 125:1>0.

Ogcodocera: 66:0>1, 82:1>0, 87:1>0.

Ylasoia: 4:0>1.

Lomatia: 134:0>1.

Comptosia: 27:0>1, 51:0>1, 57:0>1.

Antonia: 5:3>1, 32:0>1, 47:0>2, 62:0>1, 83:0>1, 113:1>0, 116:0>1, 120:1>2, 130:1>0, 141:0>1, 142:0>1, 144:0>1, 145:1>0.

Tomomyza: 24:0>1.

Amphicosmus: 7:1>0.

Myonema: 18:0>1, 26:1>0, 38:1>0, 57:1>0, 73:1>0, 76:1>0.

Docidomyia: 7:1>0, 16:2>0, 18:0>1, 33:1>0, 57:1>0.

Peringueyimyia: 24:0>1, 62:0>1, 118:0>1.

Enica: 11:1>0, 71:0>1, 111:1>2.

Cyllenia: 5:1>2, 26:1>0, 32:0>1, 38:0>1, 93:1>0, 113:0>1, 117:0>2, 139:1>0.

Amictus: 20:1>0, 57:1>0, 62:0>1, 90:1>0, 147:0>1.

Oniromyia: 5:3>2, 16:2>0, 18:0>1, 22:0>1, 62:0>1, 77:0>1, 80:0>1, 82:1>0.

Pantarbes: 9:0>1, 30:1>2, 41:0>1, 62:0>1, 93:1>0, 125:1>2.

Neosardus: 26:1>0, 96:0>1.

Megapalpus: 10:1>0, 87:0>1, 134:0>1.

Mariobezzia: 7:1>0, 20:0>1, 32:0>1, 57:0>1, 127:1>0, 138:1>0.

Corsomyza: 7:1>0, 30:1>0, 77:0>1.

Sericosoma: 9:0>1, 82:1>0, 111:1>2, 145:1>0.

Cytherea: 9:0>1, 26:1>0, 50:0>1, 82:1>0, 110:1>0, 125:1>2.

Cyrtomyia: 138:1>0.

Eclimus: 35:0>1, 41:2>1, 68:0>1.

Thevenetimyia: 1:1>0, 51:0>1.

Lepidophora: 3:0>1, 11:0>1, 35:0>1, 41:2>0, 72:0>1.

Marmasoma: 1:1>0, 5:3>1, 16:2>0, 42:1>0, 74:0>1, 82:1>0, 83:0>1, 91:0>1, 110:0>1, 111:1>2, 116:1>0, 118:0>1, 131:0>1.

Heterostylum: 5:3>2, 47:0>1, 62:0>1, 96:0>1.

Eusurbus: no autapomorphies.

Paratoxophora: 28:1>0, 43:1>0, 110:0>1, 113:0>1, 116:1>0, 118:0>1, 125:1>2, 147:0>1.

Dischistus: 4:0>1, 7:1>0, 11:0>1, 24:0>1, 44:0>1.

Aldrichia: 5:2>1, 7:1>0, 134:0>1.

Conophorus: no autapomorphies.

Eurycarenus: 47:0>1, 50:1>2, 76:0>1, 105:0>1, 116:1>0.

Bombylius androgynus: 125:1>0, 127:1>0, 139:1>0.

Bombylius major: 50:1>0, 66:0>1.

Acrophthalmyda: 4:0>1, 43:0>1, 105:0>1, 146:0>1.

Lordotus: 24:0>1, 51:0>1, 57:0>1, 66:1>0, 82:1>0, 83:0>1, 90:1>0, 106:0>1.

Crocidium: 87:0>1, 132:2>0.

Desmatomyia: 5:2>1, 7:1>2, 19:0>1, 41:1>0, 42:1>0, 79:1>0, 111:1>2, 113:0>1, 116:0>2, 144:0>1, 145:1>0.

Heterotropus: 42:1>0, 79:1>0, 110:1>0, 111:1>0, 117:0>2, 145:1>0, 148:1>0, 150:2>1.

Toxophora compta: no autapomorphies.

Toxophora virgata: no autapomorphies.

Zaclava: no autapomorphies.

Dolichomyia: no autapomorphies.

Systropus: 1:0>1, 3:0>1, 35:1>0, 86:0>1, 94:0>1.

Oligodranes: 26:1>0, 27:1>0, 87:0>1, 92:0>1, 110:1>0, 113:1>0, 116:0>1.

Usia: 10:1>0, 11:0>1, 103:0>1.

Apolysis: 5:3>2, 69:1>0, 110:1>0, 113:1>0, 116:0>1.

Poecilognathus: 87:0>1, 111:1>2, 116:0>2.

Phthiria: 42:1>0, 80:0>1, 105:1>0.

Geron albaria: no autapomorphies.

Geron grandis: 10:0>1.

Cephalodromia: 32:0>1.

Paraconsors: 41:1>2, 49:0>1, 117:0>2, 119:0>1.

Acridophagus: 33:0>1, 41:1>2, 117:0>2, 144:0>1.

Glabellula: 7:2>1, 41:1>0, 52:1>0.

Mythicomyia: 10:0>1, 11:1>0, 64:1>0.
Apystomyia: 41:1>0, 43:0>1, 93:0>1, 111:1>2.
Hilarimorpha: 29:0>1, 52:0>1, 64:0>1, 92:0>1, 105:1>0.
Mydas: 135:1>0, 139:1>0.
Apiophora: 16:0>2, 68:0>1, 116:2>1.
Neorhaphiomidas: 5:2>1, 18:0>1, 29:1>0, 43:0>1, 62:0>1, 74:0>1, 82:1>0, 83:0>1, 88:0>1, 93:0>1.
Apiocera: 5:1>2, 18:0>1, 19:0>1, 41:0>1, 55:0>1, 58:0>1, 74:0>1, 80:0>1, 135:0>1.
Apsilocephala: 109:0>1, 113:0>1, 139:1>0, 147:0>1.
Bonjeania: 27:0>1, 41:0>1, 45:0>1, 119:1>0, 120:0>3, 123:0>1, 147:0>1.
Phycus: 7:0>1, 102:0>1, 110:0>1, 134:2>1.
Thereva: 5:1>2, 11:1>0, 26:0>1, 93:0>1, 113:0>1, 125:1>2.
Propebrevitrichia: 62:0>1.
Scenopinus: 117:1>2, 129:1>0, 139:1>0, 144:0>1.
Prorates: 14:0>1, 24:0>1, 27:1>0, 35:0>1, 41:0>1, 87:0>1, 111:1>2, 116:0>2, 147:0>1.
Caenotus: 27:1>0, 76:1>0, 111:1>0, 120:0>3, 134:2>1.
Leptarthrus: 87:1>0, 105:2>0, 106:0>1.
Stenopogon: 16:0>2, 66:1>0.
Dioctria: 7:1>2, 24:1>0, 27:0>1, 105:2>1.
Leptogaster: 12:0>1, 29:0>1, 68:0>1, 76:0>1, 77:0>1, 85:0>1, 86:0>1, 96:0>1, 101:0>1, 143:0>1, 144:1>0, 145:0>1.
Eulonchus: 14:0>1.
Lasia: 26:1>2, 117:0>1.
Trichophthalma: 16:0>2, 142:0>1
Hirmoneura: 19:0>1, 36:0>1, 40:0>1
Arthroceras: no autapomorphies
Rhagio: 16:0>2, 27:1>0.