PHYLOGENY OF ASILIDAE INFERRED FROM MORPHOLOGICAL CHARACTERS OF IMAGINES (INSECTA: DIPTERA: BRACHYCERA: ASILOIDEA)

TORSTEN DIKOW

Division of Invertebrate Zoology
American Museum of Natural History
and
Department of Entomology, Cornell University,
Ithaca, NY 14853
(torsten@tdvia.de)

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 319, 175 pp., 131 figures, 8 tables
Issued March 17, 2009

ISSN 0003-0090

CONTENTS

ABSTRACT

A phylogenetic hypothesis is proposed for higher-level relationships within Asilidae, based on a sample of 158 species from 140 genera representing all 11 previously recognized subfamily taxa and 39 of the 42 tribal taxa and 220 discrete, parsimony informative, morphological characters from all tagmata of the imagines. Cladistic analysis results in 720 most parsimonious trees of 2760 steps in length, and a strict consensus topology of 2965 steps. The strict consensus cladogram is well resolved except for species of Apocleinae and Asilinae, which form a large polytomy. Monophyly of Asilidae is corroborated and supported by five autapomorphies: (1) labella of labium fused to prementum at least ventrally; (2) hypopharynx heavily sclerotized; (3) hypopharynx with dorsal seta-like spicules; (4) labrum short and at most half as long as labium; (5) cibarium trapezoidal. The clade Apioceridae + Mydidae is the sister group to Asilidae. The phylogenetic hypothesis indicates that five out of the 11 previously recognized subfamily taxa are non-monophyletic, i.e., Apocleinae, Asilinae, Dasypogoninae, Laphystiinae, and Stenopogoninae. The present cladistic analysis forms the most comprehensive phylogenetic study on Asilidae to date and is used to revise the taxon's phylogenetic classification in which 14 subfamily taxa are recognized. Ommatiinae, Trigonomiminae, and Stichopogoninae are recovered as monophyletic and contain the same genera as previously postulated. Dioctriinae and Leptogastrinae are also recovered as monophyletic, but the genera *Myelaphus* and *Acronyches* are transferred to them, respectively. Asilinae comprises all Apocleinae and Asilinae species and Laphriinae comprises all Laphriinae and Laphystiinae species sensu previous authors. Dasypogoninae and Stenopogoninae are divided into several taxa at phylogenetically unrelated positions in the cladogram. The Dasypogoninae comprises only Blepharepiini, Dasypogonini, Lastauracini, Megapodini (including Cyrtophryina, Lagodiina, Megapodina, and Senobasina), Molobratiini, Saropogonini, and Thereutriini as well as the unplaced genera *Archilestris*, *Diogmites*, and *Lestomyia*. The remaining taxa possessing either a large prothoracic tibial spine, i.e., Brachyrhopalini and Chrysopogonini, or a small S-shaped spur, i.e., *Cophura*, *Leptarthrus*, and *Nicocles*, are part of the Brachyrhopalinae (new status). The Stenopogoninae comprises only Enigmomorphini, Plesiommatini, and Stenopogonini as well as the unplaced genera *Ancylorhynchus* and *Scylaticus*. Bathypogoninae (new status), Phellinae (new status), Tillobromatinae (new status), and Willistonininae (new status) are new subfamilial taxa previously assigned to Stenopogoninae. The remaining Stenopogoninae sensu previous authors represented here, i.e., Cyrtopogonini, Ceraturgini, *Heteropogon*, *Holopogon*, *Metapogon*, and *Rhabdogaster*, are assigned to the Brachyrhopalinae (new status). The genera *Coleomyia* and *Oligopogon* remain incertae sedis as neither genus groups with any other Asilidae, and are positioned as adelphotaxa to speciose clades. The higher-level relationships are: (Laphriinae ((Asilinae + Ommatiinae) (Bathypogoninae (Phellinae ((Tillobromatinae (*Coleomyia* incertae sedis + Dasypogoninae + Stenopogoninae)) (Willistonininae (*Oligopogon* incertae sedis ((Dioctriinae (Leptogastrinae + Trigonomiminae)) (Brachyrhopalinae + Stichopogoninae)))))))).

INTRODUCTION

Asilidae ("robber flies," "assassin flies") are a distinct part of the global insect fauna, which most entomologists quickly recognize and appreciate because of their obvious predatory behavior and generally large body size in the imago stage. To date, slightly more than 7000 species have been described from all zoogeographical regions, making Asilidae one of the most diverse taxa within Diptera. Assassin flies range in size from 5–60 mm and are morphologically very diverse (figs. 2–13). They live in a wide variety of habitats, though they are most speciose in desert to semidesert environments (e.g., Londt, 1998) and tropical lowland forests (e.g., Fisher, in press; figs. 14–25). They play a major ecological role as predominantly insect predators. Despite ongoing interest in species-level revisionary studies or behavioral and ecological studies, the phylogenetic relationships among taxa within the Asilidae are very poorly known. There is, however, no doubt that the Asilidae is a monophyletic taxon. In the present phylogenetic study, morphological features of the imagines used in classifications by previous authors are combined with yet unreported character complexes to resolve the phylogenetic relationships of 158 species sampled among 140 genera from around the world (fig. 1; table 2).

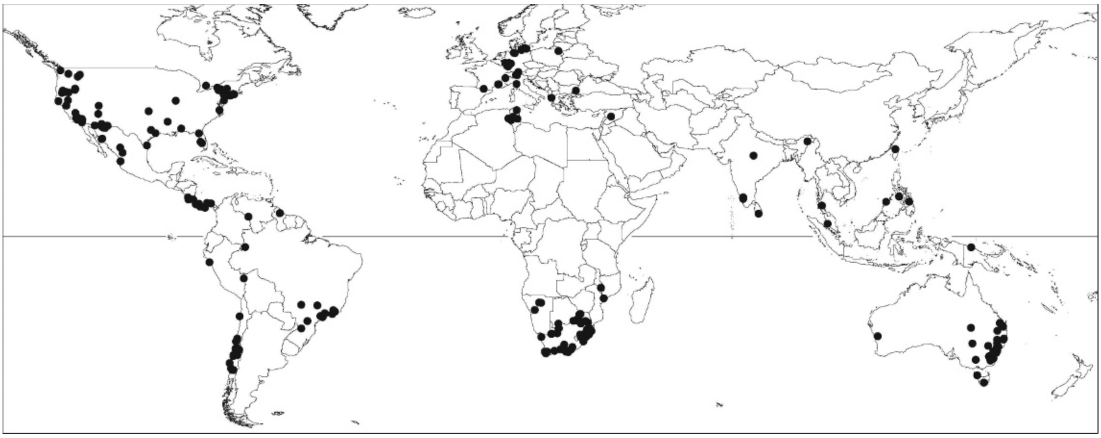


Fig. 1. Map of the world with collecting localities of Asilidae species included in the present study marked with filled circles.

Assassin flies have lived on earth for a long time. The oldest fossils that can be unambiguously assigned to the Asilidae are Cretaceous (Gallic epoch) in origin, from the Crato Formation in Brazil (Albian, approximately 110 Mya, Grimaldi, 1990) and from New Jersey amber in the United States (Turonian, 94–90 Mya, Grimaldi and Cumming, 1999; Grimaldi and Engel, 2005). A few compression fossils from the Karabastau Formation of southern Kazakhstan (Late Jurassic, Malm epoch, approximately 160 Mya) are interpreted as belonging to the Asilidae (Mostovski, 1999), but it remains to be seen whether these fossils actually belong to the stem lineage of the Asilidae or are stem lineage representatives of Asiloidea. Hull (1962) postulated a diagram of relationships of robber flies with a timeline of their diversification based on the then-known fossils and concluded that robber flies diversified as recently as the Tertiary (Palaeogene, Eocene epoch, approximately 45 Mya). Later, Lehr (1969) also postulated a diagram of relationships, concluding that the Asilidae (referred to as Asilomorpha) diversified after the mid-Jurassic (approximately 180 Mya). Artigas et al. (2005) postulated a Gondwanan origin for a taxon composed of *Hypenetes* Loew, 1858, from southern Africa and *Tillobroma* Hull, 1962, from South America (Stenopogoninae: Tillobromatini sensu Artigas and Papavero, 1991) based on a hypothesis of vicariance and a sister-group relationship between the two genera. The minimum age of 180 Million years for this taxon as proposed by Artigas et al. (2005) is not supported by any fossil evidence. In fact, not a single species that can be unambiguously assigned to any extant Asiloidea family taxon has been reported from the mid-Jurassic, and the hypothesis of an origin of a taxon comprising these two genera is highly controversial and not based on empirical evidence (see Discussion for phylogenetic relationships of these two genera). Origin and earliest diversification of the Asilidae may be postulated to be latest Jurassic to earliest Cretaceous (150–140 Mya; D. Grimaldi, personal commun.).

The Asilidae Latreille, 1802, is placed in the Asiloidea (e.g., Hennig, 1972; Woodley, 1989; Griffiths, 1994; Yeates, 1994, 2002; Yeates and Wiegmann, 1999, 2005; Grimaldi and Engel, 2005) together with five relatively speciose family taxa (i.e., Apioceridae Bigot, 1857, Bombyliidae Latreille, 1802, Mydidae Latreille, 1809, Scenopinidae Fallén, 1817, and Therevidae Newman, 1834), and three to four minor family taxa (i.e., Apsilocephalidae Nagatomi et al., 1991, Evocoidae Yeates et al., 2003, Mythicomyiidae Melander, 1902 [sensu Evenhuis, 1994; but see Yeates, 1994], and Hilarimorphidae Williston, 1896 [sensu Webb, 1974; Yeates, 1994]). The Asiloidea sensu Woodley (1989) (= Pleroneura sensu Lameere, 1906; Griffiths, 1994; = Asilidea sensu Hennig, 1954; = Asiliformia sensu

Figs. 2–7. Photographs of some Asilidae species included in the present analysis. **2.** *Asilus sericeus* (Asilinae; Cromwell Meadows Wildlife Management Area, Middlesex County, Connecticut, 2004); **3.** *Pogonioefferia pogonias* (Asilinae; Windham, Windham County, Connecticut, 2004); **4.** *Dioctria hyalipennis* (Dioctriinae; Great Swamp Wildlife Management Area, South Kingston, Washington County, Rhode Island); **5.** *Ceraturgus fasciatus* (Brachyrhopalinae; Hadley, Hampshire County, Massachusetts, 2004); **6.** *Atomosia puella* (Laphriinae; Matianuck Natural Preserve Area, Windsor, Hartford County, Connecticut, 2005); **7.** *Laphria aktis* (Laphriinae; Matianuck Natural Preserve Area, Windsor, Hartford County, Connecticut, 2004). All photographs taken by Michael Thomas.

Hennig, 1972, 1973; = Asilomorpha sensu Grimaldi and Engel, 2005) is considered to be a monophyletic taxon although only supported morphologically by the position of the larval posterior spiracle in the penultimate abdominal segment (e.g., Hennig, 1972, 1973; Woodley, 1989; Yeates, 2002). Griffiths (1994) also proposed the presence of a divided abdominal tergite 10 into acanthophorite plates in the females and the complex

Figs. 8–13. Photographs of some Asilidae species included in the present analysis. **8.** *Laxenecera albicincta* (Laphriinae; Mhlopeni Nature Reserve, KwaZulu-Natal, South Africa, 2004); **9.** *Tipulogaster glabrata* (Leptogastrinae; Skinner State Park, Hampshire County, Massachusetts, 2004); **10.** *Ommatius tibialis* (Ommatiinae; Simsbury, Hartford County, Connecticut, 2004); **11.** *Stichopogon trifasciatus* (Stichopogoninae; Simsbury, Hartford County, Connecticut, 2006); **12.** *Holcocephala calva* (Trigonomiminae; Hillsborough River State Park, Hillsborough County, Florida, 2006); **13.** *Nicocles politus* (Brachyrhopalinae; Matianuck Natural Preserve Area, Windsor, Hartford County, Connecticut, 2004). *Laxenecera albicincta* photographed by Torsten Dikow, *Tipulogaster glabrata* by Giff Beaton, and all remaining photographs taken by Michael Thomas.

14

15

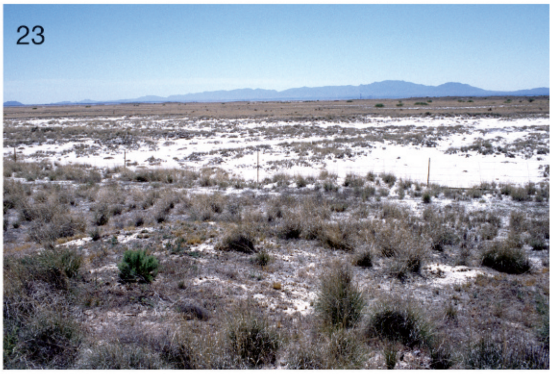
16

17

18

19

Figs. 14–19. Photographs of habitats of Asilidae with a list of species that have been collected in them and are included in the present analysis: **14.** Sand dune in Hohe Düne, Rostock, Mecklenburg-Western Pomerania, Germany (1998): *Dysmachus trigonus* and *Philonicus albiceps* (Asilinae); **15.** Forest margin, Rostocker Heide, Rostock, Mecklenburg-Western Pomerania, Germany (1998): *Dioctria atricapillus* and *Dioctria rufipes* (Dioctriinae), *Lasiopogon cinctus* (Stichopogoninae), *Philonicus albiceps* and *Tolmerus atricapillus* (Asilinae); **16.** European Alps, near Garmisch-Partenkirchen, Bavaria, Germany (2002): *Leptarthrus brevirostris* (Brachyrhopalinae); **17.** Montane grassland in Injesuthi, Drakensberg Mountains, KwaZulu-Natal, South Africa (2000): *Rhabdogaster pedion* (Brachyrhopalinae), *Damalis monochaetes* (Trigonomiminae); **18.** Acacia savannah in Mhlopeni Nature Reserve, KwaZulu-Natal, South Africa (2000): *Afroestricus chiastoneurus* (Ommatiinae), *Connomyia varipennis* (Stenopogoninae), *Hoplistomerus nobilis* and *Laxenecera albicincta* (Laphriinae), *Lasiocnemus lugens* (Leptogastrinae); **19.** Sparsely vegetated exposed hillside, Tierberg Nature Reserve, near Keimoes, Northern Cape, South Africa (2004): *Lycostommyia albifacies* (Tillobromatinae), *Trichoura* sp. (Tierberg) (Willistonininae). All photographs taken by Torsten Dikow.



Figs. 20–25. Photographs of habitats of Asilidae and Apioceridae with a list of species that have been collected in them and are included in the present analysis: **20.** White sand dunes in Witsand Nature Reserve, Northern Cape, South Africa (2004): *Stiphrolamyra angularis* (Laphriinae); **21.** Acacia savannah and white sand dunes in Witsand Nature Reserve, Northern Cape, South Africa (2004): *Acnephalum cylindricum* (Willistonininae), *Daspletis stenoura* (Stenopogoninae), *Trichardis effrena* (Laphriinae); **22.** Tropical rainforest in Central Catchment Nature Reserve, Singapore (2006): *Clephydroneura* sp. (Kepong) (Asilinae); **23.** Sand dunes adjacent to salt pan, Willcox, Arizona (2005): *Ablautus coquilletti* (Willistonininae), *Apiocera painteri* (Apioceridae); **24.** Sand dune near Borax Lake, Oregon (2005): *Diogmites grossus* (Dasypogoninae), *Laphystia tolandi* (Laphriinae), *Ospriocerus aeacus* (Stenopogoninae); **25.** Forest margin and open sand area near Ithaca, New York (2003): *Holcocephala calva* (Trigonomiminae), *Pogonioefferia pogonias* (Asilinae). All photographs taken by Torsten Dikow.

intromittent organ with an internal endoaedeagal tube (sensu Sinclair et al., 1994) in the males as autapomorphies of this lineage. Asiloidea and its sister group Eremoneura are grouped in the Heterodactyla, a monophyletic taxon based on the presence of a setiform empodium situated between the paired claws (e.g., Woodley, 1989) and reduction of the epiproct (Sinclair et al., 1994). Heterodactyla and its sister group, the Nemestrinoidea (sensu Woodley, 1989), are grouped in the Muscomorpha (sensu Woodley, 1989) characterized by the reduction of antennal flagellomeres to four or fewer, reduction of tibial spurs, one-segmented cerci in females, males with base of epandrium articulated with gonocoxites, and males with gonostyli moving in a dorsoventral fashion (Woodley, 1989; Sinclair et al., 1994).

The sister group to Asilidae is still debated in the Diptera literature and six alternative hypotheses are: (1) Asilidae and Apioceridae are sister taxa (Hull, 1962; Yeates, 1994); (2) either Apioceridae or Mydidae is the sister group to Asilidae (Hennig, 1973); (3) Asilidae and Mydidae form a sister taxon (Wood, 1981); (4) Asilidae is the sister taxon to either Apioceridae and Mydidae or Scenopinidae and Therevidae (Woodley, 1989); (5) Apioceridae and Mydidae form the sister group to Asilidae (Yeates and Irwin, 1996); and (6) Asilidae is the sister taxon to the remaining Asiloidea except Bombyliidae (Yeates, 2002; Bybee et al., 2004). Hermann (1909), in describing the first southern African Apioceridae in the genus *Ripidosyrma* Hermann, 1909, discussed the relationships of Apioceridae, Asilidae, and Mydidae and concluded that the Asilidae is most closely related to *Apiocera* Westwood, 1835, i.e., Australian Apioceridae, based on certain characters of the wing venation. Recent studies focusing on the Therevidae and their phylogenetic relationships to Apsilocephalidae, Evocoidae, and Scenopinidae revealed the so-called "therevoid clade" consisting of these family taxa, which is the sister taxon to a clade composed of Apioceridae, Asilidae, and Mydidae (S. Winterton and M. Hauser, personal commun.). Irwin and Wiegmann (2001) attempted in a molecular study to place the enigmatic southern African genus *Tongamya* Stuckenberg, 1966 (Mydidae: Megascelinae), and included Apioceridae, Mydidae, Scenopinidae, and Therevidae as outgroup taxa, but unfortunately they did not include any robber flies.

The monophyly of Asilidae has never been questioned. Hardy (1927a: fig. 2) presented a diagram of postulated relationships of Asiloidea in which the Asilidae is paraphyletic with respect to Apioceridae, Mydidae, and Therevidae. He did not provide any conclusive morphological evidence supporting this hypothesis, however. Hennig (1973) discussed three derived ground-pattern character states as supporting the monophyly of Asilidae, i.e., (1) abdomen constricted proximally (attributed to Hull, 1962), (2) labella of labium reduced and sclerotized, and (3) densely bristled legs. The sunken vertex was interpreted by Hennig (1973) to be shared with the Mydidae. Woodley (1989) listed three autapomorphies for the Asilidae all relating to the imagines: (1) labella of labium strongly reduced and fused with prementum, (2) hypopharynx strongly sclerotized, modified into a hypodermic, needlelike structure, and (3) face with a vestiture of strong macrosetae called the mystax. Yeates (1994) and Sinclair et al. (1994) independently postulated a feature of the male terminalia as an autapomorphy for assassin flies, i.e., base of the epandrium articulated with anterodorsal prolongation of hypandrium. Further support for monophyly is exhibited by the predatory behavior found in both the adult as well as the larval life stage, which is unique among Asiloidea.

Fifty-eight available, valid family-group names have been proposed to group the 537 genera of Asilidae (Sabrosky, 1999; Dikow, 2004; Geller-Grimm, 2004; note: nine additional genera have been described or reclassified since Geller-Grimm's generic catalogue in 2004, which lists 528 valid genera). Eleven names have been previously in use and recognized at the subfamilial rank, i.e., Apocleinae Papavero, 1973a, Asilinae Latreille, 1802, Dasypogoninae Macquart, 1838, Dioctriinae Enderlein, 1936, Laphriinae Macquart, 1838, Laphystiinae Hendel, 1936, Leptogastrinae Schiner, 1862, Ommatiinae Hardy, 1927, Stenopogoninae Hull, 1962, Stichopogoninae Hardy, 1930, and Trigonomiminae Enderlein, 1914 (e.g., Geller-Grimm, 2004; but see Artigas and Papavero, 1997, in regard to Apocleinae), whereas 42 family-group names have been used previously to divide the subfamily taxa into subordinate taxa referred to as tribal taxa (Dikow, 2004). The taxa subordinate to subfamily level have not often been applied on a worldwide basis. The majority of names were proposed by a few authors and for particular zoogeographical regions only, e.g., Artigas and Papavero (1988–1991) established 10 Neotropical taxa; Hardy (1926–1948) postulated nine taxa of which three are limited to Australia; Papavero (1973–1975) published six Neotropical taxa; and Hull (1962) proposed six taxa. The present study includes a worldwide sample of Asilidae species (fig. 1; table 2) and can therefore test the monophyly of geographically restricted tribal taxa, and accordingly modify the delimitation, scope, and composition of these taxa.

BRIEF HISTORICAL REVIEW OF CLASSIFICATIONS OF ASILIDAE

The eminent dipterist Thomas Becker is quoted in Hermann (1920: 161, see translation below):

> Es bricht sich das Empfinden und die Erkenntnis Bahn, daß eine Revision in der Einteilung der Gattungen der Asiliden als ein höchst notwendiges Postulat und als ein sehr dankbares Feld der Tätigkeit angesehen werden muß.

Harold Oldroyd, an influential dipterist at the British Museum (Natural History), published the following two comments on classifying Asilidae in 1974:

> A tribal classification, like any other, can be approached from different directions. Ideally, no doubt, it should be austerely scientific, and express as completely as possible the ancestry and present relationships of the genera. This must always be a matter of opinion. Traditional taxonomic methods of examining as many individual specimens as possible and comparing the results are laborious and incomplete…. We record resemblances and differences, but every generalisation has its exceptions

and

> I think our present classification of Asilidae will remain largely intuitive and utilitarian for a long time to come, perhaps for ever (Oldroyd, 1974a: 8–9).

Becker stated that a classification of the genera of Asilidae was needed and that such a project would be worthwhile and rewarding, whereas Oldroyd was pessimistic concerning the results derivable from studying many specimens in detail, comparing their morphology and using character states to propose a hypothesis of relationships. The present study goes against Oldroyd's viewpoint by initiating the study of a representative sample of the 7000 Asilidae species and coding them for 220 morphological characters of the imagines in order to postulate a well-corroborated hypothesis of phylogenetic relationships of higher-level taxa within Asilidae.

The earliest studies dealing with classifications in the form of a dichotomous key were published by Macquart (1838) and Schiner (1862). Hull (1962) summarized the taxonomic work of early authors from the 18th and 19th centuries. Papavero (1973a) provided a detailed summary of the different classifications to 1970 and postulated his own view on the relationships of taxa. Table 1 summarizes classificatory/phylogenetic studies dealing with the entire Asilidae that have been published since 1900. Only a molecular study of 26 Asilidae species (Bybee et al., 2004; fig. 130) can be regarded as a first higher-level phylogenetic analysis of Asilidae involving all previously recognized subfamily taxa (except for Dioctriinae). A few other post-Hennigian publications, published between 1959 and 1996, address the classification of Asilidae as a whole (table 1), but with the exception of Karl (1959; fig. 129) they are not grounded in modern phylogenetic theory. Hull's (1962) and Papavero's (1973a) extensive reviews of the world genera and classification of Asilidae include diagrams of relationships of subordinate taxa. Upon close examination it is apparent that neither of the studies employed a Hennigian character polarization and no sister-group relationships based on apomorphic character states were proposed. Papavero (1973a: 220) cited Darlington (1971) for his general methodology and it is here repeated to illustrate the fact that Papavero did not work in a cladistic framework:

TABLE 1

Summary of publications addressing the classification or phylogeny of Asilidae based on morphology of imagines except where noted

Publication	Analysis Method	Remarks
Hermann, 1920	similarity and diagnostic key	
Hardy, 1927a	similarity	Asiloidea, Asilidae is paraphyletic
Hardy, 1927b	similarity and diagnostic key	
Hardy, 1934	similarity	
Karl, 1959	phylogenetic	
Hull, 1962	non–matrix-based similarity	
Lehr, 1969	non–matrix-based similarity	
Artigas, 1971	phenetic	Chilean Asilidae only
Papavero, 1973a	non–matrix-based similarity	
Oldroyd, 1974a	non–matrix-based similarity	
Lehr, 1996	non–matrix-based similarity	
Bybee et al., 2004	phylogenetic	16S, 18S, 28S rDNA, COII mtDNA

> The methods I use are essentially subjective: comparison of specimens, detection of similarities and differences, and reaching conclusions based primarily on personal judgements and experience rather than on statistical analyses or other objective tests. I have tried to make my taxonomy conform to phylogeny and reflect the existence of variability as well as the interrelationships of populations in nature…. Their phylogenies must therefore be deduced, and taxonomists are sure to make mistakes about them (Darlington, 1971: 144).

Darlington (1971: 144) also stated, "In general, I think taxonomists using less arbitrary methods can do as well or better than cladists in fitting their classifications to phylogenies and in interpreting geographical patterns." In summary, Hull's (1962) and Papavero's (1973a) reviews provided classifications of the genera of Asilidae and identification keys to them, and are thus important contributions to the knowledge of Asilidae, but are not phylogenetic hypotheses of evolutionary relationships of taxa of robber flies. A few phylogenetic hypotheses of relationships of subordinate taxa were published, e.g., Adisoemarto and Wood (1975) on Dioctriini and Echthodopini (Dioctriinae) and Cannings (2002) on Stichopogoninae. Two unpublished Ph.D. dissertations dealt with taxa of Laphriinae, i.e., Andrenosomatini (Fisher, 1986) and the entire Laphriinae (Mazzarolo, 1999).

MATERIALS AND METHODS

Morphological terminology mainly follows that recommended in *Manual of Nearctic Diptera* (McAlpine, 1981). Terminology of the antennae follows Hennig (1972), Stuckenberg (1999), and Dikow and Londt (2000), and terms pertaining to male terminalia follow Sinclair et al. (1994). All abbreviations for wing veins and wing cells follow McAlpine (1981), and abdominal tergite and sternite are abbreviated by a capital T and S, respectively. A distinction is made between regular setae and macrosetae relating to their thickness. Macrosetae also often exhibit a well-developed socket. Other terms used herein correspond to those in *The Torre-Bueno Glossary of Entomology* (Nichols, 1989). The female and male terminalia and heads were first excised and macerated in 10% potassium hydroxide (KOH) in an incubator at 50° C for 45–90 minutes. They were temporarily stored in 75% ethanol for examination and illustration and eventually sealed in polyethylene genitalia vials containing 100% glycerol and attached to the specimen's pin. Morphological features were drawn with the aid of a 10 × 10 ocular grid on an Olympus SZ60 stereomicroscope, the drawings scanned on a flatbed scanner, and digitally redrawn and labeled using Adobe Illustrator® software. Scanning electron micrographs were taken with a Hitachi S4700

Field Emission Scanning Electron Microscope. The wings were temporarily slide-mounted in glycerol and photographed with a Microptics® digital macro unit and later attached to the specimen's pin on a piece of label paper.

TAXON SAMPLING

More than 7000 species have been described in the Asilidae to date, and reflecting this species diversity is of immense importance for any phylogenetic analysis. The present study includes 158 species from 140 genera, representing all 11 previously recognized subfamily taxa with multiple exemplars (table 2), thereby establishing a worldwide sampling (fig. 1). Most of the 42 valid tribal taxa are also represented by multiple exemplars, if applicable. Only the three monogeneric tribal taxa Archilaphriinae Enderlein, 1914 (Dasypogoninae, *Archilaphria* Enderlein, 1914), Dasylechiini Artigas et al., 1988 (Laphriinae, *Dasylechia* Williston, 1907), and Neophoneini Artigas et al., 1988 (Laphriinae, *Neophoneus* Williston, 1889) are not included because too few specimens are available for morphological dissections. To better represent the species diversity additional species are included for every subfamily taxon in which only a few subordinate taxa have been proposed, i.e., Apocleinae, Asilinae, Leptogastrinae, Ommatiinae, Stichopogoninae, and Trigonomiminae. Three species formerly assigned to the Isopogonini Hardy, 1948, which is an unavailable name (Sabrosky, 1999; Dikow, 2004), are included to represent this taxon, which has been applied in previous classifications (e.g., Hardy, 1948; Hull, 1962; Papavero, 1973b). Artigas and Papavero (1997) divided the Asilinae, including the Apocleinae sensu Artigas and Papavero (1988) and Geller-Grimm (2004), into generic groups without formal establishment of family-group names. Seven of these nine generic-group taxa are represented in the present analysis (table 2). The majority of the species are represented by male and female specimens with only three species represented by specimens of the female gender only (table 2). The arrangement of genera in table 2 follows the latest generic classification by Geller-Grimm (2004). An effort is made to represent the included family-group taxa and genera by their respective type genus and type species when material has been available for study. In 11 cases for which the species identification is not certain, i.e., referred to as "sp.," it has been verified that all specimens belong to a single species and an additional epithet is included in parentheses denoting their collecting locality or unpublished name for future reference. These species are either undescribed, or belong to speciose genera which need to be revised before species identifications can be undertaken.

Outgroup sampling is also of outstanding importance in a comprehensive phylogenetic analysis. Monophyly of Heterodactyla has been corroborated in a number of analyses (e.g., Yeates, 2002; Yeates and Wiegmann, 2005) and Eremoneura is indisputably a clade (e.g., Grimaldi and Engel, 2005; Yeates and Wiegmann, 2005; Sinclair and Cumming, 2006), so only 16 species representing the Asiloidea have been used as outgroup taxa to polarize the ingroup data (table 2). *Neorhynchocephalus volaticus* (Williston, 1883) (Nemestrinoidea: Nemestrinidae: Trichopsideinae) is included to represent a taxon outside of Asiloidea and Heterodactyla and is always used as the root of the cladograms presented below. Although the present paper is primarily intended to shed light on the phylogenetic relationships within the Asilidae, it also aims to provide a hypothesis of the sister taxon to Asilidae. Therefore special attention is given to include a number of Apioceridae and Mydidae species, which had historically been discussed as probable sister taxa to Asilidae (see Introduction).

Institutions providing specimens are listed below, together with the abbreviations of the depositories and the people who kindly assisted in lending the specimens:

AMNH	American Museum of Natural History, New York City, New York
AMS	Australian Museum, Sydney, New South Wales, Australia (D. Bickel, D. Britton)
ANIC	Australian National Insect Collection, Canberra, Australian Capital Territory, Australia (C. Lambkin, D. Yeates)

TABLE 2

Exemplar species of Asilidae and outgroup taxa in the present analysis

Arrangement of genera within subfamily taxa of Asilidae follows Geller-Grimm (2004). Abbreviations: Tg = type genus of family-group name; Tsp = type species of genus; U = E. Fisher unpublished (CSCA); Generic groups *sensu* Artigas and Papavero (1997): EF = *Efferia* Group, EI = *Eichoichemus* Group, G = *Glaphyropyga* Group, L = *Lochmorhynchus* Group, MA = *Mallophora* Group, MY = *Myaptex* Group, P = *Proctacanthus* Group

Subfamily taxon: Tribal taxon	Species	Depository	Country of origin	Notes
Apocleinae: Apocleini	*Apoclea algira* (Linnaeus, 1767)	CODI, COGG	Tunisia	Tg; Tsp
Apocleinae	*Blepharotes splendidissimus* (Wiedemann, 1830)	ANIC	Australia	Tsp
Apocleinae	*Dasophrys crenulatus* Londt, 1981	NMSA	South Africa	
Apocleinae	*Eichoichemus pyrrhomystax* (Wiedemann, 1828)	AMNH CAS	Brazil	EI
Apocleinae	*Lochmorhynchus albicans* (Carrera and Andretta, 1953)	AMNH	Peru	L
Apocleinae	*Megaphorus pulchrus* (Pritchard, 1935)	CUIC	USA	MA
Apocleinae	*Myaptex brachyptera* (Philippi, 1865)	UCCC	Chile	MY
Apocleinae	*Neolophonotus bimaculatus* Londt, 1986	NMSA	South Africa	Londt, 2004
Apocleinae	*Nomomyia murina* (Philippi, 1865)	UCCC	Chile	Tsp; G
Apocleinae	*Philodicus tenuipes* Loew, 1858	NMSA	South Africa	
Apocleinae	*Pogonioefferia pogonias* (Wiedemann, 1821)	CODI	USA	Tsp; EF
Apocleinae	*Proctacanthus philadelphicus* Macquart, 1838	CUIC	USA	Tsp; P
Apocleinae	*Promachus amastrus* (Walker, 1849)	NMSA	South Africa	
Asilinae: Asilini	*Asilus crabroniformis* Linnaeus, 1758	AMNH	Italy	Tsp; Tg
Asilinae: Asilini	*Asilus sericeus* Say, 1823	CUIC	USA	
Asilinae: Asilini	*Satanas gigas* (Eversmann, 1855)	ZSMC	Syria	Tsp
Asilinae: Lycomyini	*Lycomya germainii* Bigot, 1857	UCCC	Chile	Tsp; Tg
Asilinae: Machimini	*Machimus chrysitis* (Meigen, 1820)	COGG	Italy, Switzerland	Tsp; Tg
Asilinae: Machimini	*Machimus occidentalis* (Hine, 1909)	CODI	USA	homonym
Asilinae: Neomochtherini	*Afromochtherus mendax* (Tsacas, 1969)	NMSA	South Africa	
Asilinae: Neomochtherini	*Dysmachus trigonus* (Meigen, 1804)	CODI	Germany	Tsp
Asilinae: Neomochtherini	*Neomochtherus pallipes* (Meigen, 1820)	CODI, COGG	Italy, Germany	Tsp; Tg
Asilinae: Philonicini	*Philonicus albiceps* Loew, 1849	CODI	Germany	Tsp; Tg
Asilinae	*Clephydroneura sundaica* (Jaennicke, 1867)	CAS, USNM	India, Thailand	
Asilinae	*Clephydroneura* sp. (Kepong)	CODI	Malaysia	
Asilinae	*Colepia rufiventris* (Macquart, 1838)	ANIC	Australia	Tsp
Asilinae	*Congomochtherus inachus* Londt and Tsacas, 1987	NMSA	South Africa	
Asilinae	*Heligmonevra laevis* Engel, 1927	NMSA	South Africa	homonym
Asilinae	*Neoitamus cyanurus* (Loew, 1849)	CODI, COGG	Germany	Tsp
Asilinae	*Threnia carbonaria* (Wiedemann, 1828)	AMNH USNM	Brazil	Tsp
Asilinae	*Tolmerus atricapillus* (Fallén, 1814)	CODI, COGG	Germany	
Asilinae	*Zosteria rosevillensis* (Hardy, 1935)	ANIC	Australia	
Dasypogoninae: Blepharepiini	*Blepharepium cajennensis* (Fabricius, 1787)	AMNH	British Guyana, Peru	Tg
Dasypogoninae: Brachyrhopalini	*Brachyrhopala ruficornis* Macquart, 1847	ANIC	Australia	Tsp; Tg
Dasypogoninae: Brachyrhopalini	*Cabasa pulchella* (Macquart, 1846)	ANIC	Australia	Tsp
Dasypogoninae: Chrysopogonini	*Chrysopogon pilosifacies* Clements, 1985	ANIC	Australia	Tg
Dasypogoninae: Cyrtophryina	*Cyrtophrys attenuatus* (Loew, 1851)	MZSP	Brazil	Tsp; Tg

TABLE 2
(Continued)

Subfamily taxon: Tribal taxon	Species	Depository	Country of origin	Notes
Dasypogoninae: Cyrtophryina	*Deromyia fuscipennis* (Blanchard, 1852)	UCCC, USNM	Chile	Tsp
Dasypogoninae: Dasypogonini	*Austrosaropogon nigrinus* (Macquart, 1850)	AMS, ANIC	Australia	
Dasypogoninae: Dasypogonini	*Dasypogon diadema* Meigen, 1803	CODI	Germany	Tsp; Tg
Dasypogoninae: Dasypogonini	*Lestomyia fraudiger* Williston, 1883	CAS	USA	
Dasypogoninae: Lagodiina	*Pegesimallus laticornis* (Loew, 1858)	NMSA	South Africa	Tg
Dasypogoninae: Lastauracini	*Diogmites grossus* Bromley, 1936	CODI	USA	
Dasypogoninae: Lastauracini	*Neodiogmites melanogaster* (Wiedemann, 1821)	MZSP	Brazil	Tsp; Tg
Dasypogoninae: Megapodini	*Megapoda labiata* (Fabricius, 1805)	MZSP	Brazil	Tg
Dasypogoninae: Megapodini	*Pseudorus distendens* (Wiedemann, 1838)	USNM	Panama	
Dasypogoninae: Molobratiini	*Molobratia teutonus* (Linnaeus, 1767)	COGG	Bulgaria	Tsp; Tg
Dasypogoninae: Saropogonini	*Saropogon dispar* Coquillett, 1902	BYU	USA	Tg
Dasypogoninae: Saropogonini	*Saropogon luteus* Coquillett, 1904	AMNH	USA	
Dasypogoninae: Senobasina	*Senobasis corsair* Bromley, 1951	CSCA	Panama	Tg
Dasypogoninae: Thereutriini	*Thereutria amaraca* (Walker, 1949)	AMNH ANIC	Australia	Tsp; Tg
Dasypogoninae	*Cophura brevicornis* (Williston, 1883)	CUIC	USA	
Dasypogoninae	*Leptarthrus brevirostris* (Meigen, 1804)	CODI	Germany	Tsp
Dasypogoninae	*Nicocles politus* (Say, 1823)	CUIC	USA	
Dioctriinae: Dioctriini	*Broticosia paramonovi* Hull, 1962	AMS, ANIC	Australia	♂ only
Dioctriinae: Dioctriini	*Dioctria atricapillus* Meigen, 1804	COGG, CODI	Germany	Tg
Dioctriinae: Dioctriini	*Dioctria hyalipennis* (Fabricius, 1794)	CODI	USA	
Dioctriinae: Dioctriini	*Dioctria rufipes* (DeGeer, 1776)	CODI, COGG	Germany	
Dioctriinae: Dioctriini	*Nannodioctria* sp. (*formicaphaga*)	CSCA	USA	U
Dioctriinae: Echthodopini	*Dicolonus simplex* Loew, 1866	USNM	USA	Tsp
Dioctriinae: Echthodopini	*Echthodopa pubera* Loew, 1866	CUIC, USNM	USA	Tsp; Tg
Dioctriinae: Echthodopini	*Eudioctria albius* (Walker, 1849)	AMNH	Canada, USA	Tsp
Laphriinae: Andrenosomatini	*Andrenosoma cyrtoxys* Séguy, 1952	COGG	France, Greece, Spain	Tg
Laphriinae: Andrenosomatini	*Dasyllis funebris* Artigas, Papavero, and Pimentel 1988	CSCA	Costa Rica, Panama	
Laphriinae: Andrenosomatini	*Hyperechia nigripennis* (Wiedemann, 1830)	NMSA	South Africa	
Laphriinae: Andrenosomatini	*Pilica formidolosa* (Walker, 1860)	CSCA	Costa Rica, Panama	
Laphriinae: Andrenosomatini	*Proagonistes praeceps* (Walker, 1855)	NMSA	South Africa	Tsp
Laphriinae: Atomosiini	*Aphestia annulipes* (Macquart, 1838)	MZSP	Brazil	Tsp
Laphriinae: Atomosiini	*Atomosia puella* (Wiedemann, 1828)	AMNH	USA	Tg
Laphriinae: Atomosiini	*Cerotainia albipilosa* Curran, 1930	CUIC	USA	
Laphriinae: Atomosiini	*Goneccalypsis argenteoviridis* (Hermann, 1907)	NMSA	Malawi	Tsp
Laphriinae: Atomosiini	*Loewinella nigripes* Engel, 1929	NMSA	Mozambique	
Laphriinae: Ctenotini	*Lamyra gulo* (Loew, 1851)	NMSA	Namibia, South Africa	Tsp
Laphriinae: Ctenotini	*Stiphrolamyra angularis* (Loew, 1858)	NMSA	South Africa	
Laphriinae: Dasytrichini	*Orthogonis scapularis* (Wiedemann, 1828)	CAS, USNM	Philippines	Tsp
Laphriinae: Dasytrichini	*Smeryngolaphria numitor* (Osten-Sacken, 1877)	USNM	Panama	
Laphriinae: Laphriini	*Choerades bella* (Loew, 1858)	NMSA	South Africa	
Laphriinae: Laphriini	*Lampria clavipes* (Fabricius, 1805)	AMNH	British Guyana	Tsp
Laphriinae: Laphriini	*Laphria flava* (Linnaeus, 1761)	CODI, COGG	Germany	Tg
Laphriinae: Laphriini	*Laphria aktis* McAtee, 1919	CODI	USA	
Laphriinae: Laphriini	*Laxenecera albicincta* Loew, 1852	CODI	South Africa	

TABLE 2
(Continued)

Subfamily taxon: Tribal taxon	Species	Depository	Country of origin	Notes
Laphriinae: Laphriini	*Maira aenea* (Fabricius, 1805)	USNM	Papua New Guinea	
Laphriinae: Laphriini	*Nusa infumata* (Loew, 1851)	NMSA	South Africa	
Laphystiinae: Hoplistomerini	*Hoplistomerus nobilis* Loew, 1858	CODI	South Africa	Tg
Laphystiinae: Laphystiini	*Laphystia aegyptiaca* Efflatoun, 1937	COGG	Tunisia	Tg
Laphystiinae: Laphystiini	*Laphystia tolandi* Wilcox, 1960	CODI	USA	
Laphystiinae	*Perasis transvaalensis* Ricardo, 1925	NMSA	South Africa	
Laphystiinae	*Protometer* sp. (El Tuparro)	CSCA	Colombia	
Laphystiinae	*Psilocurus modestus* (Williston, 1893)	CUIC, USNM	USA	
Laphystiinae	*Trichardis effrena* Londt, 2008	CODI	South Africa	Tsp
Laphystiinae	*Zabrops tagax* (Williston, 1883)	USNM	USA	Tsp
Leptogastrinae: Leptogastrini	*Leptogaster cylindrica* (DeGeer, 1776)	CODI	Germany	Tsp; Tg
Leptogastrinae: Leptogastrini	*Leptogaster arida* Cole, 1919	CSCA	USA	
Leptogastrinae	*Beameromyia bifida* (Hardy, 1942)	FSCA	USA	
Leptogastrinae	*Euscelidia pulchra* Dikow, 2003	NMSA	South Africa	
Leptogastrinae	*Lasiocnemus lugens* Loew, 1858	NMSA	South Africa	
Leptogastrinae	*Tipulogaster glabrata* (Wiedemann, 1828)	AMNH	USA	Tsp
Ommatiinae: Ommatiini	*Afroestricus chiastoneurus* (Speiser, 1910)	CODI	South Africa	
Ommatiinae: Ommatiini	*Ommatius incurvatus* Scarbrough, 1993	AMNH	Costa Rica	Tg
Ommatiinae: Ommatiini	*Ommatius tibialis* Say, 1823	CUIC	USA	
Ommatiinae	*Cophinopoda chinensis* (Fabricius, 1794)	USNM	India	
Ommatiinae	*Emphysomera conopsoides* (Wiedemann, 1828)	CAS	Taiwan	Tsp; ♂ only
Ommatiinae	*Emphysomera pallidapex* (Bigot, 1891)	CODI	South Africa	
Ommatiinae	*Michotamia aurata* (Fabricius, 1794)	USNM	India	
Stenopogoninae: Acronychini	*Acronyches maya* Martin, 1968	CSCA	Costa Rica	Tg
Stenopogoninae: Bathypogonini	*Bathypogon nigrinus* Ricardo, 1912	ANIC	Australia	Tg
Stenopogoninae: Ceraturgini	*Ceraturgus fasciatus* (Walker, 1849)	CUIC	USA	Tg
Stenopogoninae: Ceraturgini	*Myelaphus melas* (Bigot, 1882)	CSCA	USA	
Stenopogoninae: Cyrtopogonini	*Ablautus coquilletti* Wilcox, 1935	CODI	USA	
Stenopogoninae: Cyrtopogonini	*Afroholopogon peregrinus* (Engel, 1929)	NMSA	South Africa	
Stenopogoninae: Cyrtopogonini	*Cyrtopogon lateralis* (Fallén, 1814)	COGG	Germany	Tg
Stenopogoninae: Cyrtopogonini	*Cyrtopogon rattus* Osten-Sacken, 1877	CODI	USA	
Stenopogoninae: Cyrtopogonini	*Dasycyrton gibbosus* Philippi, 1865	UCCC	Chile	Tsp
Stenopogoninae: Cyrtopogonini	*Heteropogon manicatus* (Meigen, 1820)	COGG	France	
Stenopogoninae: Cyrtopogonini	*Holopogon priscus* (Meigen, 1820)	CODI	Poland	
Stenopogoninae: Cyrtopogonini	*Metapogon punctipennis* Coquillett, 1904	CAS	USA	
Stenopogoninae: Cyrtopogonini	*Nannocyrtopogon lestomyiformis* Wilcox and Martin, 1936	CAS	USA	
Stenopogoninae: Cyrtopogonini	*Rhabdogaster pedion* Londt, 2006	NMSA	South Africa	
Stenopogoninae: Enigmomorphini	*Archilestris magnificus* (Walker, 1854)	AMNH	Mexico	
Stenopogoninae: Enigmomorphini	*Creolestes nigribarbis* (Philippi, 1865)	UCCC	Chile	Tsp
Stenopogoninae: Enigmomorphini	*Microstylum* sp. (Karkloof)	NMSA	South Africa	
Stenopogoninae: Enigmomorphini	*Prolepsis tristis* (Walker, 1851)	CUIC	USA	
Stenopogoninae: Phellini	*Obelophorus terebratus* (Macquart, 1850)	CUIC	Chile	Tsp
Stenopogoninae: Phellini	*Phellus olgae* Paramonov, 1953	ANIC	Australia	Tg
Stenopogoninae: Plesiommatini	*Plesiomma* sp. (Guanacaste)	AMNH CSCA	Costa Rica	Tg
Stenopogoninae: Stenopogonini	*Acnephalum cylindricum* Oldroyd, 1974	NMSA	South Africa	
Stenopogoninae: Stenopogonini	*Ancylorhynchus fulvicollis* (Bigot, 1879)	NMSA	South Africa	♂ only

TABLE 2
(Continued)

Subfamily taxon: Tribal taxon	Species	Depository	Country of origin	Notes
Stenopogoninae: Stenopogonini	*Daspletis stenoura* Londt, 1983	NMSA	South Africa	
Stenopogoninae: Stenopogonini	*Gonioscelis ventralis* Schiner, 1867	NMSA	South Africa	
Stenopogoninae: Stenopogonini	*Lycostommyia albifacies* (Hermann, 1907)	NMSA	South Africa	Tsp
Stenopogoninae: Stenopogonini	*Oligopogon* sp. (Cape Recife)	NMSA	South Africa	
Stenopogoninae: Stenopogonini	*Ospriocerus aeacus* (Wiedemann, 1828)	CUIC	USA	Tsp
Stenopogoninae: Stenopogonini	*Scleropogon subulatus* (Wiedemann, 1828)	CUIC	USA	
Stenopogoninae: Stenopogonini	*Scylaticus costalis* (Wiedemann, 1819)	NMSA	South Africa	
Stenopogoninae: Stenopogonini	*Sisyrnodytes* sp. (Gamka)	NMSA	South Africa	
Stenopogoninae: Stenopogonini	*Stenopogon sabaudus* (Fabricius, 1794)	CODI, USNM	France	Tsp; Tg
Stenopogoninae: Stenopogonini	*Stenopogon rufibarbis* Bromley, 1931	AMNH CSCA	USA	
Stenopogoninae: Tillobromatini	*Tillobroma punctipennis* (Philippi, 1865)	UCCC	Chile	Tsp; Tg
Stenopogoninae: Tillobromatini	*Coleomyia setigera* Cole in Cole and Lovett, 1919	USNM	USA	Tsp
Stenopogoninae: Tillobromatini	*Hypenetes stigmatias* Loew, 1858	NMSA	South Africa	Tsp
Stenopogoninae: Willistoninini	*Willistonina bilineata* (Williston, 1884)	AMNH USNM	USA	Tsp; Tg
Stenopogoninae	*Codula limbipennis* Macquart, 1850	ANIC	Australia	Tsp
Stenopogoninae	*Connomyia varipennis* (Ricardo, 1925)	CODI	South Africa	
Stenopogoninae	*Trichoura* sp. (Tierberg)	NMSA	South Africa	
Stichopogoninae: Stichopogonini	*Stichopogon elegantulus* (Wiedemann, 1820)	COGG	Tunisia	Tsp; Tg
Stichopogoninae: Stichopogonini	*Stichopogon punctum* Loew, 1851	NMSA	South Africa	
Stichopogoninae: Stichopogonini	*Stichopogon trifasciatus* (Say, 1823)	CUIC	USA	
Stichopogoninae	*Lasiopogon aldrichii* Melander, 1923	AMNH	USA	
Stichopogoninae	*Lasiopogon cinctus* (Fabricius, 1781)	CODI	Germany	
Stichopogoninae	*Lissoteles aquilonius* Martin, 1961	AMNH	Mexico	
Stichopogoninae	*Townsendia albomacula* Martin, 1966	CSCA	Mexico	
Trigonomiminae: Trigonomimini	*Trigonomima* sp. (*anamaliensis*)	CSCA	India	Tg; U
Trigonomiminae: Xenomyzini	*Damalis annulata* Loew, 1858	NMSA	South Africa	Tg
Trigonomiminae: Xenomyzini	*Damalis monochaetes* Londt, 1989	NMSA	South Africa	
Trigonomiminae: Xenomyzini	*Damalis* sp. (Palatupana)	USNM	Sri Lanka	
Trigonomiminae	*Holcocephala abdominalis* (Say, 1823)	CODI	USA	Tsp
Trigonomiminae	*Holcocephala calva* (Loew, 1872)	CODI	USA	
Trigonomiminae	*Rhipidocephala* sp. (Harold Johnson)	NMSA	South Africa	
Apioceridae	*Apiocera* (*Pyrocera*) *aldrichi* Painter, 1936	AMNH	USA	outgroup
Apioceridae	*Apiocera* (*Pyrocera*) *painteri* Cazier, 1963	AMNH CODI	USA	outgroup
Apsilocephalidae	*Apsilocephala longistyla* Kröber, 1914	CODI	USA	outgroup
Bombyliidae: Bombyliinae	*Bombylius major* Linnaeus, 1758	AMNH	USA	outgroup
Bombyliidae: Phthiriinae	*Poecilognathus* sp. (El Hacha)	AMNH	Costa Rica	outgroup
Mydidae: Diochlistinae	*Mitrodetus dentitarsis* (Macquart, 1850)	AMNH	Chile	outgroup
Mydidae: Ectyphinae	*Opomydas townsendi* (Williston, 1898)	AMNH CODI	USA	outgroup
Mydidae: Leptomydinae	*Nemomydas brachyrhynchus* (Osten-Sacken, 1889)	CODI	USA	outgroup; ♂ only
Mydidae: Leptomydinae	*Pseudonomoneura hirta* (Coquillett, 1904)	AMNH	USA	outgroup
Mydidae: Megascelinae	*Neorhaphiomidas* sp. (Mandurah)	ANIC	Australia	outgroup
Mydidae: Mydinae	*Mydas clavatus* (Drury, 1773)	AMNH	USA	outgroup
Mydidae: Rhaphiomidinae	*Rhaphiomidas maehleri* Cazier, 1941	AMNH	USA	outgroup
Mydidae: Syllegomydinae	*Afroleptomydas* sp. (Clanwilliam)	CODI	South Africa	outgroup
Nemestrinidae: Trichopsideinae	*Neorhynchocephalus volaticus* (Williston, 1883)	AMNH	USA	outgroup
Scenopinidae: Proratinae	*Prorates* sp. (Escalante)	CODI	USA	outgroup
Therevidae: Phycinae	*Phycus frommeri* Webb and Irwin, 1988	CODI	USA	outgroup
Therevidae: Xestomyzinae	*Hemigephyra atra* Lyneborg, 1972	CODI	South Africa	outgroup

BYU	Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (R. Nelson)
CAS	California Academy of Sciences, San Francisco, California (C. Griswold)
CODI	Collection of Torsten Dikow, New York City, New York
COGG	Collection of Fritz Geller-Grimm, Frankfurt am Main, Hessen, Germany
CSCA	California State Collection of Arthropods, Sacramento, California (E. Fisher)
CUIC	Cornell University Insect Collection, Ithaca, New York (J. Liebherr, E. Hoebeke)
FSCA	Florida State Collection of Arthropods, University of Florida, Gainesville, Florida (G. Steck)
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (C. Lamas)
NMSA	Natal Museum, Pietermaritzburg, KwaZulu-Natal, South Africa (J. Londt)
UCCC	Museo de Zoologia, Universidad de Concepción, Concepción, Chile (J. Artigas)
USNM	United States National Museum, Smithsonian Institution, Washington, DC (F. Thompson)
ZSMC	Zoologische Staatssammlung, München, Bayern, Germany (M. Kotrba)

PHYLOGENETIC ANALYSIS

MacClade (version 4.08, Maddison and Maddison, 2005) is used to enter the data and visualize cladograms found by the parsimony analysis. WinClada (version 0.9.99.88beta, Nixon, 2001) is used to evaluate character optimization/distribution and length of cladograms. The nomenclature for character optimizations applied follows WinClada, i.e., unambiguous, slow (= DELTRAN of MacClade), and fast (= ACCTRAN of MacClade). The parsimony analysis is conducted in TNT (version 1.0 [July 2004], Goloboff et al., 2001) under UNIX on a 1.33 GHz Apple PowerBook G4 computer. The following provides the commands issued to search for the most parsimonious trees: log 'file name'; mxram 200; proc 'file name'; tsave* 'file name'; hold 150000; mult300; ratchet=iter1500; drift=iter1500; save; nelsen*; save/; log/; (explanation of commands: open log file, set RAM to 200 MB, read matrix, open tree file, hold up to 150000 trees in memory, build 300 random addition sequence Wagner trees and perform TBR branch swapping (RAS+TBR), do 1500 iterations of the parsimony ratchet (Nixon, 1999), do 1500 iterations of tree drifting (Goloboff, 1999), save all trees, do strict consensus, save strict consensus as last tree to file and close tree file, close log file). Bremer support (Bremer, 1988, 1994) and relative Bremer support (Goloboff and Farris, 2001) are calculated in TNT. The Bremer support search is done in an incremental way as described by Giannini and Bertelli (2004) searching for suboptimal trees of one step longer than the most parsimonious tree, then two steps longer, and so on up to eight steps longer, holding an additional 5000 trees for each replicate (commands in script used: macro=; log 'file name'; mxram200; proc 'file name'; tsave* 'file name'; var 99; set 99 1; loop 1 8 subopt '99'; hold+5000; mult300; ratchet=iter1500; drift=iter1500; set 99 '99' + 1; stop save; bsupport=1; bsupport]; save/; log/; proc/; note: the number 99 is only a name for the variable and the set and does not affect the calculations). This search is started with the command "run 'file name'" and followed the same exhaustiveness as the searches for most parsimonious trees to sample the tree space as thoroughly as possible for suboptimal topologies. Relative Bremer support takes character conflict into account and provides a proportion as indicated in percent of the number of characters supporting a clade versus the number of characters contradicting the clade (Goloboff and Farris, 2001; Giannini and Bertelli, 2004).

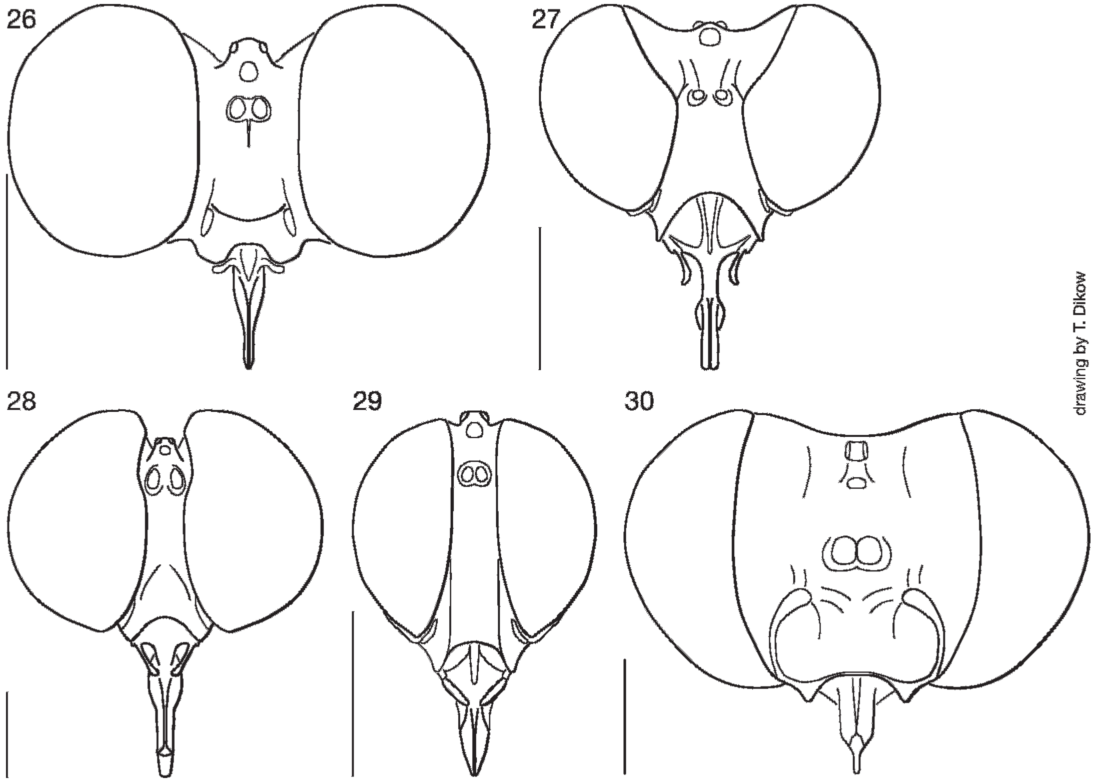
FIGURE ABBREVIATIONS FOR MORPHOLOGICAL CHARACTERS

The following abbreviations are found in the figures:

anatg = anatergite; **anepm** = anepimeron (mesothoracic); **anepst** = anepisternum (mesothoracic); **ant bas** = anterior basalare; **aprn** = antepronotum; **ax cord** = axillary cord; **cerc** = cercus/i; **cerv scl** = cervical sclerite; **cx** = coxa; **d** = dorsal; **d aed shea** = dorsal aedeagal sheath; **ej apod** = ejaculatory apodeme; **epand** = epandrium; **fem** = femur/femora; **goncx** = gonocoxite; **gonst** = gonostylus/i; **hlt** = halter/es; **hypand** = hypandrium; **hyphar** = hypopharynx; **kepm** = katepimeron (mesothoracic); **kepst** = katepisternum (mesothoracic); **ktg** = katatergite; **lat** = lateral; **lat ej proc** = lateral ejaculatory process; **lat pr gonst** = lateral process/es of gonostyli; **lbl** = labella (labium); **lbr** = labrum; **mes** = mesothoracic; **mes pnot** = mesopostnotum; **mes spr** = mesothoracic spiracle; **mes wg** = mesothoracic wing; **met** = metathoracic; **met spr** = metathoracic spiracle; **mr** = meron; **mtanepst** = metanepisternum; **mtepm** = metepimeron; **mtkepst** = metkatepisternum; **mtn** = metanotum; **mx** = maxilla; **plr wg proc** = pleural wing process; **post bas** = posterior basalare; **post ment** = postmentum (labium); **pprn** = postpronotum; **pprn lb** = postpronotal lobe; **pr epand** = proximal part of epandrium; **prepm** = proepimeron; **prepst** = proepisternum; **pre ment** = prementum (labium); **pro** = prothoracic; **sct** = scutum (mesonotum); **sctl** = scutellum (mesothoracic); **sur** = surstylus/i; **trn sut** = transverse suture; **troch** = trochanter; **v aed shea** = ventral aedeagal sheath.

CHARACTER ANALYSIS

Many of the characters employed here have been applied implicitly or explicitly in morphological and classificatory studies on Asilidae by previous authors. Of particular relevance are the studies by Hermann (1912, 1920), Melin (1923), Hardy (1927a, 1930, 1944, 1948), Reichardt (1929), Karl (1959), Hull (1962), Martin (1968), Papavero (1973a), and Theodor (1976). Additional morphological studies of other Diptera taxa containing useful information on characters were published by Hennig (1954, 1972, 1973, 1976), Woodley (1989), Sinclair et al. (1994), Yeates (1994), and Yeates and Irwin (1996). Many informative character complexes have emerged only during the detailed study of the many robber-fly species represented in the present analysis. The data matrix of 220 discrete, morphological features of imagines compiled from 175 species (158 Asilidae species and 17 outgroup species) is presented in appendix 1. Characters 1–67 pertain to structures of the head, characters 68–127 to thoracic structures including the legs, and characters 128–150 deal with structures of the wing. Characters 151–220 code for features of the abdomen, of which nine (characters 151–159) involve both females and males as semaphoronts and the remaining are divided into female (characters 160–185) and male (characters 185–220) structures. Characters 3 (vertex shape) and 128 (anterior margin of wings) are considered only in females and males, respectively. The majority of characters are binary (114 characters) and 106 characters are multistate. Thirty-one of the multistate characters could be considered to be part of an evolutionary transformation series (see table 8 and Discussion). All characters are treated as nonadditive (unordered), i.e., no constraints on evolutionary transformation sequences are imposed, and are parsimony informative. Following each character-state list, the optimization of the particular character on one of the most parsimonious cladograms (fig. 118) is provided, i.e., length in steps, consistency index (CI), and retention index (RI). A short character description and comments on the character-state distribution among the studied robber flies and Asiloidea is provided. Taxon names, e.g., Andrenosomatini and Willistonininae, refer to the concept of the newly proposed classification outlined in the Results section and summarized in table 6 to minimize confusion of the use of previous and new delimitations of taxa. Due to the nature of the exemplar approach employed here, the presence/absence of particular character states is based only on the species represented in the present analysis and no general statement of the distribution of character states in yet unstudied congeneric species is taken into consideration. This can be done only by including additional species in a larger, more comprehensive analysis using all characters employed here. Tables 2 and 6 list all included species and genera, respectively, with author and year of descrip-



Figs. 26–30. Heads in frontal view. **26.** *Holcocephala calva* (Trigonomiminae). **27.** *Stichopogon trifasciatus* (Stichopogoninae). **28.** *Clephydroneura* sp. (Kepong) (Asilinae). **29.** *Gonioscelis ventralis* (Stenopogoninae). **30.** *Opomydas townsendi* (Mydidae: Ectyphinae). Antennae and vestiture omitted. Scale lines = 1 mm.

tion and this information is omitted below. For outgroup taxa, the family name is always added in parentheses to the species name and when listed by itself refers only to the respective species included in the present study.

HEAD

1. SHAPE OF HEAD: (0) wider than high; (1) circular (as wide as high) (length = 2; CI = 0.50; RI = 0.80). The head of Asilidae is usually wider than high in anterior view (state 0; figs. 26–28). In *Broticosia paramonovi* (Dioctriinae) and *Gonioscelis ventralis*, *Ospriocerus aeacus*, *Scleropogon subulatus*, and *Stenopogon* species (all Stenopogoninae), the head is circular in anterior view (state 1; fig. 29). Among the outgroup taxa, the head is always wider than high (state 0).

2. COMPOUND EYE SEPARATION: (0) females and males dichoptic; (1) females dichoptic and males holoptic (length = 1; CI = 1.00; RI = 1.00). In Asilidae both genders possess dichoptic compound eyes (state 0; figs. 26–29). Among the outgroup taxa, the compound eyes of male representatives of Bombyliidae, Nemestrinidae, and Scenopinidae are holoptic (state 1).

3. VERTEX SHAPE BETWEEN COMPOUND EYES (IN DICHOPTIC FEMALES): (0) vertex and compound eyes at same level; (1) vertex slightly depressed (less than 60° angle on median margin of compound eyes); (2) vertex sharply depressed (90° angle on median margin of compound eyes) (length = 26; CI = 0.07; RI = 0.60). Hardy (1927a), Hennig (1973), and Oldroyd (1974a) discussed the depressed vertex in Asilidae and Mydidae. Woodley (1989) postulated the depressed

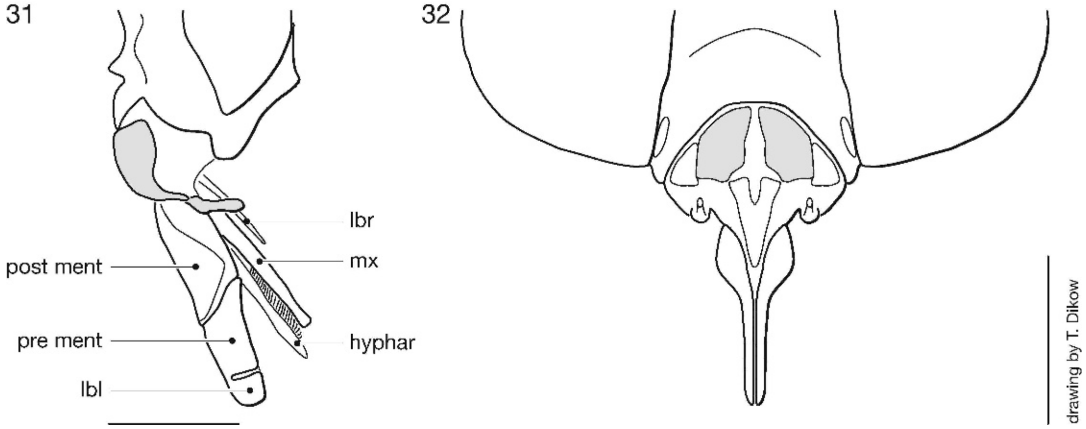
vertex in Mydidae as a possible autapomorphy and concluded that it has arisen independently in robber flies and mydas flies. Here, two different states for the depressed vertex are considered. A slightly depressed vertex is found in the majority of Asilidae (state 1; figs. 26–27). A sharply depressed vertex in which the median margin of the compound eyes is at an angle of 90° is found in Asilinae; most Dioctriinae; Laphriinae; Ommatiinae; and some other species (state 2; fig. 28). Among the outgroup taxa, the vertex is at the same level as the compound eye in most species (state 0), but in Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, a slightly depressed vertex is developed (state 1; fig. 30).

4. Extent of facial swelling: (0) not developed; (1) lower facial margin slightly protruding; (2) extending over lower facial half; (3) extending over lower three quarters; (4) extending over entire face (length = 60; CI = 0.06; RI = 0.52). Most species of Asilidae have a well-developed facial swelling of varying extent on which the mystax is situated (states 2, 3, 4). In *Afroholopogon peregrinus*, *Heteropogon manicatus*, *Holopogon priscus*, and *Metapogon punctipennis* (all Brachyrhopalinae) and Trigonomiminae, with the exception of *Damalis annulata* and *Damalis monochaetes*, the face is not developed (state 0). In Leptogastrinae except *Acronyches maya*; Stichopogoninae except *Lasiopogon* species; Willistonininae except *Acnephalum cylindricum*; and a few other robber-fly species, only the lower facial margin is slightly protruding (state 1). Among the outgroup taxa, the face extends over the entire height in Mydidae except *Neorhaphiomidas* sp. (Mandurah) (state 4), but not developed in the remaining outgroup taxa (state 0).

5. Division of face: (0) entire, no division evident; (1) divided, distinct ventral and dorsal halves developed; (2) divided, prominent ventral part and narrow dorsal part developed (length = 2; CI = 1.00; RI = 1.00). The face generally comprises a single sclerite and no transverse subdivision is evident (state 0; fig. 27). In species of *Holcocephala* (Trigonomiminae) it is divided into a ventral and a dorsal half of equal extent (state 1; fig. 26). Among the outgroup taxa, the face is usually undivided (state 0), but in Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, a large ventral part and a narrow dorsal part are separated by a transverse indentation (state 2; fig. 30).

6. Mystax: (0) absent; (1) present (length = 4; CI = 0.25; RI = 0.70). The mystax is considered to be an autapomorphic feature of the Asilidae (Oldroyd, 1974a; Woodley, 1989) composed of as little as two setae just dorsal of the fronto-clypeal suture to many setae covering the entire face (see character 7). The only Asilidae species without any mystacal setae is *Pseudorus distendens* (Dasypogoninae) (state 0). In Mydidae except *Neorhaphiomidas* sp. (Mandurah), the face is covered with macrosetae very similar in arrangement and extent to assassin flies and these species are therefore coded as possessing a mystax (state 1). This has previously been observed by Hardy (1927a) and Woodley (1989), although neither author homologized the setae in mydas and robber flies. Woodley (1989) stated that the mystax in robber flies is composed of strong macrosetae in contrast to other Diptera with only weak facial setae, but many robber flies, e.g., species of Leptogastrinae and Trigonomiminae, possess only very weak mystacal setae as well. The facial setae in Mydidae are separated medially by an asetose area, with the exception of *Mydas clavatus* and *Rhaphiomidas maehleri*, which is never found among Asilidae species.

7. Extent of mystax: (0) restricted to lower facial margin; (1) extending over lower half; (2) extending over lower three quarters, (3) extending over entire face (length = 60; CI = 0.05; RI = 0.46). The extent of the mystacal setae is often associated with the extent of the facial swelling (see character 4), but in a number of species, e.g., *Holopogon priscus* (Brachyrhopalinae) and *Connomyia varipennis* (Stenopogoninae), the mystax covers the entire face while the facial swelling is considerably less developed. In some Brachyrhopalinae; many Dasypogoninae; Dioctriinae; Leptogastrinae; Stichopogoninae except *Lasiopogon* species; and a few other species the mystax is restricted to the lower facial margin (state 0). All remaining char-



Figs. 31–32. Mouthparts. **31.** Head of *Apoclea algira* (Asilinae) in lateral view. Labrum, maxillae, and hypopharynx protruding from labium; stipites and maxillary palpus grey. For abbreviations see Materials and Methods. **32.** Head of *Choerades bella* (Laphriinae) in frontal view, clypeal sclerites grey. Vestiture omitted. Scale lines = 1 mm.

acter states are found widely within the major taxa of Asilidae. All outgroup taxa lacking a mystax are coded as inapplicable (-).

8. SHAPE OF MYSTAX: (0) setae loosely arranged; (1) setae tightly packed, forming a distinct shield (length = 2; CI = 0.50; RI = 0.80). The mystax is composed of loosely arranged setae that extend anteriorly over the proboscis (state 0). In *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae) as well as *Trichoura* sp. (Tierberg) and *Willistonina bilineata* (Willistonininae), the median setae are closely arranged, forming a shield covering the proboscis (state 1). All outgroup taxa lacking a mystax are coded as inapplicable (-).

9. CLYPEUS: (0) inverted U-shaped sclerite; (1) inverted U-shaped sclerite, dorsal half sclerotized to form a plate; (2) sclerites extended medially, nearly forming a single plate (length = 7; CI = 0.28; RI = 0.37). In Asilidae, the clypeus appears to be composed of a single plate with a median longitudinal suture (state 2; fig. 32). Among the outgroup taxa, the same configuration is also found in Apioceridae, Apsilocephalidae, *Afroleptomydas* sp. (Clanwilliam) (Mydidae), Scenopinidae, and Therevidae (state 2). In *Poecilognathus* sp. (El Hacha) (Bombyliidae), *Mitrodetus dentitarsis*, *Nemomydas brachyrhynchus*, *Neorhaphiomidas* sp. (Mandurah), and *Opomydas townsendi* (all Mydidae), and Nemestrinidae, the clypeus consists only of an inverted U-shaped sclerite (state 0). *Bombylius major* (Bombyliidae), *Mydas clavatus*, *Pseudonomoneura hirta*, and *Rhaphiomidas maehleri* (all Mydidae) possess an inverted U-shaped sclerite with the dorsal half forming a plate (state 1).

10. CLYPEAL-FACIAL MARGIN (FRONTOCLYPEAL SUTURE): (0) forming a distinct ridge; (1) smoothly rounded, not particularly pronounced (length = 5; CI = 0.20; RI = 0.33). The clypeal-facial margin is usually well developed and pronounced in Asilidae (state 0; fig. 31). A smoothly rounded and not particularly pronounced clypeal-facial margin is found in *Rhipidocephala* sp. (Harold Johnson) and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae) (state 1). Among the outgroup taxa, state 1 is also found in Apsilocephalidae, Nemestrinidae, Scenopinidae, and Therevidae.

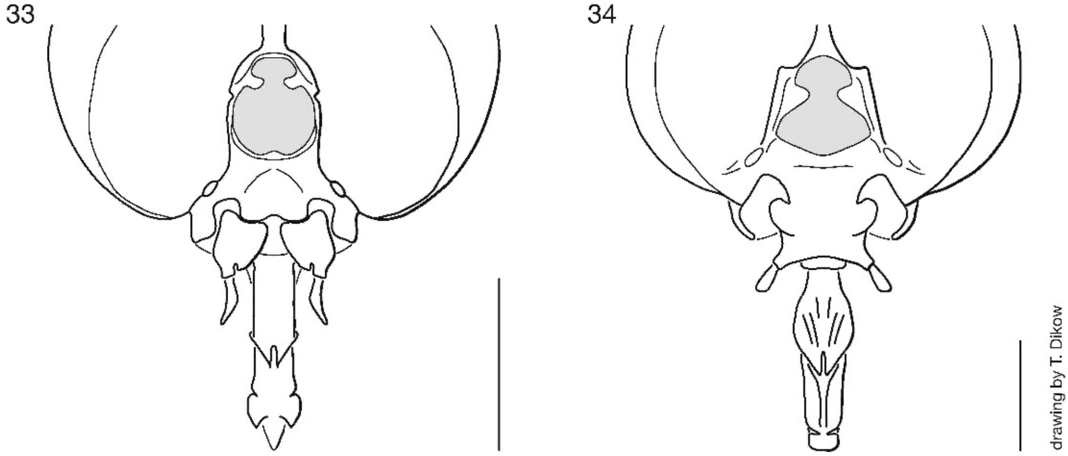
11. MAXILLARY PALPUS: (0) one-segmented; (1) two-segmented (length = 17; CI = 0.05; RI = 0.81). The number of maxillary palpomeres has been used extensively in Asilidae classifications in the past, e.g., Karl (1959), Hull (1962), Papavero (1973a), and Oldroyd (1974a). In the identification key to taxa provided by Hull (1962), it is used in the first couplet to divide the Asilidae into two large groups highlighting the diagnostic usefulness of this character in separating

species of Asilidae. However, Oldroyd (1974a) pointed out that it can be very difficult to count the palpomeres because genal setae often cover the maxillary palpi. Therefore, the heads are macerated here to be able to count the number of palpomeres correctly. One-segmented palpi are found in Asilinae; Bathypogoninae; Andrenosomatini, *Cerotainia albipilosa*, Ctenotini, *Goneccalypsis argenteoviridis*, *Loewinella nigripes*, *Orthogonis scapularis*, and *Smeryngolaphria numitor* (all Laphriinae); Leptogastrinae; Ommatiinae; *Townsendia albomacula* (Stichopogoninae); Trigonomiminae except *Rhipidocephala* sp. (Harold Johnson); and a few other species (state 0). Two-segmented palpi are found in Brachyrhopalinae; most Dasypogoninae and Dioctriinae; the remaining Laphriinae; Phellinae; Stenopogoninae, with the exception of *Daspletis stenoura* and *Microstylum* sp. (Karkloof); and Tillobromatinae (state 1). Among the outgroup taxa, the one-segmented palpi in Mydidae are interpreted as autapomorphic for this taxon by Woodley (1989) (state 0). Apioceridae, Apsilocephalidae, Scenopinidae, and Therevidae have two palpomeres (state 1) whereas Bombyliidae and Nemestrinidae possess only a single palpomere (state 0).

12. Sensory pit in distal palpomere: (0) absent; (1) present (length = 15; CI = 0.05; RI = 0.81). Sensory openings in palpomeres are often found among "nematoceran" Diptera. Yeates (1994) used this character in the Bombyliidae and some species of Asilidae possess a pit in the distal palpomere as well. It is found in one-segmented as well as two-segmented palpi (see character 11). A sensory pit is present in Brachyrhopalinae, with the exception of *Afroholopogon peregrinus* and *Dasycyrton gibbosus*; Dasypogoninae, with the exception of *Pegesimallus laticornis*, *Senobasis corsair*, *Megapoda labiata*, and *Pseudorus distendens*; *Echthodopa pubera* (Dioctriinae); *Hoplistomerus nobilis*, *Psilocurus modestus*, *Protometer* sp. (El Tuparro), and *Trichardis effrena* (all Laphriinae); Leptogastrinae; Stenopogoninae; with the exception of *Daspletis stenoura* and *Microstylum* sp. (Karkloof), Stichopogoninae; Tillobromatinae; *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae); and Willistonininae (state 1). Among the outgroup taxa, sensory pits are found in Apioceridae, Apsilocephalidae, *Bombylius major* (Bombyliidae), *Opomydas townsendi* (Mydidae), Scenopinidae, and Therevidae (state 1). E. Fisher (personal commun.) pointed out in his review of this publication that Laphriinae (except Andrenosomatini and possibly Atomosiini) always possess a sensory pit in contrast to my observations. In this study, the heads have been macerated to be able to examine the palpi in detail; moreover, no SEM micrographs were taken, which would have increased the chances of detecting a pit. I do not believe, although I cannot claim to know the truth, that my possible miscodings of a few Laphriinae species (and possibly other species) would change the cladistic relationships of the studied Asilidae species. I, therefore, suggest that future studies pay particular attention to this character and use SEM micrographs to verify the presence/absence of pits in the maxillary palpi.

13. Distal palpomere: (0) cylindrical; (1) laterally compressed (leaflike) (length = 2; CI = 0.50; RI = 0.83). The distal palpomere is usually cylindrical in Asilidae (state 0; fig. 31). Fisher (1986) employed the laterally compressed distal palpomere in species of Andrenosomatini (Laphriinae) as an autapomorphic feature. State 1 is found in all Andrenosomatini and Apioceridae and all remaining taxa have a simple, cylindrical distal palpomere (state 0).

14. Stipites fusion: (0) fused entirely medially; (1) fused medially, but with V-shaped indentation; (2) divided medially; (3) not sclerotized (length = 35; CI = 0.08; RI = 0.62). The stipites of the maxilla are two separated sclerites bearing the maxillary palpi in Diptera (McAlpine, 1981). In the Asilidae, the stipites are large platelike sclerites at the base of the proboscis (fig. 31) that can be fused medially or divided medially. In most Brachyrhopalinae, in Dasypogoninae, Leptogastrinae, and Trigonomiminae, and in some other species of various taxa the stipites are fused medially and form a single sclerite (state 0; fig. 34). In many Asilinae and Laphriinae; Ommatiinae; *Connomyia varipennis*, *Creolestes nigribarbis*, *Daspletis stenoura*, *Microstylum* sp. (Karkloof), and *Prolepsis tristis* (all Stenopogoninae); Tillobromatinae; and a few other species, the two



Figs. 33–34. Heads in posterior view. **33.** *Stichopogon trifasciatus* (Stichopogoninae). **34.** *Apoclea algira* (Asilinae). Occipital foramina grey; vestiture omitted. Scale lines = 1 mm.

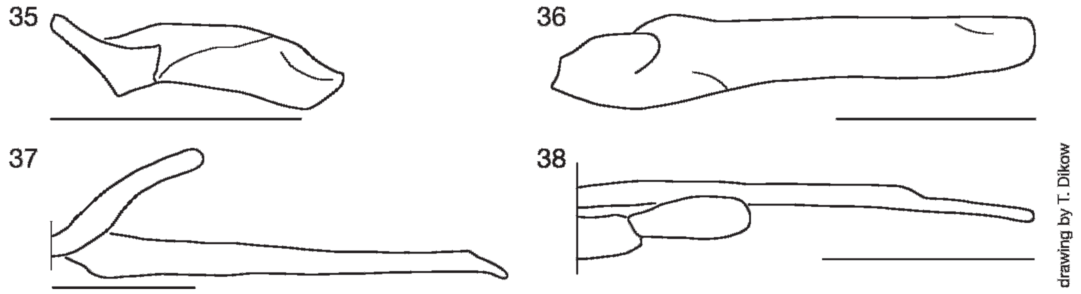
stipites are fused only partly and a V-shaped indentation is developed medially (state 1). In some Asilinae; Bathypogoninae; Dioctriinae; Laphriinae; *Gonioscelis ventralis*, *Ospriocerus aeacus*, *Scleropogon subulatus*, and *Stenopogon* species (all Stenopogoninae); Stichopogoninae; and other species the stipites are divided medially and a longitudinal fissure is evident that ends at the fusion line with the postgenae (state 2; fig. 33). Among the outgroup taxa, some Mydidae and Therevidae possess divided stipites (state 2) and the stipites in Nemestrinidae are not sclerotized (state 3).

15. Stipites fusion to postgenae: (0) separated; (1) fused (length = 3; CI = 0.33; RI = 0.86). The medioventral area of the posterior head of Diptera is formed by a sclerotized hypostomal bridge and called the postgenae (McAlpine, 1981). In Asilidae except *Holcocephala calva* (Trigonomiminae), the stipites are fused to the postgenae and only the lateral apices are free (state 1; figs. 33–34). Among the outgroup taxa, only Apioceridae also possesses fused stipites and postgenae (state 1) and in all other species the stipites are separated from the postgenae (state 0).

16. Medial projection of postgenae: (0) absent; (1) present (length = 2; CI = 0.50; RI = 0.66). In general, the postgenae are flat medially and this state is found in all Asilidae (state 0). Among the outgroup taxa, Apioceridae and *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* (Mydidae) possess a median projection on the postgenae (state 1).

17. Shape of proboscis: (0) straight; (1) angled slightly and evenly ventrally; (2) angled sharply ventrally and posteriorly; (3) distal tip angled slightly and evenly dorsally (length = 5; CI = 0.60; RI = 0.33). Most Asilidae species possess a more or less straight proboscis (state 0; fig. 31), but in a few species, the proboscis is angled dorsally or ventrally. An evenly ventrally angled proboscis is found in *Archilestris magnificus* and *Megapoda labiata* (Dasypogoninae) (state 1) and the distal tip is evenly angled dorsally in *Dasyllis funebris*, *Pilica formidolosa*, and *Proagonistes praeceps* (Laphriinae) (state 3). *Ancylorhynchus fulvicollis* (Stenopogoninae) is unique in that the proboscis is sharply angled ventrally and slightly posteriorly (state 2). Oldroyd (1974b) discussed the function and morphology of the proboscis in *Ancylorhynchus* in detail. Among the outgroup taxa, all species possess a straight proboscis (state 0).

18. Cross section of prementum proximally: (0) circular; (1) dorsoventrally flattened; (2) laterally compressed; (3) square; (4) not sclerotized (length = 14; CI = 0.28; RI = 0.78). The sclerotized labium in Asilidae forms a ventral sheath surrounding the maxillae and hypopharynx (fig. 31). In con-



Figs. 35–38. Labia and maxillary palpus and lacinia in lateral view. **35.** *Dioctria atricapillus* (Dioctriinae) labium. **36.** *Choerades bella* (Laphriinae) labium. **37.** *Colepia rufiventris* (Asilinae) lacinia. **38.** *Diogmites grossus* (Dasypogoninae) lacinia. Vestiture omitted. Scale lines = 1 mm.

trast to Crampton (1942: fig. 2F) and Wood (1981: 550), I consider the proximal part of the labium to be the postmentum and not the prementum (see fig. 31). In most Asilidae the prementum is more or less circular in diameter (state 0). A dorsoventrally flattened prementum is found in *Lycomya germainii* (Asilinae) and Andrenosomatini (Laphriinae) (state 1). A laterally compressed prementum is most pronounced in all Laphriini (Laphriinae; fig. 32) in which the proboscis appears knifelike, but the prementum is also laterally compressed although to a lesser degree in *Ceraturgus fasciatus*, *Chrysopogon pilosifacies*, and *Codula limbipennis* (all Brachyrhopalinae); Dasypogoninae, with the exception of *Dasypogon diadema*, *Lestomyia fraudiger*, *Saropogon* species, and *Threnia carbonaria*; *Daspletis stenoura* and *Microstylum* sp. (Karkloof) (Stenopogoninae); *Hypenetes stigmatias* (Tillobromatinae); and Trigonomiminae, with the exception of *Rhipidocephala* sp. (Harold Johnson) and *Trigonomima* sp. (*anamaliensis*) (state 2). A square cross section is found in *Dioctria* species and *Nannodioctria* sp. (*formicaphaga*) (Dioctriinae) (state 3). Among the outgroup taxa, an unsclerotized prementum without a distinct cross section is found in most species (state 4), with the exception of Bombyliidae, *Rhaphiomidas maehleri* (Mydidae), and Nemestrinidae, which have a circular prementum (state 0).

19. Ventral development of postmentum: (0) ventral margin entirely smooth; (1) median groove only in distal part; (2) median groove on entire length (length = 25; CI = 0.08; RI = 0.57). The postmentum, the proximal part of the labium (fig. 31), is usually smooth on its ventral surface and appears platelike in Asilidae (state 0). A median groove is developed in a number of species and the extent of this groove is variable. A short median groove restricted to the distal postmentum is present in *Blepharotes splendidissimus* (Asilinae); Bathypogoninae; *Ceraturgus fasciatus*, *Nannocyrtopogon lestomyiformis*, *Nicocles politus*, *Metapogon punctipennis*, and *Rhabdogaster pedion* (all Brachyrhopalinae); *Blepharepium cajennensis* (Dasypogoninae); Dioctriinae except *Broticosia paramonovi*; *Andrenosoma cyrtoxys*, *Dasyllis funebris*, *Hoplistomerus nobilis*, *Perasis transvaalensis*, *Proagonistes praeceps*, and *Smeryngolaphria numitor* (all Laphriinae); Phellinae; Stenopogoninae, with the exception of Stenopogonini; *Stichopogon punctum* (Stichopogoninae); and Willistoninae (state 1). A long median groove extending over the entire length of the postmentum is found in *Austrosaropogon nigrinus*, *Cophura brevicornis*, *Dasycyrton gibbosus*, and *Holopogon priscus* (all Brachyrhopalinae) and most Dasypogoninae (state 2). Among the outgroup taxa, state 2 is also found in Therevidae. All remaining outgroup taxa possess a smooth ventral margin (state 0).

20. Ventral margin of postmentum: (0) platelike, straight; (1) platelike, arched (length = 1; CI = 1.00; RI = 1.00). The ventral margin of the postmentum is usually straight in Asilidae (state 0; fig. 36) and only *Dioctria* species and *Nannodioctria* sp. (*formicaphaga*) (Dioctriinae) possess an arched postmentum (state 1; fig. 35). Among the

outgroup taxa, the postmentum is always platelike and straight (state 0).

21. POST- AND PREMENTUM FUSION: (0) not fused; (1) entirely fused (length = 4; CI = 0.25; RI = 0.81). The post- and prementum are generally separated by a membranous area and appear not entirely fused in most Asilidae (state 0; fig. 35). In *Megapoda labiata*, *Pseudorus distendens*, and *Senobasis corsair* (all Dasypogoninae), and Andrenosomatini, Ctenotini, Laphriini, *Hoplistomerus nobilis*, and *Perasis transvaalensis* (all Laphriinae), the post- and prementum are entirely fused (state 1; fig. 36). Among the outgroup taxa, post- and prementum are never fused (state 0).

22. DORSAL FLANGE MEDIALLY ON PREMENTUM: (0) absent; (1) present (length = 22; CI = 0.04; RI = 0.50). The two median, dorsal margins of the prementum can be elevated and form a flange that can be seen easily in lateral view. Most species of Asilidae lack such a median flange, i.e., Asilinae except *Proctacanthus philadelphicus*; Laphriinae; Leptogastrinae; Ommatiinae; Stichopogoninae except *Lasiopogon aldrichii*; Trigonomiminae except *Damalis* sp. (Palatupana); and some other species (state 0). Many Brachyrhopalinae; Dasypogoninae; Stenopogoninae; Willistonininae; and some other species possess a dorsal flange (state 1). Among the outgroup taxa, a dorsal flange is never developed (state 0).

23. LABELLA: (0) well developed and separated from prementum; (1) reduced, fused to prementum only ventrally; (2) reduced, fused to prementum entirely (length = 13; CI = 0.15; RI = 0.84). In Diptera the labella are generally enlarged lobes at the tip of the proboscis that function to take up liquids, yeasts, bacteria, spores, pollen, or other fine particles for nutrition. Hennig (1973) and Woodley (1989) recognized the reduced labella and the fusion to the prementum as an autapomorphy of Asilidae related to the predatory habit of the imagines. Upon close examination, it becomes apparent that the labella are not always entirely fused to the prementum, which has been highlighted for Dioctriinae species by Adisoemarto and Wood (1975), who used the presence/absence of a "subapical notch" dividing the labella dorsally from the prementum as a character. In Asilinae; Bathypogoninae; most Brachyrhopalinae; Ommatiinae; Phellinae; Stichopogoninae; and Willistonininae; and most Stenopogoninae, the labella are only partly fused to the prementum (state 1; fig. 31). In *Chrysopogon pilosifacies* and *Codula limbipennis* (Brachyrhopalinae); Dasypogoninae, with the exception of *Dasypogon diadema*, *Lestomyia fraudiger*, *Saropogon luteus*, and *Thereutria amaraca*; Laphriinae, with the exception of *Laphystia* species, *Laxenecera albicincta*, *Nusa infumata*, *Orthogonis scapularis*, *Protometer* sp. (El Tuparro), *Psilocurus modestus*, *Smeryngolaphria numitor*, *Trichardis effrena*, and *Zabrops tagax*; Leptogastrinae except *Acronyches maya*; *Daspletis stenoura* and *Microstylum* sp. (Karkloof) (Stenopogoninae); *Hypenetes stigmatias* and *Lycostommyia albifacies* (Tillobromatinae); and Trigonomiminae, the labella are entirely fused to the prementum (state 2; figs. 35–36). Among the outgroup taxa, the labella and prementum are always separated (state 0).

24. APEX OF LABELLA: (0) rounded; (1) pointed; (2) blunt; (3) enlarged, pseudotracheae present (length = 23; CI = 0.13; RI = 0.76). In the Asilidae the sclerotized labella can be of varying shape. In most species the tip is simple and rounded, i.e., in most Asilinae; Bathypogoninae; Leptogastrinae; Ommatiinae; Phellinae; and Willistonininae (state 0; fig. 31). A pointed proboscis is found in most Brachyrhopalinae; Dasypogoninae; Stenopogoninae; and Trigonomiminae (state 1). Within Laphriinae, states (0), (1), and (2) are found: Andrenosomatini, *Atomosia puella*, and *Perasis transvaalensis* possess a pointed proboscis (state 1), Ctenotini, *Cerotainia albipilosa*, Laphriini, *Orthogonis scapularis*, and *Smeryngolaphria numitor* possess a blunt tip (state 2; fig. 36; see also McAlpine, 1981; fig. 54), and the remaining taxa possess a rounded tip (state 0). Among the outgroup taxa, broadened labella with pseudotracheae are developed (state 3).

25. LENGTH OF LABELLA: (0) small, only forming distal tip of proboscis; (1) large, occupying from one-third to one-half the length of proboscis (length = 25; CI = 0.04; RI = 0.71). The length of the labella varies considerably in Asilidae and two character states are recognized here. Small labella,

which only form the distal tip of the proboscis, are found in Asilinae, with the exception of *Asilus crabroniformis*, *Blepharotes splendidissimus*, *Proctacanthus philadelphicus*, and *Satanas gigas*; Bathypogoninae; many Brachyrhopalinae; Leptogastrinae; Ommatiinae; Stichopogoninae; and Willistonininae, with the exception of *Acnephalum cylindricum* and *Sisyrnodytes* sp. (Gamka) (state 0; fig. 31). Large labella are found in Dasypogoninae except *Saropogon luteus*; Dioctriinae except *Broticosia paramonovi*; most Laphriinae; Phellinae; Stenopogoninae; Tillobromatinae; and Trigonomiminae (state 1; figs. 35–36). Among the outgroup taxa, both character states are present.

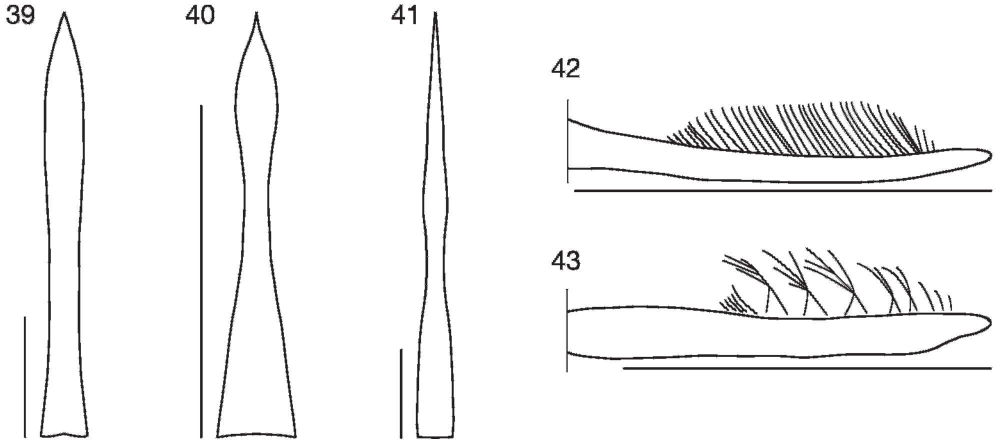
26. EXTENT OF SENSORY SETAE ON PREMENTUM AND LABELLA: (0) setae on prementum and labella; (1) setae restricted to labella (length =11; CI = 0.09; RI = 0.52). The labella and sometimes also the prementum possess sensory setae on the anterior, dorsal, and ventral surfaces and the extent of these setae varies among Asilidae. In general, the setae are restricted to the labella (state 1), but a few species, i.e., *Cabasa pulchella*, *Ceraturgus fasciatus*, *Cophura brevicornis*, *Heteropogon manicatus*, *Holopogon priscus*, *Nannocyrtopogon lestomyiformis*, *Nicocles politus*, and *Rhabdogaster pedion* (all Brachyrhopalinae); *Archilestris magnificus* and *Saropogon luteus* (Dasypogoninae); *Broticosia paramonovi* and *Myelaphus melas* (Dioctriinae); most Laphriinae; and *Coleomyia setigera*, possess setae on the labella and the prementum (state 0). All species in which the labella and prementum are entirely fused (see character 23) are coded as inapplicable (-) because no decision can be made concerning the border between the structures. Among the outgroup taxa, sensory setae are only developed on the labella (state 1).

27. LACINIA LENGTH: (0) shorter than labrum; (1) longer than labrum (length = 3; CI = 0.33; RI = 0.77). I follow Hennig (1973) and McAlpine (1981) in naming the maxillary blade (= endite) of the maxilla the lacinia. Martin (1968) stated that the maxillae of Leptogastrinae are only very poorly developed, a finding not supported here. The length of the lacinia does not vary among species of Asilidae, where it is always longer than the labrum (state 1), but in the outgroup taxa. Mydidae, Scenopinidae, and *Hemigephyra atra* (Therevidae) possess a shortened lacinia that is shorter than the labrum (state 0).

28. SHAPE OF LACINIA (LATERAL VIEW): (0) same height throughout; (1) proximally high, distal tip distinctly narrower: (2) tapered gradually toward tip (length = 18; CI = 0.11; RI = 0.74). Melin (1923) illustrated the laciniae of a number of robber flies and it can be seen that the shape of the laciniae varies greatly within Asilidae species. The laciniae are of equal height throughout and only the very distal tip might be narrowed as in Asilinae, with the exception of *Blepharotes splendidissimus* and *Proctacanthus philadelphicus*; Bathypogoninae; Dioctriinae; most Laphriinae; Leptogastrinae; Ommatiinae; most Stenopogoninae; Trigonomiminae; Tillobromatinae except *Lycostommyia albifacies*; and Willistonininae (state 0; fig. 37). A proximally high, distinctly narrowed lacinia distally with a dorsal notch is found in most Brachyrhopalinae; Dasypogoninae; Andrenosomatini except *Dasyllis funebris* and Ctenotini (all Laphriinae); Phellinae; and a few Stenopogoninae (state 1; fig. 38). A gradually tapered lacinia is found in *Blepharotes splendidissimus* (Asilinae); *Dasyllis funebris* (Laphriinae); and *Acnephalum cylindricum* (Willistonininae) (state 2). Among the outgroup taxa, state 2 is also found in Apsilocephalidae, Mydidae, Nemestrinidae, and *Phycus frommeri* (Therevidae) whereas all remaining species possess state 0. It is sometimes difficult to distinguish between states (1) and (2).

29. TIP OF LACINIA: (0) blunt; (1) pointed (length = 4; CI = 0.25; RI = 0.91). The tip of the lacinia is generally pointed in Asilidae (state 1; figs. 37–38), but in Asilinae, with the exception of *Asilus crabroniformis* and *Colepia rufiventris*; Ommatiinae; and *Willistonina bilineata* (Willistonininae) the tip is blunt (state 0; fig. 31). Among the outgroup taxa, blunt laciniae occur (state 0).

30. HYPOPHARYNX: (0) only weakly sclerotized; (1) heavily sclerotized (length = 1; CI = 1.00; RI = 1.00). The unpaired hypopharynx lies between the labrum and labium as a tonguelike structure. It is generally weakly sclerotized in Diptera, as is here found in all outgroup taxa (state 0), and more heavily sclerotized in blood sucking flies, e.g., Culic-



drawing by T. Dikow

Figs. 39–43. Hypopharynces in dorsal and lateral view. **39.** *Colepia rufiventris* (Asilinae) dorsal. **40.** *Acronyches maya* (Leptogastrinae) dorsal. **41.** *Archilestris magnificus* (Dasypogoninae) dorsal. **42.** *Stenopogon rufibarbis* (Stenopogoninae) tip in detail (lateral). **43.** *Acronyches maya* tip in detail (lateral). Spicules omitted from 39–41. Scale lines = 1 mm.

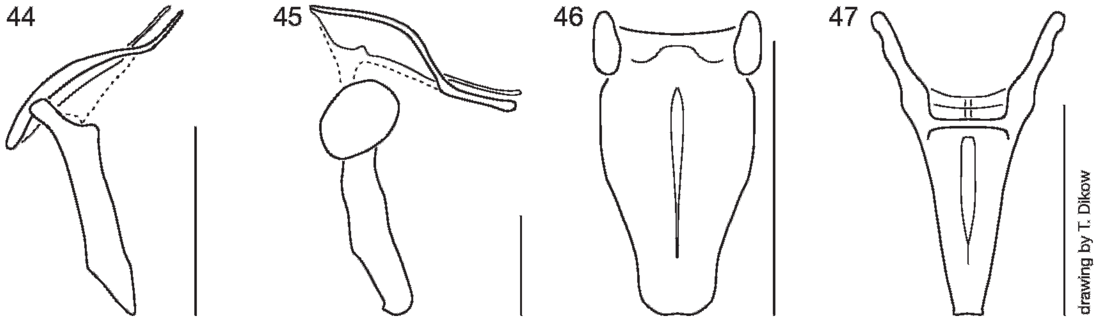
idae, Tabanidae, and Pupiparia, and predatory flies. Woodley (1989) recognized the heavily sclerotized, needlelike hypopharynx in all robber flies as an autapomorphy (state 1; figs. 39–41).

31. HYPOPHARYNX LENGTH: (0) short, shorter than labium; (1) long, as long as labium (length = 2; CI = 0.50; RI = 0.92). Yeates (1994) discussed the different lengths of the hypopharynx in several Asiloidea taxa and pointed out that it is relatively longer in Asilidae. Asilidae is coded to possess a long hypopharynx (state 1; fig. 31). Among the outgroup taxa, the hypopharynx is as long as the labium in *Bombylius major* (Bombyliidae) and Nemestrinidae (state 1) whereas it is shorter than the labium in all remaining taxa (state 0).

32. SHAPE OF SCLEROTIZED HYPOPHARYNX: (0) parallel-sided throughout, only distal tip suddenly pointed; (1) parallel-sided in proximal half, distal half much narrower; (2) tapering gradually toward distal tip (length = 15; CI = 0.13; RI = 0.76). The shape of the hypopharynx varies within Asilidae and most species have a parallel-sided hypopharynx with a suddenly pointed tip, i.e., Asilinae; Bathypogoninae; Dioctriinae, with the exception of *Broticosia paramonovi* and *Myelaphus melas*; Laphriinae; Leptogastrinae; Ommatiinae; most Stenopogoninae; Stichopogoninae; and Trigonomiminae (state 0; figs. 39–40). A proximally parallel-sided and distally gradually tapering hypopharynx is found in most Brachyrhopalinae; Dasypogoninae; Phellinae; Tillobromatinae; and a few other species (state 1; fig. 41). Among the outgroup taxa, most species possess a gradually tapering hypopharynx (state 2), with the exception of Apioceridae and Nemestrinidae, which exhibit state 0.

33. HYPOPHARYNX DORSAL PROTUBERANCES: (0) absent; (1) present, seta-like spicules spaced close together; (2) present, seta-like spicules spaced far apart (length = 4; CI = 0.50; RI = 0.91). Melin (1923) illustrated the strong seta-like spicules on the dorsal margin of the hypopharynx and called it “bristly covering.” These spicules are only present in Asilidae, but two different developments are apparent. In the majority of species, they are spaced close together (state 1; fig. 42), but in Leptogastrinae; *Plesiomma* sp. (Guanacaste) (Stenopogoninae); and *Trichoura* sp. (Tierberg) (Willistonininae) these spicules are spaced far apart (state 2; fig. 43). Among the outgroup taxa, spicules are absent (state 0).

34. LENGTH OF LABRUM: (0) long, as long as labium (or nearly so); (1) short, at most half the length of labium (length = 1; CI = 1.00; RI = 1.00). All Asilidae possess a short labrum that is at most half as long as the labium (state 1; fig. 31) whereas all outgroup taxa possess a long labrum (state 0).



Figs. 44–47. Cibarium. 44–45. Cibarium with attached pharyngeal pump in lateral view (dotted lines indicate unsclerotized cuticle connecting both structures, anterior = left). **44.** *Dioctria hyalipennis* (Dioctriinae). **45.** *Lycomya germainii* (Asilinae). 46–47. Cibarium in posterior view. **46.** *Willistonina bilineata* (Willistonininae). **47.** *Dioctria hyalipennis*. Scale lines = 0.5 mm.

35. DORSOPOSTERIOR MARGIN OF CIBARIUM: (0) simple, no particular ridge connecting cornua; (1) one transverse ridge connecting cornua, cornua originating from ridge; (2) one transverse ridge connecting cornua, cornua not originating from ridge (length = 9; CI = 0.22; RI = 0.89). Yeates (1994) pioneered the study of internal head structures across Asiloidea by illustrating the cibarium and tentorium for many representatives. The cibarium functions as a food pump and is associated with the hypopharynx (Snodgrass, 1944; McAlpine, 1981). Its shape varies within Asilidae and the transverse ridges between the cornua (see character 37) are absent only in Ctenotini (Laphriinae); *Cophinopoda chinensis* (Ommatiinae); *Gonioscelis ventralis* (Stenopogoninae); and *Willistonina bilineata* (Willistonininae) (state 0; fig. 46). A single transverse ridge from which the cornua originate is present in Brachyrhopalinae; Dasypogoninae; Dioctriinae; Laphriinae except Ctenotini; *Acronyches maya* (Leptogastrinae); Phellinae; Stenopogoninae except Stenopogonini; Stichopogoninae; Tillobromatinae; and Trigonomiminae (state 1; fig. 47). In Asilinae; Bathypogoninae; the remaining Leptogastrinae; Ommatiinae; and Stenopogoninae a single transverse ridge is found, but the cornua do not originate from this ridge (state 2). Among the outgroup taxa, no transverse ridges are developed (state 0).

36. SHAPE OF CIBARIUM: (0) trapezoidal; (1) smoothly rounded; (2) dorsally narrow and ventrally broad (length = 2; CI = 1.00; RI = 1.00). Yeates (1994) found that the shape of the cibarium varies within Asiloidea and all Asilidae species he studied possess a trapezoidal cibarium. This is confirmed here and only Asilidae have a trapezoidal cibarium (state 0; figs. 46–47). Among the outgroup taxa, all species possess a smoothly rounded cibarium (state 1), with the exception of *Mydas clavatus* (Mydidae), which has a dorsally narrow and ventrally broad cibarium (state 2; see figs. in Yeates, 1994).

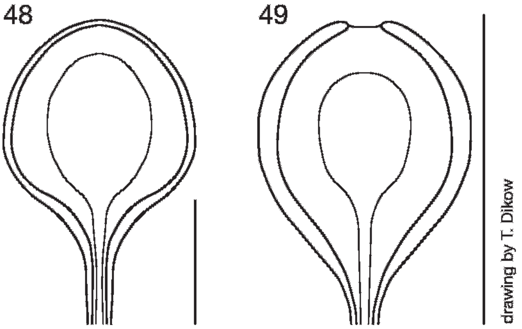
37. DEVELOPMENT OF CORNUA OF CIBARIUM: (0) well developed in anteroposterior orientation; (1) well developed in dorsoventral orientation; (2) reduced or absent (length = 12; CI = 0.16; RI = 0.82). Melin (1923) illustrated the cibarium (referred to as pharynx) in lateral view, highlighting the cornua pharyngis, i.e., the dorsolateral attachment of the protractor muscles, which can be oriented differently. Following Owsley (1946), these muscle attachment projections are here simply termed cornua. Martin (1968) stated that all Leptogastrinae possess only reduced cornua, a finding not supported here. Yeates (1994) called the cornua "posterior arms of cibarium" and discussed the different orientation in Bombyliidae. In Asilidae, the orientation varies as well and in Asilinae; *Holopogon priscus* (Brachyrhopalinae); *Loewinella nigripes* (Laphriinae); Leptogastrinae, with the exception of *Acronyches maya* and *Beameromyia bifida*; Ommatiinae, with the exception of *Cophinopoda chinensis* and *Ommatius tibialis*; Stenopogonini except *Gonioscelis ventralis* (Stenopogo-

ninae); and Stichopogoninae the cornua are oriented in an anterior-posterior fashion (state 0; fig. 45). In the remaining Asilidae and outgroup taxa the cornua are oriented in a dorsoventral fashion (state 1; fig. 44). In *Beameromyia bifida* (Leptogastrinae); *Mydas clavatus* (Mydidae), and Nemestrinidae, the cornua are reduced or absent (state 2).

38. Median longitudinal ridge on cibarium: (0) absent; (1) present (length = 2; CI = 0.50; RI = 0.93). Yeates (1994) mentioned that all Asilidae studied possess a median longitudinal ridge on the cibarium. This ridge is found here in all Asilidae and *Neorhaphiomidas* sp. (Mandurah) (Mydidae) (state 1; figs. 46–47), but absent in all remaining outgroup taxa (state 0).

39. Pharyngeal pump: (0) absent; (1) present (length = 3; CI = 0.33; RI = 0.71). Melin (1923) referred to the pumping structure dorsal to the cibarium as the swollen esophagus, which is later termed pharyngeal pump by Owsley (1946). The anterior part of this pump is situated between or just dorsal of the cornua (Owsley, 1946). It is present in all Asilidae and most outgroup taxa (state 1; figs. 44–45), with the exception of Bombyliidae and some Mydidae species (state 0).

40. Pharyngeal pump development: (0) laterally without sclerotized ring; (1) laterally with sclerotized ring, but medio-anteriorly unsclerotized; (2) with entirely sclerotized ring (length = 11; CI = 0.18; RI = 0.75). The lateral margin of the pharyngeal pump can be unsclerotized or possess a sclerotized ring of varying extent. The lateral margin is unsclerotized in Phellinae; Stenopogoninae, with the exception of *Creolestes nigribarbis* and *Plesiomma* sp. (Guanacaste); Tillobromatinae; and Willistonininae except *Ablautus coquilletti* (state 0). A sclerotized ring that is not entirely closed medio-anteriorly is found in the majority of Asilidae and all outgroup taxa (state 1; fig. 49). An entirely sclerotized ring is present in *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Megapoda labiata*, and *Pseudorus distendens* (all Dasypogoninae); Atomosiini except *Smeryngolaphria numitor* and Laphriini (Laphriinae); as well as *Plesiomma* sp. (Guanacaste) (Stenopogoninae) (state 2; fig. 48). All species not possessing a pharyngeal pump (see character 39) are coded as inapplicable (-).

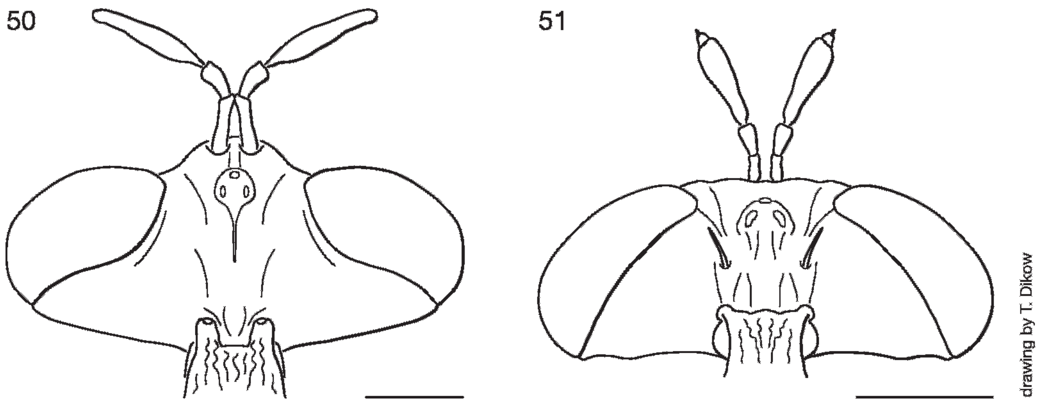


Figs. 48–49. Pharyngeal pump in dorsal view. **48.** *Orthogonis scapularis* (Laphriinae). **49.** *Dioctria hyalipennis* (Dioctriinae). Scale lines = 0.5 mm.

41. Pharyngeal pump shape (dorsal view): (0) circular; (1) triangular (length = 10; CI = 0.10; RI = 0.47). In dorsal view, the pharyngeal pump is generally circular (state 0; figs. 48–49), but in a few species it is more or less of triangular shape, i.e., *Dasypogon diadema* and *Lestomyia fraudiger* (Dasypogoninae); Phellinae; Stenopogoninae, with the exception of *Ancylorhynchus fulvicollis*, *Gonioscelis ventralis*, *Plesiomma* sp. (Guanacaste), and *Prolepsis tristis*; Tillobromatinae except *Hypenetes stigmatias*; and *Sisyrnodytes* sp. (Gamka) (Willistonininae) (state 1). Among the outgroup taxa, Apsilocephalidae is the only taxon with a triangular pharyngeal pump (state 1). All species not possessing a pharyngeal pump (see character 39) are coded as inapplicable (-).

42. Dorsal margin of postocciput: (0) simple, no projections; (1) triangular projection present (length = 3; CI = 0.33; RI = 0.93). The dorsal margin of the postocciput is usually not particularly pronounced although in some instances a narrow ridge is developed (state 0; fig. 51). In *Dasycyrton gibbosus* (Brachyrhopalinae); *Myelaphus melas* (Dioctriinae); and Laphriinae, a prominent triangular projection is present that is best seen in dorsal view (state 1; fig. 50). Among the outgroup taxa, all species exhibit state 0.

43. Shape of occipital foramen: (0) a single foramen; (1) two apparent foramina divided by a bridge (length = 1; CI = 1.00; RI = 1.00). Yeates (1994) highlighted the variation in development of the occipital foramina in Asiloidea and here the majority of species possess a single foramen (state 0;



Figs. 50–51. Heads in dorsal view. **50.** *Dasyllis funebris* (Laphriinae). **51.** *Pegesimallus laticornis* (Dasypogoninae). Vestiture omitted except for setae on median occipital sclerite. Scale lines = 1 mm.

figs. 33–34). Two distinct foramina are present only in Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* (state 1).

44. ANTERIOR TENTORIAL PITS: (0) small, slitlike, inconspicuous, ventrally located; (1) well developed, conspicuous, anteroventrally located; (2) well developed, conspicuous, anteromedially located; (3) absent (not observable) (length = 5; CI = 0.60; RI = 0.84). Papavero (1973a) used the development of the anterior tentorial pits (referred to as deep, mediogenal grooves), as a diagnostic character for the Trigonomiminae. In most Asilidae species, the tentorial pits are small, slitlike, and inconspicuously positioned more or less ventrally (state 0; figs. 27–29, 32). In all Trigonomiminae, they are well developed, conspicuous, and positioned anteroventrally on the head (state 1; fig. 26). In *Phellus olgae* (Phellinae) and *Plesiomma* sp. (Guanacaste) (Stenopogoninae), the tentorial pits are positioned much more dorsal on the head and this position is coded as a separate character state (state 2). Among the outgroup taxa, state 0 is primarily found, but state 2 is observed in Mydidae (fig. 30), with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, and in *Poecilognathus* sp. (El Hacha) (Bombyliidae) the anterior tentorial pits appear to be absent (state 3).

45. FACIAL SETAE: (0) only circular setae; (1) circular and dorsoventrally flattened setae laterally in males and females; (2) circular and dorsoventrally flattened mystacal setae in males; (3) circular and dorsoventrally flattened mystacal setae in males and females (length = 9; CI = 0.33; RI = 0.25). In Asilidae, the well-developed facial setae are usually only circular (state 0), but a few species possess setae of different cross section. The facial setae are sometimes differently developed among female and male specimens of a single species. Circular as well as dorsoventrally flattened setae that are positioned laterally to the mystax in males and females are found only in Laphriini except *Laphria flava* (Laphriinae) (state 1). Circular and dorsoventrally flattened mystacal setae are present in males only of *Goneccalypsis argenteoviridis*, *Orthogonis scapularis*, and *Perasis transvaalensis* (all Laphriinae) (state 2). The same mystacal setae are present in females and males of *Smeryngolaphria numitor* (Laphriinae); *Lissoteles aquilonius* (Stichopogoninae); and *Ablautus coquilletti* and *Sisyrnodytes* sp. (Gamka) (Willistonininae) (state 3). *Pseudorus distendens* (Dasypogoninae), which does not possess any facial setae, is coded as inapplicable (-). Among the outgroup taxa, only circular setae are developed (state 0).

46. SIZE OF ANTERIOR MEDIAN OMMATIDIA: (0) all same size; (1) at least some median ommatidia distinctly larger (length = 26; CI = 0.03; RI = 0.64). As early as Walker (1851), dipterists realized that the median ommatidia of the flattened compound eyes of an assassin fly are often enlarged. Although it

is sometimes difficult to determine whether the median ommatidia are larger than surrounding lateral ones, I attempted to code this character. The majority of Asilidae species possess larger ommatidia medially (state 1) with notable exceptions of all Bathypogoninae; Phellinae; and Stenopogoninae, in which all ommatidia are of the same size (state 0). Among the outgroup taxa, all ommatidia are of the same size (state 0).

47. POSTGENAE: (0) posterior margin simple, smoothly rounded; (1) posterior margin with large flangelike projection (length = 1; CI = 1.00; RI = 1.00). The posterior margin of the postgenae is generally smoothly rounded in Asilidae and all outgroup taxa (state 0). In *Lamyra gulo* and *Stiphrolamyra angularis* (Laphriinae) it is developed as a flangelike projection. Londt (1988) used this character (referred to as posterior margin of lower occiput) in an identification key to Afrotropical Laphriinae diagnosing the two genera. See character 16. Among the outgroup taxa, the postgenae are smoothly rounded (state 0).

48. SHAPE OF FRONS (AT LEVEL OF ANTENNAL INSERTION): (0) more or less parallel-sided; (1) markedly and suddenly diverging laterally; (2) markedly approximating medially (length = 5; CI = 0.40; RI = 0.70). The frons is usually parallel-sided as wide at the ventral margin as at the level of antennal insertion in Asilidae (state 0; figs. 26, 28–29). In a few species, i.e., *Cerotainia albipilosa* (Laphriinae); Stichopogoninae; as well as *Trichoura* sp. (Tierberg) and *Willistonina bilineata* (Willistonininae), the frons is markedly and suddenly diverging laterally (state 1; fig. 27). The opposite case is found in *Acronyches maya* (Leptogastrinae) and *Plesiomma* sp. (Guanacaste) (Stenopogoninae), in which the compound eyes approximate each other markedly at the level of the antennal insertion (state 2). Among the outgroup taxa, a parallel-sided frons is present (state 0).

49. MACROSETAE ON LATERAL MARGIN OF FRONS, DORSAL TO ANTENNAL INSERTIONS: (0) absent; (1) present (length = 30; CI = 0.03; RI = 0.40). Asilidae usually possess setae on the lateral margin of the frons dorsal to the antennal insertions. These setae can be particularly well developed and form strong macrosetae. Regular setae are present in Brachyrhopalinae; Leptogastrinae; Ommatiinae; Tillobromatinae; Trigonomiminae; and Willistonininae (state 0) whereas all remaining major taxa have at least some representatives possessing stronger macrosetae (state 1). Among the outgroup taxa, no macrosetae are developed (state 0).

50. LONGITUDINAL RIDGE MEDIALLY ON FRONS, DORSAL TO ANTENNAL INSERTION: (0) absent; (1) present, connecting antennae and ocellar triangle (length = 2; CI = 0.50; RI = 0.50). A longitudinal ridge medially on the frons is developed in *Cerotainia albipilosa*, *Goneccalypsis argenteoviridis*, and *Loewinella nigripes* (all Laphriinae) (state 1) whereas it is absent in all remaining Asilidae (state 0). Among the outgroup taxa, a longitudinal ridge is absent (state 0).

51. POSITION OF ANTENNAE ON HEAD: (0) in ventral half; (1) in dorsal half (length = 5; CI = 0.20; RI = 0.42). The position of the antennae on the head varies within Asiloidea. In all Asilidae, the antennae are positioned in the dorsal half of the head (state 1; figs. 26–29). Among the outgroup taxa, in Apsilocephalidae, *Bombylius major* (Bombyliidae), and Mydidae except *Neorhaphiomidas* sp. (Mandurah) the antennae are positioned in the dorsal half (state 1), but in the remaining taxa, the antennae originate in the ventral half of the head (state 0).

52. DISTANCE BETWEEN SCAPICES: (0) scapices close together, touching; (1) scapices separated (length = 2; CI = 0.50; RI = 0.83). Yeates and Irwin (1996) established the very closely associated scapices as an autapomorphy of Mydidae. In the present analysis, only Mydidae except *Neorhaphiomidas* sp. (Mandurah) possess closely associated scapices (state 0; fig. 30) and all remaining taxa possess separated scapices (state 1; figs. 26–29).

53. ELEVATION OF ANTENNAL INSERTION: (0) not elevated; (1) elevated above eye margin in lateral view, with distinct protuberance (length = 8; CI = 0.12; RI = 0.61). The antennal insertion is usually not visible in lateral view on a robber-fly head. A few species possess a protuberance on which the antennae originate and the base of the scape is therefore visible in lateral view, i.e., *Austrosaropogon nigrinus* and *Cabasa pul-*

chella (Brachyrhopalinae); *Cyrtophrys attenuatus* and *Saropogon luteus* (Dasypogoninae); Dioctriinae except *Broticosia paramonovi*; *Cerotainia albipilosa* and Laphriini (Laphriinae); and *Ospriocerus aeacus* (Stenopogoninae) (state 1). Among the outgroup taxa, the antennal insertion is not elevated (state 0).

54. SHAPE OF POSTPEDICEL: (0) tapering distally; (1) cylindrical, same diameter throughout; (2) medially broadest, long; (3) elongated and distinctly clubbed distally; (4) proximal bulb with elongated distal part; (5) medially broadest, short (length = 44; CI = 0.11; RI = 0.66). In Brachycera the postpedicel is situated distal to the pedicel. In Asilidae and other "orthorrhaphous" taxa, it is "a compound structure formed by sequential distal fusion of the third segment with successive distal segments" (Stuckenberg, 1999: 41) of varying length. All parts distal to the postpedicel are considered here to comprise the stylus (see characters 57–58) (Stuckenberg, 1999). Contrary to the view of Hennig (1972: fig. 29), the postpedicel of Mydidae is considered to entail the cylindrical proximal part and the expanded distal part, which are separated by an unsclerotized part (see character 56). The shape of the postpedicel varies considerably in Asilidae and five character states (fig. 52) are employed here to account for this morphological diversity. The character-state distribution is as follows: Asilinae: state 1, *Lycomya germainii*; state 2, *Threnia carbonaria*; state 5, *Dasophrys crenulatus*, *Eichoichemus pyrrhomystax*, *Lochmorhynchus albicans*, *Philodicus tenuipes*, *Pogonioefferia pogonias*, *Proctacanthus philadelphicus*, and *Promachus amastrus*; state 0, all remaining species; Bathypogoninae, state 2; Brachyrhopalinae: state 0, *Dasycyrton gibbosus*, *Holopogon priscus*, and *Heteropogon manicatus*; state 2, *Brachyrhopala ruficornis* and *Cabasa pulchella*; state 1, all remaining species; Dasypogoninae: state 1, *Archilestris magnificus*, *Cyrtophrys attenuatus*, and *Dasypogon diadema*; state 2, all remaining species; Dioctriinae: state 2, *Eudioctria albius* and *Nannodioctria* sp. (*formicaphaga*); state 1, all remaining species; Laphriinae: state 1, *Atomosiini*, *Hoplistomerus nobilis*, *Laphystia aegyptiaca*, and *Perasis transvaalensis*; state 2, all remaining species; Leptogastrinae: state 1, *Acronyches maya*; state 0, all remaining species; Ommatiinae: state 0, *Michotamia aurata*; state 5, all remaining species; Phellinae: state 1, *Phellus olgae*; state 2, *Obelophorus terebratus*; Stenopogoninae: state 0, *Scleropogon subulatus* and *Stenopogon* species; state 2, *Creolestes nigribarbis*, *Daspletis stenoura*, and *Microstylum* sp. (Karkloof); state 1, all remaining species; Stichopogoninae: state 1, *Lasiopogon cinctus* and *Townsendia albomacula*; state 5, *Lissoteles aquilonius*; state 0, all remaining species; Tillobromatinae: state 1, *Lycostommyia albifacies*; state 2, all remaining species; Trigonomiminae: state 4, *Damalis* species; state 1, all remaining species; Willistonininae: state 2, *Ablautus coquilletti* and *Willistonina bilineata*; state 0, all remaining species. Outgroup taxa: state 0, Apsilocephalidae, *Bombylius major* (Bombyliidae), and Scenopinidae; state 1, *Poecilognathus* sp. (El Hacha) and Therevidae; state 2, *Rhaphiomidas maehleri* (Mydidae); state 3, Mydidae except other mentioned species; state 5, Apioceridae and *Neorhaphiomidas* sp. (Mandurah) (Mydidae).

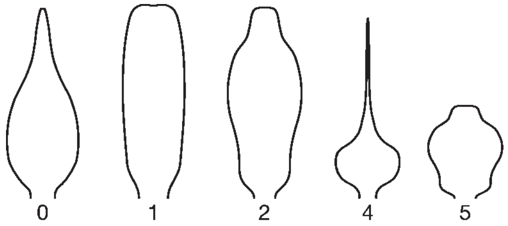
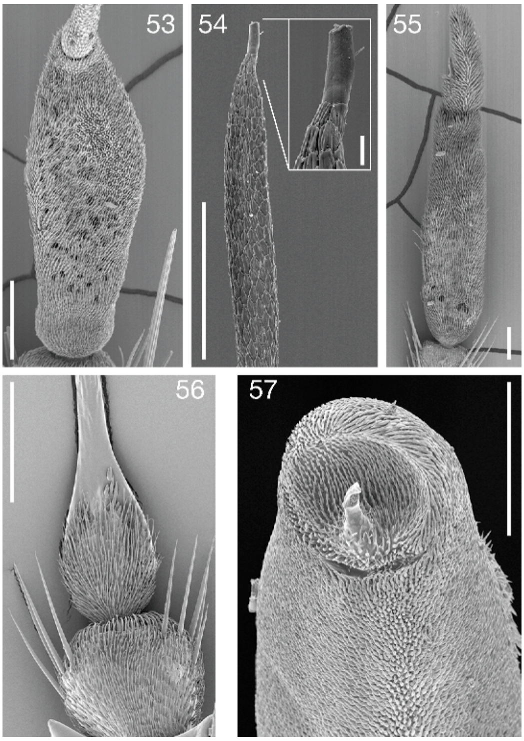


Fig. 52. Schematic drawing of shape of postpedicel coded in character 54 with character states indicated. Character state 3, which is only found in Mydidae, not illustrated; vestiture omitted; not to scale.

55. SETAE DORSALLY ON POSTPEDICEL: (0) absent; (1) present (length = 32; CI = 0.03; RI = 0.63). Many species of Asilidae possess setae on the dorsal surface of the postpedicel (state 1; fig. 53). Setae are absent in Bathypogoninae; Leptogastrinae; Phellinae; Tillobromatinae; and several other species (state 0). *Lampria clavipes* (Laphriinae) and *Ospriocerus aeacus* (Stenopogoninae) are coded polymorphic (0/1), as individuals with and without setae are examined. Among the outgroup taxa, setae are present only in Apioceridae, *Poecilognathus* sp. (El Hacha)



Figs. 53–57. SEM micrographs of antennae in lateral view. **53.** *Dysmachus trigonus* (Asilinae) postpedicel. **54.** *Philonicus albiceps* (Asilinae) stylus and enlarged apical "seta-like" sensory element. **55.** *Dioctria atricapillus* (Dioctriinae) postpedicel and stylus. **56.** *Damalis femoralis* Ricardo, 1925 (Trigonomiminae), base of postpedicel with apical "seta-like" sensory element. **57.** *Hoplistomerus nobilis* (Laphriinae) tip of postpedicel with apical "seta-like" sensory element. Scale lines = 100 μm except for inset scale line = 10 μm.

(Bombyliidae), as well as *Neorhaphiomidas* sp. (Mandurah), *Opomydas townsendi*, and *Rhaphiomidas maehleri* (all Mydidae) (state 1).

56. Sclerotization of postpedicel: (0) entirely sclerotized; (1) cylindrical proximal part and bulbous distal part separated by unsclerotized area (length = 1; CI = 1.00; RI = 1.00). Asiloidea species usually possess an entirely sclerotized postpedicel (state 0), but in Mydidae, with the exception *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, an unsclerotized median part is developed (state 1, see character 54).

57. Position of apical 'seta-like' sensory element: (0) apically on stylus; (1) apically in cavity on stylus; (2) subapically in cavity on postpedicel; (3) subapically and laterally on stylus; (4) apically in cavity on postpedicel; (5) subapically and laterally on postpedicel (length = 31; CI = 0.16; RI = 0.69). Papavero (1973a) discussed the development and position of the stylus in Asilidae in detail. The nomenclature pertaining to these parts is adjusted here to make more meaningful homology statements, however. The stylus in "orthorrhaphous" Brachycera (= part of flagellum sensu McAlpine, 1981) was defined by Stuckenberg (1999: 41) as, "the structure consisting of any free segments distal to the pedicel, hypothesized to terminate apically in segment 10." Hennig (1972) called the terminal element of the stylus that corresponds to the tip of segment 10 *Endgriffel*, and this element was termed *apical "seta-like" sensory element* by Dikow and Londt (2000). As the stylus is fused to the postpedicel in stepwise fashion (Stuckenberg, 1999, see characters 54 and 58), only the apical "seta-like" sensory element is differentiable and its position on the stylus or postpedicel varies greatly within Asilidae. In Asilinae; Bathypogoninae; most Brachyrhopalinae; Leptogastrinae; Ommatiinae; most Willistonininae; and several other species the apical "seta-like" element is situated apically on the stylus (state 0; figs. 53–54). In *Austrosaropogon nigrinus* and *Cyrtopogon rattus* (Brachyrhopalinae); *Dasypogon diadema*, *Lestomyia fraudiger*, *Megapoda labiata*, *Pegesimallus laticornis*, and *Saropogon* species (all Dasypogoninae); *Hoplistomerus nobilis*, *Laphystia species*, *Nusa infumata*, *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), *Psilocurus modestus*, *Trichardis effrena*, and *Zabrops tagax* (all Laphriinae); *Phellus olgae* (Phellinae); *Ancylorhynchus fulvicollis*, *Ospriocerus aeacus*, *Plesiomma* sp. (Guanacaste), and *Scylaticus costalis* (all Stenopogoninae); Tillobromatinae; *Willistonina bilineata* (Willistonininae); and *Coleomyia setigera* the apical "seta-like" element is situated apically on the stylus, but in a distinct apical cavity (state 1; fig. 57). In *Chrysopogon pilosifacies* and *Codula limbipennis* (Brachyrhopalinae); *Deromyia fuscipennis* (Dasypogoninae); and *Damalis* species (Trigonomiminae), the apical "seta-like" element is situated in a subapical cavity on

the postpedicel (state 2, e.g.; fig. 56). In *Ceraturgus fasciatus* (Brachyrhopalinae); Dioctriinae; *Townsendia albomacula* (Stichopogoninae); and *Rhipidocephala* sp. (Harold Johnson) (Trigonomiminae); the apical "seta-like" element is situated subapically laterally on the stylus (state 3; fig. 55). A "seta-like" element is situated in an apical cavity on the postpedicel in *Brachyrhopala ruficornis* and *Cabasa pulchella* (Brachyrhopalinae); most Dasypogoninae; Andrenosomatini, Ctenotini, Laphriini, and *Laxenecera albicincta* (all Laphriinae); *Daspletis stenoura* and *Prolepsis tristis* (Stenopogoninae); and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae) (state 4). It is situated subapically and laterally on the postpedicel in *Cyrtophrys attenuatus* (Dasypogoninae) and Atomosiini (Laphriinae) (state 5). Among the outgroup taxa, *Hemigephyra atra* (Therevidae) and Scenopinidae exhibit state 1 and *Poecilognathus* sp. (El Hacha) (Bombyliidae) and Mydidae exhibit state 4 whereas all remaining taxa possess an apical "seta-like" sensory element apically on the stylus (state 0).

58. Stylus: (0) three elements; (1) two elements; (2) one element; (3) reduced, only apical "seta-like" sensory element present (length = 33; CI = 0.09; RI = 0.68). The stylus (see characters 54 and 57) in Asilidae is generally composed of one or two elements (states 1 and 2). In *Brachyrhopala ruficornis*, *Cabasa pulchella*, *Chrysopogon pilosifacies*, and *Codula limbipennis* (all Brachyrhopalinae); most Dasypogoninae; Andrenosomatini, Atomosiini, Ctenotini, Laphriini, and *Laxenecera albicincta* (all Laphriinae); *Daspletis stenoura* and *Prolepsis tristis* (Stenopogoninae); and *Damalis* species and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae), the stylus is only represented by the apical "seta-like" sensory element (state 3). Among the outgroup taxa, a three-segmented stylus is only present in Nemestrinidae (state 0) and the remaining states are also represented in the outgroup taxa.

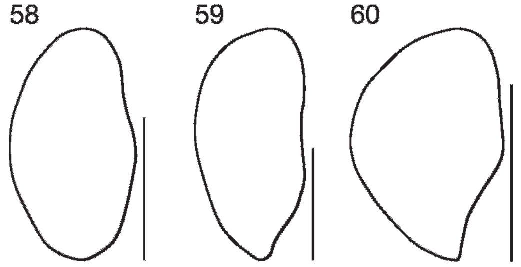
59. Setae on stylus: (0) absent; (1) present on anterior surface only; (2) present on all surfaces (length = 2; CI = 1.00; RI = 1.00). Hardy (1927a), in erecting the tribe Ommatiini, pointed out the setose antennae of species of *Ommatius* Wiedemann, 1821 and other genera. All Ommatiinae are found here to possess setae on the anterior surface of the stylus (state 1) and *Oligopogon* sp. (Cape Recife) possesses setae on all surfaces of the stylus (state 2). Among the outgroup taxa, all species lack setae on the stylus (state 0). All species, in which the stylus is reduced to the apical "seta-like" element (see character 58), are coded as inapplicable (-).

60. Ocelli on ocellar triangle: (0) three ocelli on a single ocellar triangle; (1) anterior ocellus separate, situated anteriorly (length = 1; CI = 1.00; RI = 1.00). In Diptera the three ocelli are usually situated on a single ocellar triangle (McAlpine, 1981) and this is found in all Asilidae (state 0; figs. 26–29, 50–51). Among the outgroup taxa, in Apioceridae and Mydidae, the anterior ocelli are separated and are situated more anteriorly (state 1; fig. 30) whereas they are situated on a single ocellar triangle in the remaining species (state 0).

61. Development of posterior ocelli: (0) circular or slightly oval; (1) distinctly elongated (length = 1; CI = 1.00; RI = 1.00). Yeates and Irwin (1996) highlighted the distinct elongation of the posterior ocelli in Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, and this is confirmed here (state 1; fig. 30). All remaining taxa have three equally large, circular to slightly oval ocelli (state 0; figs. 26–29, 50–51).

62. Ocellar (oc) setae: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 36; CI = 0.05; RI = 0.60). Hardy (1930) described the development of ocellar setae in Australian robber flies in detail. Most Asilidae species possess setae or macrosetae on the ocellar triangle (states 1 and 2), but they are found to be absent in Leptogastrinae (state 0). Among the outgroup taxa, there are either no setae (state 0) or only regular setae developed (state 1).

63. Shape of postcranium: (0) flat to convex; (1) concave (length = 2; CI = 0.50; RI = 0.87). Yeates (1994) observed a distinctly concave postcranium in many Bombyliidae. In the present analysis, a concave postcranium is found in Bombyliidae, Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, and Nemestrinidae (state 1). All



Figs. 58–60. Compound eyes in lateral view. **58.** *Pegesimallus laticornis* (Dasypogoninae). **59.** *Pogonioefferia pogonias* (Asilinae). **60.** *Stichopogon trifasciatus* (Stichopogoninae). Anterior = left. Scale lines = 1 mm.

Asilidae and remaining outgroup taxa possess a flat to slightly convex postcranium (state 0).

64. SHAPE OF POSTERIOR COMPOUND EYE MARGIN (LATERAL VIEW): (0) straight or slightly curved anteriorly throughout; (1) sinuate in ventral quarter; (2) distinctly sinuate in ventral half (length = 7; CI = 0.28; RI = 0.85). The majority of Asilidae have a more or less oval-shaped compound eye in lateral view (state 0; fig. 58). In most Asilinae, with the exception of *Blepharotes splendidissimus*, *Clephydroneura species*, *Heligmonevra laevis*, *Lycomya germainii*, and *Satanas gigas*; as well as *Lestomyia fraudiger* (Dasypogoninae); and Willistonininae, with the exception of *Acnephalum cylindricum* and *Sisyrnodytes* sp. (Gamka), the ventral quarter is angled anteriorly and the ventral part of the eye is much narrower than the dorsal half (state 1; fig. 59). All Stichopogoninae are outstanding in that the ventral half is much narrower than the dorsal half and the compound eye appears sinuate in lateral view (state 2; fig. 60). Among the outgroup taxa, all species possess state 0.

65. MACROSETAE ON MEDIAN OCCIPITAL SCLERITE (M OCP SCL): (0) absent; (1) two distinct macrosetae; (2) more than two macrosetae (length = 10; CI = 0.20; RI = 0.55). The median occipital sclerite is situated ventral to the vertex and between the compound eyes and often entirely fused to the occiput (McAlpine, 1981). In Dasypogoninae, the sclerite is relatively easy to distinguish and in most instances, more than two macrosetae are situated on it (state 2). In *Archilestris magnificus* and *Pseudorus distendens*, no setae are developed (state 0; fig. 50) and in *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Pegesimallus laticornis*, and *Senobasis corsair*, only two macrosetae are present (all Dasypogoninae) (state 1; fig. 51). In *Heteropogon manicatus* (Brachyrhopalinae); *Hyperechia nigripennis* (Laphriinae); *Daspletis stenoura* (Stenopogoninae); *Lycostommyia albifacies* (Tillobromatinae); and *Acnephalum cylindricum* and *Sisyrnodytes* sp. (Gamka) (Willistonininae), more than two macrosetae are developed as well (state 2). Among the outgroup taxa, all species lack any macrosetae (state 0).

66. POSTOCULAR (POCL) SETAE: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 17; CI = 0.11; RI = 0.42). Postocular setae, often also labeled occipital setae in robber flies, are present in all Asilidae studied and most species possess macrosetae and regular setae (state 2). Only regular setae are developed in Phellinae; Trigonomiminae, with the exception of *Damalis monochaetes*; and a few Brachyrhopalinae; Leptogastrinae; Dasypogoninae; and other species (state 1). Among the outgroup taxa, all three character states are observed.

67. SHAPE OF POSTOCULAR (POCL) SETAE: (0) straight or only slightly angled anteriorly; (1) sharply angled anteriorly in distal half (length = 12; CI = 0.08; RI = 0.26). The postocular setae are usually straight or only slightly angled anteriorly in Asilidae (state 0). In *Dasophrys crenulatus*, *Neoitamus cyanurus*, and *Neolophonotus bimaculatus* (all Asilinae); *Nannocyrtopogon lestomyiformis* (Brachyrhopalinae); *Dicolonus simplex* and *Echthodopa pubera* (Dioctriinae); *Laphria* species (Laphriinae); *Emphysomera* species and *Ommatius incurvatus* (Ommatiinae); *Creolestes nigribarbis*, *Gonioscelis ventralis*, and *Stenopogon rufibarbis* (all Stenopogoninae); and *Lasiopogon* species (Stichopogoninae), the setae are long and sharply angled anteriorly in the distal half (state 1). Among the outgroup taxa, all species possess straight postocular setae (state 0).

THORAX

For reference; figure 61 illustrates the thoracic features of an exemplar species.

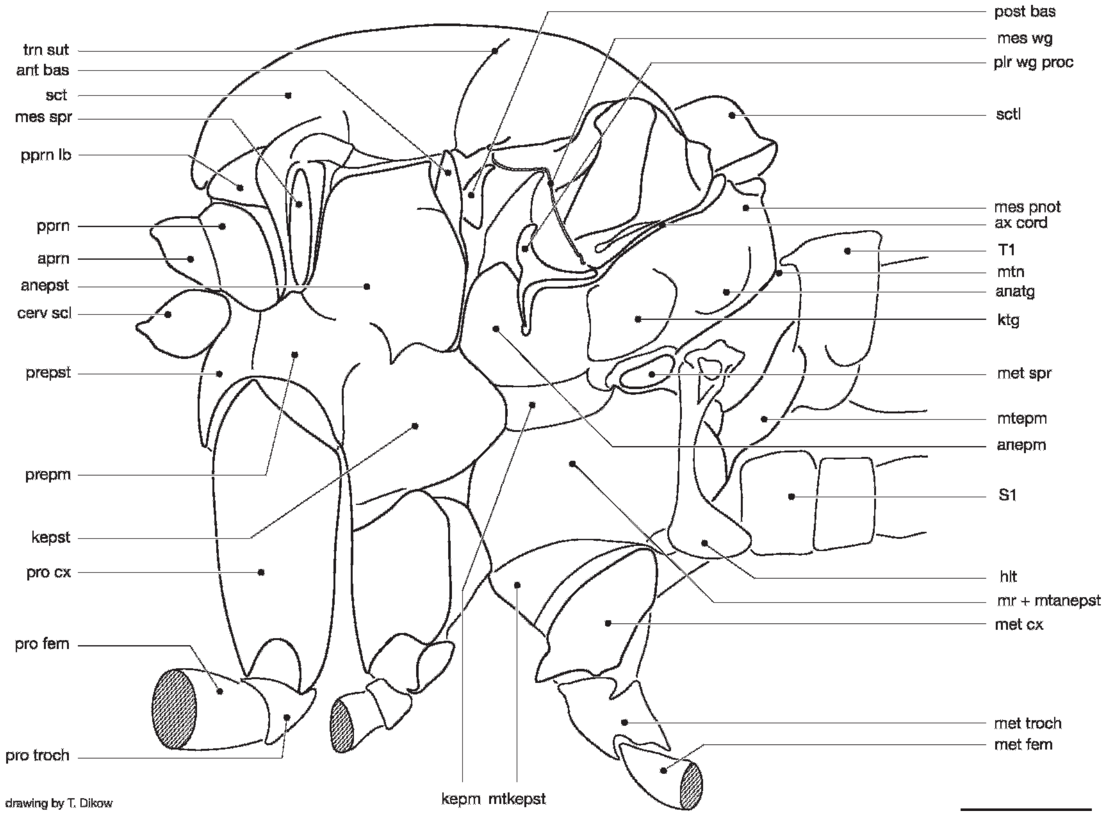


Fig. 61. Thorax of *Philonicus albiceps* (Asilinae) in lateral view with morphological features labeled. Wing and vestiture omitted; abbreviations see Materials and Methods. Scale line = 1 mm.

Osten-Sacken (1884) established a nomenclature of setae in Diptera, called *chaetotaxy*, and discussed certain setal arrangements in Asilidae. Later, Hardy (1930) provided a table summarizing the presence/absence of thoracic setae, including notopleural, postalar, supra-alar, and scutellar setae (see characters 88, 90–92, 94, 98), in Asilidae. Figure 62 provides an overview of thoracic setae coded in the present study.

68. DIVISION OF PRONOTUM: (0) only a single sclerite present; (1) divided into ante- and postpronotum (length = 1; CI = 1.00; RI = 1.00). In all Asilidae, the pronotum is divided into ante- and postpronotum (state 1; figs. 61, 64–65) (Martin, 1968). Among the outgroup taxa, the same arrangement is also found in Apioceridae, Mydidae, and Therevidae, whereas all remaining species possess a single sclerite (state 0).

69. ANTEPRONOTAL SETAE: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 28; CI = 0.07; RI = 0.67). The antepronotum is usually setose in Asilidae and setae are absent only in Leptogastrinae except *Acronyches maya* and *Nannodioctria* sp. (*formicaphaga*) (Dioctriinae) (state 0). All Stichopogoninae; most Brachyrhopalinae, Trigonomiminae, Dioctriinae, and Laphriinae possess only regular setae (state 1) while macrosetae are developed in most species of the remaining taxa (state 2). Among the outgroup taxa, all character states are found.

70. LATERAL POSTPRONOTAL (PPRN) SETAE: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 20; CI = 0.10; RI = 0.48). The lateral surfaces of the postpronotum are asetose in Leptogastrinae except *Acronyches*

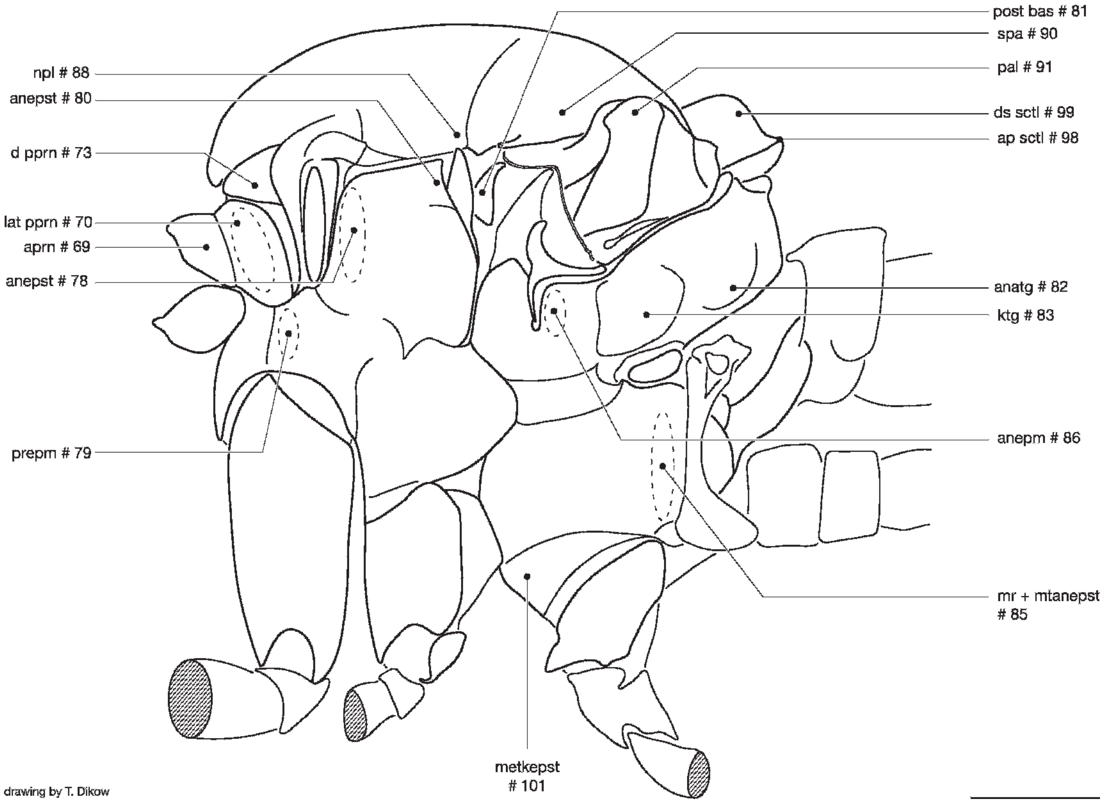
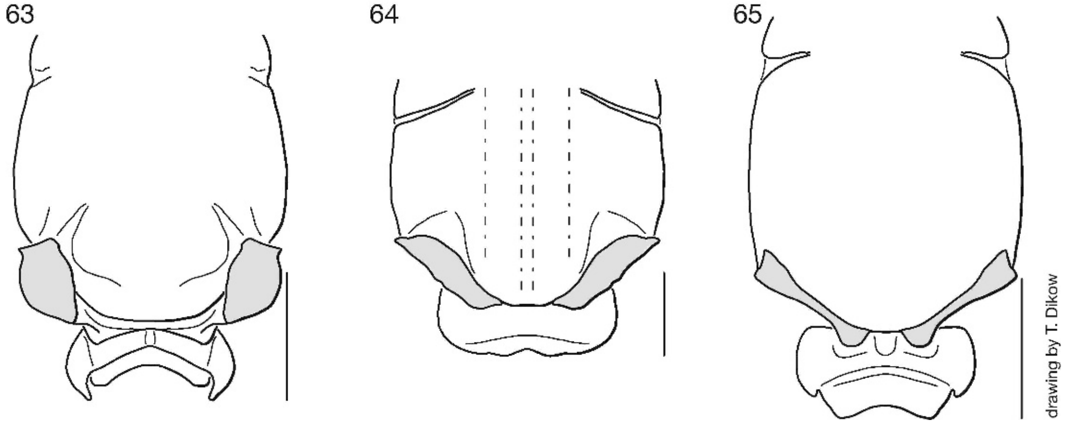


Fig. 62. Thorax of *Philonicus albiceps* (Asilinae) in lateral view with chaetotaxic characters mapped. Dotted lines indicate setose areas; wing and vestiture omitted; for abbreviations see Materials and Methods and variously numbered character descriptions. Scale line = 1 mm.

maya; *Brachyrhopala ruficornis* (Brachyrhopalinae); *Nannodioctria* sp. (*formicaphaga*) (Dioctriinae); and *Goneccalypsis argenteoviridis* and *Loewinella nigripes* (Laphriinae) (state 0). Most species possess at least some setae on the lateral postpronotum (state 1), but most Dasypogoninae, Stenopogoninae, and a few other species possess macrosetae (state 2). Among the outgroup taxa, Apioceridae and *Rhaphiomidas maehleri* (Mydidae) possess macrosetae and regular setae (state 2) whereas all remaining species possess only regular setae (state 1). All species in which the pronotum is not divided into an ante- and postpronotum (see character 68) are coded as inapplicable (-).

71. Dorsal fusion of postpronotal lobes with scutum: (0) entirely fused; (1) only partly fused, lobes elevated above scutum posteriorly (length = 2; CI = 0.50; RI = 0.90). In all Asilidae the postpronotal lobes are entirely fused with the scutum although the sutures are still discernible (state 0; figs. 64–65). Among the outgroup taxa, the lobes are elevated above the scutal surface and not fused with it posteriorly in Bombyliidae, Mydidae, Nemestrinidae, and Scenopinidae (state 1; fig. 63).

72. Postpronotal lobes: (0) confined to lateral margin of scutum; (1) extending medially, but not anteriorly; (2) extending medially and anteriorly, nearly touching medially (length = 3; CI = 0.66; RI = 0.95). Martin (1968) established the medially and anteriorly extending postpronotal lobes as an autapomorphy of his Leptogastridae. All Asilidae exhibit medially extending postpronotal lobes (state 1; fig. 64), but Leptogastrinae except *Acronyches maya* possess medially and anteriorly extending lobes (state 2; fig. 65). Among the outgroup taxa, the postpronotal lobes are usually confined to

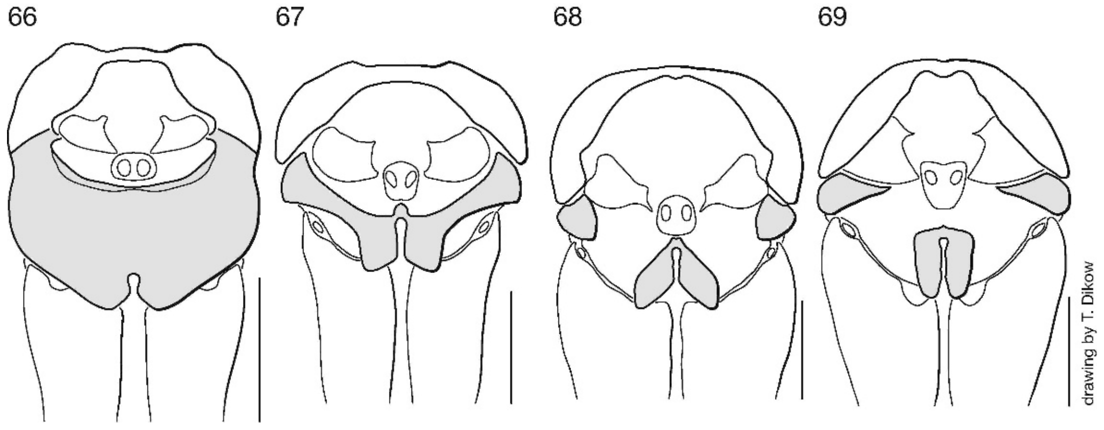


Figs. 63–65. Thoraces in anterodorsal view (anterior = bottom). **63.** *Nemomydas brachyrhynchus* (Mydidae: Leptomydinae). **64.** *Dasyllis funebris* (Laphriinae), dotted lines = acrostichal (medially) and dorsocentral (laterally) setae. **65.** *Lasiocnemus lugens* (Leptogastrinae). Postpronotal lobes grey; vestiture omitted. Scale lines = 1 mm.

the lateral scutal margin (state 0) and only in the Scenopinidae do they also extend medially (state 1).

73. Dorsal postpronotal (pprn) setae: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 23; CI = 0.08; RI = 0.50). The postpronotal setae on the anterodorsal surface of the postpronotal lobes are usually present in Asilidae and only a few species lack regular setae (state 0). The majority of species possess setae (state 1) and most Dasypogoninae and Stenopogoninae possess macrosetae (state 2). Among the outgroup taxa, setae (state 1) and macrosetae (state 2) are present.

74. Lateral fusion of prosternum to proepisternum: (0) fused, broad prosternum; (1) fused, prosternum narrow above prothoracic coxa; (2) separated, sclerite triangular, pointed dorsally; (3) separated, sclerite square to rectangular, straight dorsally; (4) separated, prosternum square and proepisternum projecting medially (nearly touching prosternum) (length = 31; CI = 0.12; RI = 0.76). Hardy (1930, 1948), Clements (1951), Hull (1962), Papavero (1973a), and Oldroyd (1974a) discussed in detail the development of the prosternum in relation to its lateral fusion to the proepisternum in Asilidae. Five character states are employed here and a completely fused, broad prosternum is present in all Stichopogoninae; Leptogastrinae, with the exception of *Acronyches maya* and *Tipulogaster glabrata*; and many Laphriinae (state 0; fig. 66). The prosternum and proepisternum are fused, but the prosternum is narrower above the coxa in all Trigonomiminae; some Asilinae and Laphriinae; and a few other species (state 1; fig. 69). A triangular, separate prosternum surrounded by membrane that is pointed dorsally is found in Tillobromatinae except *Tillobroma punctipennis*; Willistonininae except *Willistonina bilineata*; many Asilinae and Stenopogoninae; *Afroholopogon peregrinus*, *Ceraturgus fasciatus*, and *Heteropogon manicatus* (all Brachyrhopalinae); and *Obelophorus terebratus* (Phellinae) (state 2; fig. 68). A similar development is found in all Bathypogoninae and Dioctriinae; most Brachyrhopalinae and Dasypogoninae; a few Asilinae and Stenopogoninae; and some other species in that the prosternum is separate and surrounded by membrane but square to rectangular in shape with a straight dorsal margin (state 3; fig. 67). In *Ommatius* species (Ommatiinae) the prosternum is separate and square and the proepisternum is projecting medially to nearly touch the prosternum (state 4). Among the outgroup taxa, Apsilocephalidae, Mydidae, and Scenopinidae possess a fused prosternum and proepisternum (state 0) whereas they are fused and narrow above the coxa in Therevidae (state 1). The remaining outgroup taxa



Figs. 66–69. Thoraces in anterior view. **66.** *Stichopogon trifasciatus* (Stichopogoninae). **67.** *Emphysomera pallidapex* (Ommatiinae). **68.** *Pogonioefferia pogonias* (Asilinae). **69.** *Pegesimallus laticornis* (Dasypogoninae). Prosternum and proepisternum grey; vestiture omitted. Scale lines = 1 mm.

possess a free prosternum that is triangular in shape (state 2).

75. DORSAL (ANTERIOR) MARGIN OF PROSTERNUM: (0) not elevated; (1) distinct flangelike projection (length = 10; CI = 0.10; RI = 0.84). The dorsal (anterior) margin of the prosternum is usually not particularly pronounced (state 0; fig. 69), but in a few species a distinct dorsal flangelike projection is evident (state 1; fig. 66). It is found in all Laphriinae and Trigonomiminae; Leptogastrinae, with the exception of *Acronyches maya* and *Tipulogaster glabrata*; Stichopogoninae except *Lasiopogon* species; *Dicolonus simplex* and *Dioctria* species (Dioctriinae); *Hypenetes stigmatias* (Tillobromatinae); and *Oligopogon* sp. (Cape Recife) within Asilidae (state 1). Among the outgroup taxa, only Mydidae except *Rhaphiomidas maehleri* possess a flangelike projection (state 1).

76. SHAPE OF PROPRESTERNUM: (0) arrowlike sclerite; (1) square sclerite; (2) triangular sclerite (length = 3; CI = 0.66; RI = 0.90). Yeates (1994) used the shape of the propresternum in the phylogeny of Bombyliidae and emphasized the different shape within Asiloidea. All Asilidae possess a square propresternum that possesses two distinct sclerites bearing sensory setae (state 1; figs. 66–69). Among the outgroup taxa, an arrowlike sclerite is found in Apsilocephalidae, Bombyliidae, Nemestrinidae, and Therevidae (state 0). Apioceridae, *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* (Mydidae), and Scenopinidae possess a square sclerite similar to Asilidae (state 1) while the remaining Mydidae species possess a triangular sclerite (state 2).

77. DEVELOPMENT OF CERVICAL SCLERITE: (0) not extending medially to cover sensory area on propresternum; (1) extending medially to cover sensory area on propresternum (length = 2; CI = 0.50; RI = 0.87). The median margin of the cervical sclerite is closely associated with the propresternum, but usually does not come in contact with it (state 0; figs 66–69). In Mydidae and Nemestrinidae, the median margin is extended and covers the sensory setae of the propresternum partly (state 1). In all Asilidae and all remaining outgroup taxa, the cervical sclerite is not touching the propresternum (state 0).

78. ANTERIOR ANEPISTERNAL SETAE: (0) absent; (1) erect; (2) erect to appressed, pointed anteriad (length = 25; CI = 0.08; RI = 0.66). In Asilidae, the anterior and dorsal margins of the anepisternum possess usually short to long setae. These setae are absent in all Bathypogoninae and Dasypogoninae; most Stenopogoninae and Stichopogoninae; some Brachyrhopalinae and a few other species (state 0). In many Asilidae, the anterior anepisternal setae are erect and more or less perpendicular to the surface (state 1). In Leptogastrinae except *Acronyches maya*, and *Dioctria* species, *Echtho-*

dopa pubera, and *Myelaphus melas* (all Dioctriinae), the setae are directed anteriorly and lightly appressed to the surface of the anepisternum (state 2). Other species of Dioctriinae lack these setae (state 0), i.e., *Broticosia paramonovi*, *Eudioctria albius*, and *Nannodioctria* sp. (*formicaphaga*), whereas *Dicolonus simplex* possesses only erect setae (state 1). Among the outgroup taxa, anepisternal setae are usually absent (state 0) and erect setae are present in Bombyliidae, *Neorhaphiomidas* sp. (Mandurah) (Mydidae), Nemestrinidae, and *Phycus frommeri* (Therevidae) (state 1).

79. ANTERIOR PROEPIMERAL SETAE: (0) absent; (1) erect; (2) erect to appressed, pointed anteriad (length = 11; CI = 0.18; RI = 0.64). The same development of anepisternal setae (see character 78) is also found on the proepimeron. Within Asilidae, only *Pseudorus distendens* (Dasypogoninae) and *Lasiopogon* species and *Townsendia albomacula* (Stichopogoninae) lack erect proepimeral setae (state 0). In Leptogastrinae except *Acronyches maya*, and *Dioctria* species, *Echthodopa pubera*, *Eudioctria albius*, and *Myelaphus melas* (all Dioctriinae), the proepimeral setae are lightly appressed and directed anteriorly (state 2). Among the outgroup taxa, proepimeral setae are erect in *Apiocera aldrichii* (Apioceridae), Apsilocephalidae, *Bombylius major* (Bombyliidae), *Neorhaphiomidas* sp. (Mandurah and *Rhaphiomidas maehleri* (Mydidae), and Nemestrinidae (state 1) and absent in the remaining taxa (state 0).

80. MACROSETAE ON SUPEROPOSTERIOR ANEPISTERNUM: (0) absent; (1) present (length = 5; CI = 0.20; RI = 0.81). Osten-Sacken (1884) indicated the presence of setae on the mesopleura in some Asilidae and Hermann (1920) found them in all Laphriinae he studied. Later, Papavero (1973a) used the presence of at least one macroseta on the superoposterior anepisternum as a character supporting the division of Laphriinae sensu previous authors into two taxa, i.e., Laphriinae and Laphystiinae. He pointed out that all Laphriinae possess this seta whereas it may be present or absent in his Laphystiinae. Macrosetae are present in all Andrenosomatini, Ctenotini, Laphriini, Atomosiini except *Cerotainia albipilosa*, *Laxenecera albicincta*, *Nusa infumata*, and *Trichardis effrena* (all Laphriinae); *Michotamia aurata* (Ommatiinae); and *Acnephalum cylindricum* (Willistonininae) (state 1). All remaining Asilidae and outgroup taxa lack macrosetae on the superoposterior anepisternum (state 0).

81. SETAE ON POSTERIOR BASALARE (POST BAS): (0) absent; (1) present (length = 6; CI = 0.16; RI = 0.83). The posterior basalare is usually bare of setae in Asilidae (state 0). Setae are present in all Ommatiinae; Asilinae, with the exception of *Dasophrys crenulatus*, *Eichoichemus pyrrhomystax*, *Lochmorhynchus albicans*, *Myaptex brachyptera*, *Neolophonotus bimaculatus*, *Nomomyia murina*, *Pogonioefferia pogonias*, and *Proctacanthus philadelphicus*; as well as *Lampria clavipes* (Laphriinae) (state 1). Among the outgroup taxa, most species lack setae on the basalare (state 0) except *Rhaphiomidas maehleri* (Mydidae) (state 1).

82. ANATERGAL SETAE: (0) absent; (1) regular setae only (no macrosetae); (2) short, stout macrosetae (length = 12; CI = 0.16; RI = 0.71). Papavero (1973a) used the presence/absence of anatergal setae (referred to as postscutellar or metanotal setae) to divide the Asilinae of earlier authors into Apocleinae and Asilinae, but later Artigas and Papavero (1997) treated these two taxa as a single group, highlighting the point that the distribution of anatergal setae is not constant within the taxa delimited. Anatergal setae are found here to be present in Asilinae, with the exception of *Apoclea algira*, *Blepharotes splendidissimus*, *Dasophrys crenulatus*, *Eichoichemus pyrrhomystax*, *Lochmorhynchus albicans*, *Megaphorus pulchrus*, *Myaptex brachyptera*, *Neolophonotus bimaculatus*, *Nomomyia murina*, *Philodicus tenuipes*, *Pogonioefferia pogonias*, *Proctacanthus philadelphicus*, and *Promachus amastrus*; as well as *Megapoda labiata* and *Pseudorus distendens* (Dasypogoninae); *Dicolonus simplex* (Dioctriinae); *Aphestia annulipes*, *Dasyllis funebris*, *Laphria aktis*, and *Pilica formidolosa* (all Laphriinae); and *Daspletis stenoura* and *Microstylum* sp. (Karkloof) (Stenopogoninae) (state 1). Hermann (1912) highlighted the short, stout macrosetae on the anatergite of Atomosiini (Laphriinae) as a characteristic feature and these setae are found here to be present in Atomosiini with the exception of

Aphestia annulipes, *Orthogonis scapularis*, and *Smeryngolaphria numitor* (state 2). Among the outgroup taxa, most Mydidae possess anatergal setae as well (state 1), but the remaining taxa possess asetose anatergites (state 0).

83. KATATERGAL SETAE: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 19; CI = 0.10; RI = 0.62). The katatergite is usually setose with a mixture of regular setae and macrosetae in Asilidae (state 2). Katatergal setae are only absent in *Gonioscelis ventralis* and *Stenopogon* species (Stenopogoninae) and regular setae are present in Leptogastrinae except *Lasiocnemus lugens*; as well as *Megaphorus pulchrus* (Asilinae); *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Megapoda labiata*, *Molobratia teutonus*, *Pegesimallus laticornis*, *Pseudorus distendens*, and *Senobasis corsair* (all Dasypogoninae); *Atomosia puella*, *Cerotainia albipilosa*, and *Hyperechia nigripennis* (all Laphriinae); *Phellus olgae* (Phellinae); *Scleropogon subulatus* (Stenopogoninae); and some Brachyrhopalinae (state 1). Among the outgroup taxa, the katatergite is usually asetose (state 0) and *Bombylius major* (Bombyliidae), *Afroleptomydas* sp. (Clanwilliam), *Nemomydas brachyrhynchus*, *Neorhaphiomidas* sp. (Mandurah), and *Pseudonomoneura hirta* (all Mydidae), Nemestrinidae, and *Hemigephyra atra* (Therevidae) possess katatergal setae (state 1). *Phycus frommeri* (Therevidae) possesses katatergal setae and macrosetae (state 2).

84. KATATERGITE SHAPE: (0) slightly elevated sclerite; (1) cone-shaped sclerite (length = 2; CI = 0.50; RI = 0.00). The katatergite is usually a slightly elevated sclerite dorsal of the metathoracic spiracle (state 0), but in *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* (Mydidae) it is a pronounced, cone-shaped sclerite (state 1).

85. SETAE ON POSTERIOR MERON + METANEPISTERNUM: (0) absent; (1) regular setae only (no macrosetae); (2) at least one macroseta among setae (length = 21; CI = 0.09; RI = 0.77). The posterior meron + metanepisternum, often referred to as the metapleura, is usually asetose in Asilidae (state 0), but all Asilinae, Laphriinae, and Ommatiinae possess at least regular setae (state 1). Papavero (1973a) stated that these setae are present only in his Apocleinae, Asilinae, and Ommatiinae. Macrosetae among the setae are present in many Asilinae and Ommatiinae and *Daspletis stenoura* (Stenopogoninae) (state 2). Other Asilidae possessing regular setae are *Heteropogon manicatus* and *Holopogon priscus* (Brachyrhopalinae); *Megapoda labiata* and *Pseudorus distendens* (Dasypogoninae); *Dicolonus simplex* and *Echthodopa pubera* (Dioctriinae); *Phellus olgae* (Phellinae); *Creolestes nigribarbis*, *Microstylum* sp. (Karkloof), and *Prolepsis tristis* (all Stenopogoninae); *Lycostommyia albifacies* (Tillobromatinae); and *Damalis monochaetes* and *Damalis* sp. (Palatupana) (Trigonomiminae) (state 1). Among the outgroup taxa, only Bombyliidae and Nemestrinidae possess regular setae (state 1).

86. SETAE ON SUPEROPOSTERIOR ANEPIMERON: (0) absent; (1) regular setae only (no macrosetae); (2) at least one macroseta among setae (length = 22; CI = 0.09; RI = 0.70). Similar to the setose meron + metanepisternum, the anepimeron can possess setae on its superoposterior surface as well. These setae are found in all Ommatiinae; Asilinae except *Apoclea algira*; *Megapoda labiata* and *Pseudorus distendens* (Dasypogoninae); most Laphriinae; *Lasiocnemus lugens* (Leptogastrinae); *Daspletis stenoura* and *Microstylum* sp. (Karkloof) (Stenopogoninae); *Phellus olgae* (Phellinae); and *Lycostommyia albifacies* (Tillobromatinae) (state 1). *Asilus crabroniformis*, *Myaptex brachyptera*, *Neoitamus cyanurus*, *Satanas gigas*, and *Threnia carbonaria* (all Asilinae), and *Emphysomera species*, *Michotamia aurata*, and *Afroestricus chiastoneurus* (Ommatiinae) possess macrosetae and regular setae (state 2). Among the outgroup taxa, setae are found in *Bombylius major* (Bombyliidae), Mydidae, with the exception of *Nemomydas brachyrhynchus*, *Neorhaphiomidas* sp. (Mandurah), and *Rhaphiomidas maehleri*, and Nemestrinidae (state 1).

87. SHORT, STOUT, ERECT MACROSETAE ON ANTERIOR MESONOTUM: (0) absent; (1) present (length = 1; CI = 1.00; RI = 1.00). Londt (1988) used the short, stout, erect macrosetae on the anterior mesonotum as distinguishing characteristics for some Afrotropical Atomosiini genera. These setae are present only in the Afrotropical *Goneccalypsis argenteoviridis*

and *Loewinella nigripes* (Laphriinae) (state 1). Among the outgroup taxa, all species lack these setae (state 0).

88. NOTOPLEURAL (NPL) SETAE: (0) absent; (1) one seta; (2) two setae; (3) three or more setae; (4) single, short stout macroseta (length = 42; CI = 0.09; RI = 0.60). Notopleural setae are usually present in Asilidae (states 1, 2, and 3), but absent in Trigonomiminae except *Damalis* sp. (Palatupana) (state 0). The number of setae varies considerably and states (1), (2), and (3) are found widely within Asilidae. *Chrysopogon pilosifacies* and *Codula limbipennis* (Brachyrhopalinae) possess particularly short, stout macrosetae that are coded in a separate state (state 4). The following species are coded as polymorphic as more than one state is observed in different individuals, i.e., states (0) and (1) in *Myelaphus melas* (Dioctriinae), states (1) and (2) in *Protometer* sp. (El Tuparro) (Laphriinae), states (2) and (3) in *Laxenecera albicincta* (Laphriinae); *Scylaticus costalis* (Stenopogoninae); *Lasiopogon cinctus* (Stichopogoninae); and *Lycostommyia albifacies* (Tillobromatinae). Among the outgroup taxa, Apsilocephalidae and *Hemigephyra atra* (Therevidae) possess a single notopleural (npl) seta (state 1), *Phycus frommeri* (Therevidae) possesses two npl setae (state 2), and Apioceridae and *Rhaphiomidas maehleri* (Mydidae) possess three or more npl setae (state 3). All remaining species lack any npl setae (state 0).

89. TRANSVERSE (TRN) SUTURE: (0) entirely absent (not discernible); (1) distinct, at least on lateral surface (length = 1; CI = 1.00; RI = 1.00). Yeates (1994) highlighted the absence of the transverse suture in the genus *Neorhaphiomidas* Norris, 1936 (Mydidae) and Acroceridae. The transverse suture is usually well developed and present in all Asilidae (state 1). In the Mydidae except *Rhaphiomidas maehleri*, it is absent or not discernible (state 0) (fig. 63).

90. SUPRA-ALAR (SPA) SETAE: (0) absent; (1) present (length = 9; CI = 0.11; RI = 0.68). Supra-alar setae are usually present in Asilidae (state 1) and are absent only in all Trigonomiminae; *Chrysopogon pilosifacies*, *Codula limbipennis*, *Dasycyrton gibbosus*, *Holopogon priscus*, *Leptarthrus brevirostris* (all Brachyrhopalinae); *Pseudorus distendens* (Dasypogoninae); and *Lissoteles aquilonius* and *Stichopogon trifasciatus* (Stichopogoninae) (state 0). Among the outgroup taxa, supra-alar setae are absent in Bombyliidae, Mydidae except *Rhaphiomidas maehleri*, Nemestrinidae, and Scenopinidae (state 0).

91. POSTALAR (PAL) SETAE: (0) absent; (1) present (length = 12; CI = 0.08; RI = 0.66). Postalar setae are usually present in Asilidae (state 1) and are only absent in *Afroholopogon peregrinus*, *Chrysopogon pilosifacies*, *Codula limbipennis*, *Dasycyrton gibbosus*, *Leptarthrus brevirostris* (all Brachyrhopalinae); *Pseudorus distendens* (Dasypogoninae); Dioctriinae, with the exception of *Broticosia paramonovi*, *Dicolonus simplex*, and *Echthodopa pubera*; *Hyperechia nigripennis* (Laphriinae); Leptogastrinae, with the exception of *Acronyches maya* and *Leptogaster cylindrica*; and Trigonomiminae except *Damalis annulata* (state 0). Among the outgroup taxa, postalar setae are absent in Bombyliidae, Mydidae except *Rhaphiomidas maehleri*, and Nemestrinidae (state 0).

92. PRESUTURAL DORSOCENTRAL (DC) SETAE: (0) absent; (1) present (length = 43; CI = 0.02; RI = 0.44). The development of pre- and postsutural dorsocentral setae can be informative for identification of robber flies and has been reviewed by Hardy (1930). Both character states are widely found within Asilidae. It is sometimes difficult to discern the presutural dorsocentral setae and also ambiguous as to how long the seta should be to call it a well-developed dorsocentral seta. Among the outgroup taxa, presutural dorsocentral setae are present only in Apsilocephalidae and Mydidae, with the exception of *Mydas clavatus*, *Nemomydas brachyrhynchus*, and *Rhaphiomidas maehleri* (state 1).

93. PRESUTURAL ACROSTICHAL (ACR) SETAE (IN REGULAR ROWS): (0) absent; (1) present (length = 12; CI = 0.08; RI = 0.15). Presutural acrostichal setae arranged in regular rows are almost always present in Asilidae (state 1) and only absent in *Deromyia fuscipennis*, *Megapoda labiata*, and *Senobasis corsair* (all Dasypogoninae); *Goneccalypsis argenteoviridis* (Laphriinae); *Tipulogaster glabrata* (Leptogastrinae); *Ommatius incurvatus* (Ommatiinae); and *Stichopogon elegantulus* (Stichopogoninae) (state 0). Among the outgroup taxa, only a few

species lack presutural acrostichal setae (state 0).

94. Postsutural dorsocentral (dc) setae: (0) absent; (1) present (length = 16; CI = 0.06; RI = 0.31). Postsutural dorsocentral setae are usually developed in Asilidae (state 1) and absent only in *Codula limbipennis* (Brachyrhopalinae); *Molobratia teutonus* and *Pegesimallus laticornis* (Dasypogoninae); *Dioctria* species and *Myelaphus melas* (Dioctriinae); *Hoplistomerus nobilis*, *Lamyra gulo*, *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), and *Trichardis effrena* (all Laphriinae); *Tipulogaster glabrata* (Leptogastrinae); *Stichopogon trifasciatus* (Stichopogoninae); and *Holcocephala* species (Trigonomiminae) (state 0). Among the outgroup taxa, most species possess postsutural dorsocentral setae (state 1).

95. Sockets surrounding scutal setae: (0) absent (setae without large sockets); (1) present (setae with large sockets) (length = 6; CI = 0.16; RI = 0.58). The base of the scutal setae and macrosetae is usually not differentiated and no particular indentation is evident (state 0). Hermann (1912) pointed out that many Atomosiini possess large setal sockets on mesonotum and abdominal tergites (see character 151). In *Leptarthrus brevirostris* (Brachyrhopalinae); *Dioctria* species (Dioctriinae); Atomosiini, with the exception of *Orthogonis scapularis* and *Smeryngolaphria numitor*, *Hoplistomerus nobilis*, *Stiphrolamyra angularis*, and *Trichardis effrena* (all Laphriinae); and *Euscelidia pulchra* (Leptogastrinae), large sockets are evident (state 1). Among the outgroup taxa, setal sockets are not developed (state 0).

96. Development of medial setae on posterior scutum (between dc setae): (0) absent; (1) present, directed posteriorly; (2) present, directed anteriorly; (3) present, appressed to surface, directed posteriorly (length = 21; CI = 0.14; RI = 0.43). The posterior part of the mesonotum possesses generally additional setae between the two rows of dorsocentral setae. These setae are usually oriented posteriorly in Asilidae (state 1). The setae are absent in *Cyrtophrys attenuatus*, *Dasypogon diadema*, and *Megapoda labiata* (all Dasypogoninae); *Ablautus coquilletti* (Willistonininae); and *Coleomyia setigera* (state 0). In Leptogastrinae except *Beameromyia bifida*; *Apoclea algira* (Asilinae); *Goneccalypsis argenteoviridis* and *Zabrops tagax* (Laphriinae); *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae); *Hypenetes stigmatias* (Tillobromatinae); *Holcocephala* species and *Rhipidocephala* sp. (Harold Johnson) (Trigonomiminae); and *Acnephalum cylindricum* (Willistonininae) these setae are oriented anteriorly (state 2). In *Choerades bella*, *Lampria clavipes*, *Laphria aktis*, and *Maira aenea* (Laphriinae), these setae are oriented posteriorly and more or less tightly appressed to the thorax (state 3). Among the outgroup taxa, the setae are absent in Scenopinidae (state 0) and directed anteriorly in Mydidae, with the exception of *Mitrodetus dentitarsis* and *Rhaphiomidas maehleri*, and Nemestrinidae (state 2). All remaining outgroup taxa exhibit state 1.

97. Size of mesonotal scutellum: (0) small, mesopostnotum visible in dorsal view; (1) large, mesopostnotum not visible in dorsal view (length = 4; CI = 0.25; RI = 0.80). Yeates and Irwin (1996) established that the small scutellum is an autapomorphy of a subordinate taxon of Mydidae. In Asilidae, the scutellum is generally large and the mesopostnotum is not visible in dorsal view (state 1). In *Cabasa pulchella* (Brachyrhopalinae); *Blepharepium cajennensis*, *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Megapoda labiata*, *Molobratia teutonus*, *Pegesimallus laticornis*, *Pseudorus distendens*, and *Senobasis corsair* (all Dasypogoninae); and *Plesiomma* sp. (Guanacaste) (Stenopogoninae), the scutellum is small, so that the mesopostnotum is visible in dorsal view (state 0). Among the outgroup taxa, a small scutellum is found in Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* (state 0).

98. Apical scutellar (ap sctl) setae: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 31; CI = 0.06; RI = 0.58). Hardy (1930) (within Asilidae) and Yeates and Irwin (1996) (within Apioceridae and Mydidae) examined the apical scutellar setae. In Asilidae, there are usually some setae present, e.g., Dioctriinae, Leptogastrinae, Trigonomiminae, and many Brachyrhopalinae (state 1), but the majority of robber flies possess macrosetae as well as regular setae on the apical

margin of the scutellum (state 2). No apical scutellar setae are developed in *Blepharepium cajennensis*, *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Molobratia teutonus*, and *Senobasis corsair* (all Dasypogoninae); *Eudioctria albius* and *Myelaphus melas* (Dioctriinae); *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), and *Trichardis effrena* (all Laphriinae); *Michotamia aurata* (Ommatiinae); *Plesiomma* sp. (Guanacaste) (Stenopogoninae); and *Holcocephala* species, *Rhipidocephala* sp. (Harold Johnson), and *Trigonomima* sp. (*anamaliensis*) (all Trigonomiminae) (state 0). Among the outgroup taxa, Bombyliidae, Nemestrinidae, and Scenopinidae possess apical scutellar setae (state 1) and Apioceridae, Apsilocephalidae, and Therevidae possess macrosetae as well as setae (state 2). Within Mydidae, *Rhaphiomidas maehleri* possesses macrosetae and regular setae (state 2), *Mitrodetus dentitarsis* and *Neorhaphiomidas* sp. (Mandurah) possess only regular setae (state 1) and in the remaining species apical scutellar setae are absent (state 0).

99. DISCAL SCUTELLAR (DS SCTL) SETAE: (0) absent; (1) present (length = 18; CI = 0.05; RI = 0.65). The scutellar disc is generally setose in Asilidae (state 1), but a few taxa lack any setae on the scutellum. These are all Willistonininae; Dasypogoninae, with the exception of *Megapoda labiata*, *Pegesimallus laticornis*, and *Pseudorus distendens*; Stenopogoninae except Enigmomorphini; Stichopogoninae, with the exception of *Lissoteles aquilonius* and *Stichopogon punctum*; and a few other species of Brachyrhopalinae; Dioctriinae; Leptogastrinae; and Trigonomiminae (state 0). Among the outgroup taxa, only *Afroleptomydas* sp. (Clanwilliam), *Nemomydas brachyrhynchus*, and *Pseudonomoneura hirta* (all Mydidae), *Hemigephyra atra* (Therevidae), and Scenopinidae lack discal scutellar setae (state 0).

100. COXAE AND METKATEPISTERNUM (IN VENTRAL VIEW): (0) metkatepisternum small and not visible between mesothoracic and metathoracic coxae; (1) metkatepisternum large and visible between mesothoracic and metathoracic coxae (length = 7; CI = 0.14; RI = 0.81). Yeates and Irwin (1996) postulated the large metkatepisternum (referred to as metepisternum) as an autapomorphy for a subordinate taxon of Mydidae. In Asilidae, the metkatepisternum is usually small and not visible between the mes- and metathoracic coxae (state 0). In Laphriinae, with the exception of *Aphestia annulipes*, *Atomosia puella*, *Cerotainia albipilosa*, *Goneccalypsis argenteoviridis*, *Loewinella nigripes*, and *Psilocurus modestus*; as well as *Megapoda labiata* and *Pseudorus distendens* (Dasypogoninae), and *Acronyches maya* (Leptogastrinae), the metkatepisternum is large and visible in ventral view between the mes- and metathoracic coxae (state 1). Among the outgroup taxa, Mydidae except *Rhaphiomidas maehleri* and Nemestrinidae also possess a large metkatepisternum (state 1).

101. METKATEPISTERNAL SETAE: (0) absent; (1) present (length = 9; CI = 0.11; RI = 0.85). The metkatepisternum is usually asetose in Asilidae (state 0), but all Asilinae and Ommatiinae as well as *Broticosia paramonovi* (Dioctriinae); Andrenosomatini except *Andrenosoma cyrtoxys*, *Aphestia annulipes*, and *Lamyra gulo* (all Laphriinae); and *Damalis monochaetes* (Trigonomiminae), possess setae on this sclerite (state 1). Among the outgroup taxa, all species that possess a large metkatepisternum (see character 100) also possess setae (state 1).

102. POSTMETACOXAL BRIDGE: (0) absent, postmetacoxal area entirely membranous; (1) partly present laterally, membranous area medially; (2) present, visible suture between lateral halves; (3) present, entirely sclerotized (length = 26; CI = 0.11; RI = 0.56). Several authors (e.g., Hull, 1962; Papavero, 1973a) have emphasized the development of sclerotization in the postmetacoxal area in Asilidae. It is here coded into three different states. Most Asilidae possess an entirely membranous postmetacoxal area with a straight lateral margin (state 0). A partly developed postmetacoxal bridge in which the lateral sclerites fold medially, but where the median area is still membranous to a large extent, is found in *Austrosaropogon nigrinus* (Brachyrhopalinae); *Pseudorus distendens* (Dasypogoninae); Leptogastrinae, with the exception of *Acronyches maya*, *Euscelidia pulchra*, and *Lasiocnemus lugens*; as well as *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae); *Damalis annulata* and *Damalis monochaetes* (Trigonomiminae);

most Laphriinae; and a number of Asilinae (state 1). The postmetacoxal bridge is present, but a median suture is still visible dividing the two halves in *Euscelidia pulchra* and *Lasiocnemus lugens* (Leptogastrinae) and *Townsendia albomacula* (Stichopogoninae) (state 2). An entirely complete postmetacoxal bridge is developed in Atomosiini, with the exception of *Orthogonis scapularis* and *Smeryngolaphria numitor* (Laphriinae); Ommatiinae; *Rhabdogaster pedion* (Brachyrhopalinae); and *Damalis* sp. (Palatupana) (Trigonomiminae) (state 3). Among the outgroup taxa, all species possess an entirely membranous postmetacoxal area (state 0).

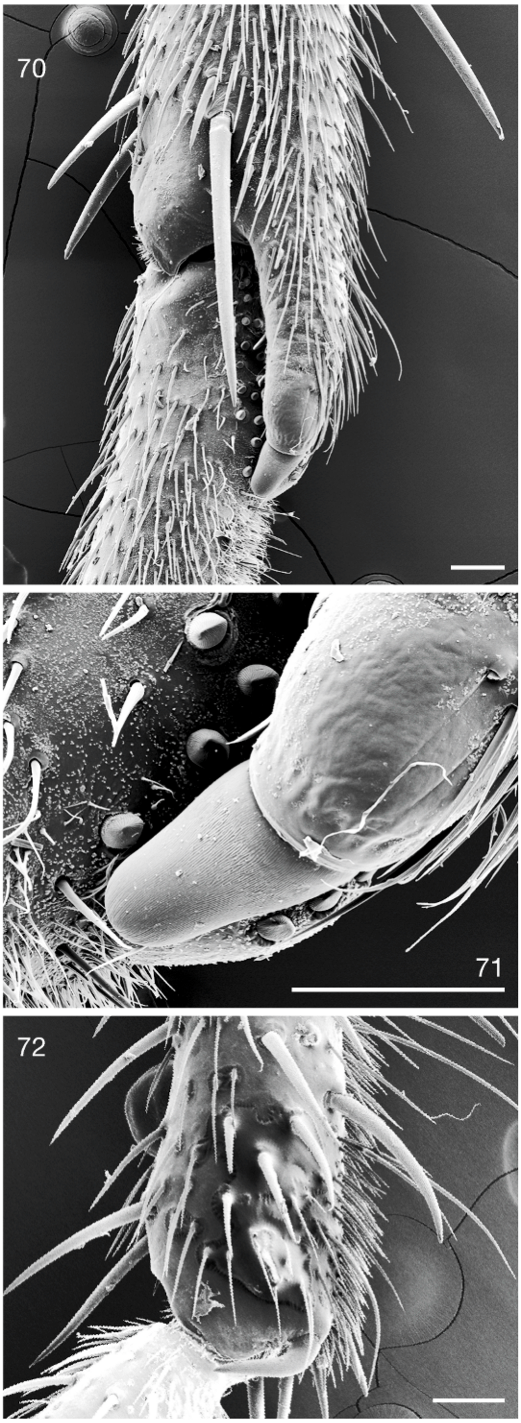
103. SHAPE OF SETAE ON LEGS: (0) only circular setae; (1) dorsoventrally flattened setae and circular setae (length = 3; CI = 0.33; RI = 0.50). Setae on all legs are usually circular in cross section in Asilidae (state 0), but Willistonininae except *Willistonina bilineata* possess dorsoventrally flattened setae as well as circular setae on the legs (state 1). Among the outgroup taxa, only *Bombylius major* (Bombyliidae) possesses dorsoventrally flattened setae (state 1).

104. LATERAL DEPRESSION ON PROTHORACIC COXA: (0) absent; (1) present (length = 3; CI = 0.33; RI = 0.85). The lateral surface of the prothoracic coxae is usually markedly depressed in Asilidae so that the coxae are not circular in cross section (state 1). This depression appears to be necessary to fold the prothoracic femora tightly against the coxae and thorax when perching. Only in Leptogastrinae do the coxae appear to be circular in cross section (state 0). Among the outgroup taxa, Apioceridae and Mydidae except *Pseudonomoneura hirta* possess indented coxae as well (state 1) whereas all remaining taxa possess circular coxae (state 0).

105. SETAE ON ANTEROVENTRAL PROTHORACIC TIBIAE: (0) absent; (1) at least three setae present (length = 10; CI = 0.10; RI = 0.72). The anteroventral surface of the prothoracic tibiae in Asilidae are found to possess at least three setae facing ventromedially. These setae are absent only in *Afroholopogon peregrinus* and *Heteropogon manicatus* (Brachyrhopalinae); *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae); Stenopogoninae, with the exception of *Ancylorhynchus fulvicollis*, *Connomyia varipennis*, *Daspletis stenoura*, *Gonioscelis ventralis*, *Scylaticus costalis*, and *Stenopogon* species; and Willistonininae except *Sisyrnodytes* sp. (Gamka) (state 0). Among the outgroup taxa, the setae are absent in all species (state 0).

106. PROJECTIONS ON PROTHORACIC TIBIAE: (0) absent; (1) small S-shaped spur, originating posteroventrally; (2) large spine, originating anteroventrally (length = 8; CI = 0.25; RI = 0.70). One of the most obvious characters used in classifications on Asilidae has been the development of spurs or spines on the prothoracic tibiae (e.g., Hermann 1912, 1920; Hull, 1962; Papavero, 1973a; Oldroyd, 1974a) and Hermann (1912) based an entire taxon on the presence of projections, i.e., Acanthocneminae (unavailable name: Sabrosky, 1999; Dikow, 2004). The majority of Asilidae species lack any projections on the prothoracic tibiae with the exception of straight macrosetae or setae. The large spine found in *Molobratia teutonus* (fig. 70) is easy to observe, but the smaller, S-shaped spur in *Leptarthrus brevirostris* (fig. 72) is difficult to see and to distinguish from the surrounding macrosetae. A detailed examination of the different tibial projections reveals that the large spines are always originating on the posteroventral surface whereas the small, S-shaped spurs originate on the anteroventral surface of the prothoracic tibiae. Hull (1962) and Oldroyd (1974a) recognized the different shapes of the projections, but not their different origin on the prothoracic tibiae. Both projections are considered here to be nonhomologous and coded as two different states. A small, S-shaped spur is found in *Cophura brevicornis*, *Leptarthrus brevirostris*, and *Nicocles politus* (all Brachyrhopalinae) and *Thereutria amaraca* (Dasypogoninae) (state 1). A large spine is found in Dasypogoninae, with the exception of *Archilestris magnificus* and *Thereutria amaraca*; as well as *Austrosaropogon nigrinus*, *Brachyrhopala ruficornis*, *Cabasa pulchella*, and *Chrysopogon pilosifacies* (all Brachyrhopalinae) (state 2). Among the outgroup taxa, tibial projections are absent (state 0).

107. BASE OF SPINE/SPUR ON PROTHORACIC TIBIA: (0) spine/spur originating directly from tibia; (1) spine/spur originating from projection of tibia (length = 3; CI = 0.33; RI =



Figs. 70–72. SEM micrographs of prothoracic tibiae in lateral view. **70.** *Molobratia teutonus* (Dasypogoninae). **71.** *Molobratia teutonus*, detail of spine with spicules on tarsomere. **72.** *Leptarthrus brevirostris* (Brachyrhopalinae). Scale lines = 200 µm.

←

0.77). The base of the prothoracic tibial projection varies in species that possess these projections and Hull (1962) mentioned the pronounced and enlarged base in *Molobratia*. The spine/spur originates directly from the tibia in all Brachyrhopalinae and *Blepharepium cajennensis*, *Diogmites grossus*, *Lestomyia fraudiger*, *Neodiogmites melanogaster*, and *Thereutria amaraca* (all Dasypogoninae) (state 0). In the remaining Dasypogoninae, the spine originates from a prominent projection on the tibia (state 1; figs. 70–71). All species not possessing spines/spurs are coded as inapplicable (-) (see character 106).

108. PROXIMAL PROTHORACIC TARSOMERE: (0) cylindrical; (1) cylindrical with short spicules; (2) expanded proximoventrally with stout spicules (length = 7; CI = 0.28; RI = 0.70). The proximal prothoracic tarsomere is usually simple and cylindrical without any projections in Asilidae (state 0). Hull (1962) commented on the different development of the prothoracic tarsomere in species possessing tibial projections. In Dasypogoninae except *Archilestris magnificus* and a few species of Brachyrhopalinae, which possess a large spine on the tibia, the proximal tarsomere often possesses projections in forms of spicules or expanded protuberances. In *Diogmites grossus*, *Lestomyia fraudiger*, *Neodiogmites melanogaster*, and *Thereutria amaraca* (all Dasypogoninae) and *Austrosaropogon nigrinus*, *Brachyrhopala ruficornis*, *Cabasa pulchella*, and *Chrysopogon pilosifacies* (all Brachyrhopalinae) the proximal tarsomere is cylindrical, but bears short spicules (state 1; fig. 71). In the remaining Dasypogoninae, the tarsomere is expanded proximoventrally and stout spicules are positioned on this elevated protuberance (state 2). Among the outgroup taxa, all species possess a cylindrical proximal tarsomere (state 0).

109. ORIENTATION OF PROTHORACIC AND MESOTHORACIC COXAE: (0) distinctly directed posteriorly; (1) more or less directed ventrally (sometimes even anteriorly) (length = 7; CI

= 0.14; RI = 0.87). In Asilidae, the pro- and mesothoracic coxae are usually directed more or less ventrally (sometimes even anteriorly), which permits them to catch and hold prey directly under the thorax (state 1; fig. 61). In *Ceraturgus fasciatus* (Brachyrhopalinae); Laphriinae except Atomosiini sensu stricto; *Megapoda labiata* and *Pseudorus distendens* (Dasypogoninae); *Creolestes nigribarbis* (Stenopogoninae); *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae); and *Tillobroma punctipennis* (Tillobromatinae), the coxae are directed posteriorly (state 0). Among the outgroup taxa, the coxae are also directed posteriorly (state 0).

110. MACROSETAE ON ANTERO-DORSAL SURFACE OF MESOTHORACIC TIBIAE: (0) absent; (1) one seta present; (2) several setae in one row present (length = 18; CI = 0.11; RI = 0.36). Hennig (1973) postulated the densely bristled legs as an autapomorphy of Asilidae. I, however, am unable to find any particular setal arrangement or characters of the legs that could be easily homologized for the entire taxon. The row of macrosetae on the anterodorsal surface of the mesothoracic tibia is the only exception. Most Asilidae possess several setae at this position (state 2), but all Leptogastrinae; *Blepharotes splendidissimus*, *Colepia rufiventris*, *Heligmonevra laevis*, *Megaphorus pulchrus*, *Pogonioefferia pogonias*, and *Zosteria rosevillensis* (all Asilinae); *Myelaphus melas* (Dioctriinae); and *Laphria* species (Laphriinae) lack any strong macrosetae on the mesothoracic tibia (state 0). *Apoclea algira*, *Lochmorhynchus albicans*, *Nomomyia murina*, and *Philodicus tenuipes* (all Asilinae) possess only a single seta (state 1). Among the outgroup taxa, most species possess a few setae (state 2) and only *Nemomydas brachyrhynchus* and *Neorhaphiomidas* sp. (Mandurah) (Mydidae), Nemestrinidae, and Scenopinidae lack setae (state 0). *Asilus sericeus* and *Lycomya germainii* (Asilinae, 0/1) and *Ommatius tibialis* (Ommatiinae, 1/2) are coded as polymorphic as several individuals possess different numbers of setae.

111. ORIENTATION OF METATHORACIC COXAE: (0) distinctly directed ventrally to posteriorly; (1) directed anteriorly (length = 1; CI = 1.00; RI = 1.00). The metathoracic coxae are directed ventrally to posteriorly in most Asilidae and all outgroup taxa (state 0). In Leptogastrinae except *Acronyches maya*, the coxae are distinctly directed anteriorly (state 1). Among the outgroup taxa, all species exhibit state 0.

112. SETAE ON LATERAL SURFACE OF METATHORACIC COXA: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 22; CI = 0.09; RI = 0.70). Robber flies usually possess setae on the lateral surface of the metathoracic coxae and often these setae are developed as strong macrosetae. Setae are absent in *Tipulogaster glabrata* and *Euscelidia pulchra* (Leptogastrinae); *Townsendia albomacula* (Stichopogoninae); and *Coleomyia setigera* (state 0). Macrosetae are generally found within Asilinae; Dasypogoninae; Ommatiinae; and Stenopogoninae (state 2), whereas the remaining taxa possess generally only regular setae (state 1). Among the outgroup taxa, all three character states are found.

113. PROTUBERANCE ON ANTERIOR SURFACE OF METATHORACIC COXA: (0) absent; (1) present, protuberance blunt distally; (2) present, peglike protuberance pointed distally (length = 16; CI = 0.12; RI = 0.39). Cannings (2002) observed the blunt protuberance on the anterior surface of the metathoracic coxa of some Stichopogoninae in contrast to species of *Lasiopogon*, and Londt (2005a) based the description of the Afrotropical genus *Ischiolobos* Londt, 2005 (placed in Stenopogoninae sensu Papavero, 1973a), on the presence of a blunt protuberance on the metathoracic coxa. The majority of Asilidae do not possess any protuberance on the metathoracic coxae (state 0). In Bathypogoninae; as well as *Cophura brevicornis*, *Holopogon priscus*, *Metapogon punctipennis*, *Nannocyrtopogon lestomyiformis* (all Brachyrhopalinae); *Creolestes nigribarbis* (Stenopogoninae); *Stichopogon* species (Stichopogoninae); *Hypenetes stigmatias* and *Tillobroma punctipennis* (Tillobromatinae); *Trichoura* sp. (Tierberg) and *Willistonina bilineata* (Willistonininae); and *Coleomyia setigera*, a blunt protuberance is present (state 1). In *Dioctria* species, *Eudioctria albius*, and *Nannodioctria* sp. (*formicaphaga*) (all Dioctriinae), a peglike, pointed protuberance is developed (state 2). Among the outgroup taxa, all Apioceridae, Apsilocepha-

lidae, Scenopinidae, and Therevidae possess a blunt protuberance on the metathoracic coxae (state 1).

114. SETAE ON MEDIAN SURFACE OF METATHORACIC TROCHANTER: (0) absent; (1) regular setae only (no macrosetae); (2) macrosetae and regular setae (length = 28; CI = 0.07; RI = 0.64). All Asilidae species possess at least regular setae on the median surface of the metathoracic trochanter (state 1) and many species of Asilinae; Bathypogoninae; Dioctriinae; Ommatiinae; Stenopogoninae; Stichopogoninae; and Tillobromatinae possess macrosetae (state 2). Among the outgroup taxa, these setae are absent in *Rhaphiomidas maehleri* (Mydidae) and most other species only possess setae (state 1).

115. SHAPE OF MEDIAN SURFACE OF METATHORACIC TROCHANTER: (0) cylindrical, medially without expansion; (1) medially with posteriorly directed expansion (length = 5; CI = 0.20; RI = 0.33). The metathoracic trochanter is usually cylindrical in Asilidae (state 0), but in *Lampria clavipes*, *Laxenecera albicincta*, and *Maira aenea* (all Laphriinae), as well as *Damalis* species (Trigonomiminae), the medial surface of the trochanter is expanded (state 1). Among the outgroup taxa, only *Mydas clavatus* (Mydidae) possesses a medially expanded trochanter (state 1).

116. SETATION ON VENTRAL SURFACE OF METATHORACIC FEMUR: (0) absent or only regular setae present; (1) macrosetae present; (2) short, stout, cone-shaped macrosetae present (length = 30; CI = 0.06; RI = 0.66). Woodley (1989) postulated that the short, stout, cone-shaped macrosetae on the ventral surface of the metathoracic femur found in many Mydidae is an autapomorphy of this taxon. Although Asilidae usually possess setae on the ventral surface of the metathoracic femur (state 0), only within Asilinae; Ommatiinae; and Stenopogoninae do the majority of species possess macrosetae (state 1). *Brachyrhopala ruficornis* (Brachyrhopalinae); *Hoplistomerus nobilis*, *Lampria clavipes*, and *Trichardis effrena* (all Laphriinae); *Hypenetes stigmatias* and *Lycostommyia albifacies* (Tillobromatinae); and *Damalis monochaetes* and *Damalis* sp. (Palatupana) (Trigonomiminae) possess short, stout, cone-shaped macrosetae (state 2). Among the outgroup taxa, cone-shaped macrosetae are only found in *Afroleptomydas* sp. (Clanwilliam) and *Mydas clavatus* within Mydidae (state 2) although all remaining species of Mydidae and Apioceridae possess macrosetae on the ventral metathoracic femora (state 1).

117. CUTICULAR FACETS MEDIALLY ON PROXIMAL SURFACE OF METATHORACIC FEMUR: (0) absent; (1) present (length = 1; CI = 1.00; RI = 1.00). Clements (1985) observed the presence of cuticular facets on the metathoracic femora in all known species of *Codula* and most species of *Chrysopogon* and absence of these in *Chryseutria* Hardy, 1928, and *Opseostlengis* White, 1914, all belonging to his concept of Chrysopogonini. These cuticular facets are found here to be present only in *Chrysopogon pilosifacies* and *Codula limbipennis* (state 1). Among the outgroup taxa, cuticular facets are lacking (state 0).

118. FRINGE OF PARALLEL SETAE VENTRALLY ON METATHORACIC FEMORA AND TIBIA: (0) absent; (1) present on tibiae only; (2) present on femora and tibiae (length = 4; CI = 0.50; RI = 0.83). Fisher (personal commun.) pointed out the fringe of parallel setae on the ventral metathoracic femora and tibiae in many Dioctriinae and Atomosiini (Laphriinae). These setae are present on the metathoracic tibiae only in *Aphestia annulipes* (Laphriinae) (state 1) and present on femora and tibiae in Dioctriinae, with the exception of *Broticosia paramonovi* and *Myelaphus melas*; and the remaining Atomosiini (all Laphriinae) (state 2). The fringe of parallel setae are absent in all remaining Asilidae and all outgroup taxa (state 0).

119. SHAPE OF METATHORACIC TIBIA: (0) straight; (1) arched laterally; (2) arched medially (length = 10; CI = 0.20; RI = 0.50). The metathoracic tibia is usually straight in Asilidae (state 0), but in a number of species of Dasypogoninae and Laphriinae, it is distinctly arched laterally or medially. Laterally arched tibiae are found in *Andrenosoma cyrtoxys*, *Dasyllis funebris*, *Hoplistomerus nobilis*, *Hyperechia nigripennis*, *Lampria clavipes*, *Laphria* species, *Laphystia aegyptiaca*, *Laxenecera albicincta*, *Maira aenea*, *Nusa infumata*, *Pilica formidolosa*, and *Trichardis effrena* (all Laphriinae) (state 1), and medially arched tibiae are found in *Blepharepium cajennensis*, *Cyrtophrys attenu-*

TABLE 3

Distribution of lengths of proximal tarsomeres (chars. 120–122)

Note that a species exhibiting state (0) on the prothoracic leg might not exhibit the same state on another leg, for example, and the columns are just counts of species; see character matrix in appendix 1 for details; number in parentheses following the taxon name equals number of species of the taxon included in the present study; state 0 = shorter or equal to the length of two following tarsomeres combined; state 1 = longer than two following tarsomeres combined

	prothoracic		mesothoracic		metathoracic	
Taxon	state 0	state 1	state 0	state 1	state 0	state 1
Asilinae (32)	21	11	20	12	4	28
Bathypogoninae (1)	–	1	–	1	–	1
Brachyrhopalinae (18)	2	16	13	5	all	–
Dasypogoninae (16)	–	all	–	all	–	all
Dioctriinae (9)	8	1	7	2	1	8
Laphriinae (29)	13	16	13	16	2	27
Leptogastrinae (7)	2	5	3	4	3	4
Ommatiinae (7)	all	–	4	3	–	all
Phellinae (2)	–	all	–	all	–	all
Stenopogoninae (13)	2	11	–	all	–	all
Stichopogoninae (7)	all	–	all	–	all	–
Tillobromatinae (3)	–	all	2	1	–	all
Trigonomiminae (7)	6	1	6	1	4	3
Willistonininae (5)	all	–	all	–	2	3
Coleomyia setigera	–	1	–	1	–	1
Oligopogon sp. (Cape Recife)	1	–	1	–	–	1

atus, *Deromyia fuscipennis*, and *Senobasis corsair* (all Dasypogoninae) (state 2). Among the outgroup taxa, *Mydas clavatus* (Mydidae) is the only species possessing a laterally arched tibia (state 1).

120. LENGTH OF PROXIMAL PROTHORACIC TARSOMERE: (0) shorter or same length as following two tarsomeres combined; (1) longer than following two tarsomeres combined (length = 24; CI = 0.04; RI = 0.70). The length of the proximal tarsomeres relative to the following tarsomeres has been used as a diagnostic and phylogenetic character within Mydidae (e.g., Papavero and Wilcox, 1974; Yeates and Irwin, 1996), but has not been evaluated across Asilidae. Here, it is only determined whether the proximal tarsomere is shorter or longer than the two following tarsomeres combined, to avoid morphometric calculations that cannot be coded as discrete character states. See table 3 for character state distribution within Asilidae. Among the outgroup taxa, most species possess longer proximal tarsomeres (state 1) and only Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah), *Opomydas townsendi*, and *Rhaphiomidas maehleri* possess shorter proximal tarsomeres (state 0).

121. LENGTH OF PROXIMAL MESOTHORACIC TARSOMERE: (0) shorter or same length as following two tarsomeres combined; (1) longer than following two tarsomeres combined (length = 29; CI = 0.03; RI = 0.67). See character 120 and table 3. Among the outgroup taxa, most species possess longer proximal tarsomeres (state 1) and only Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* possess shorter proximal tarsomeres (state 0).

122. LENGTH OF PROXIMAL METATHORACIC TARSOMERE: (0) shorter or same length as following two tarsomeres combined; (1) longer than following two tarsomeres combined (length = 14; CI = 0.07; RI = 0.50). See character 120 and table 3. Among the outgroup taxa, most species possess longer proximal tarsomeres (state 1) and only Mydidae, with the exception of *Mitrodetus dentitarsis*, *Neorhaphiomidas* sp. (Mandurah), *Opomydas townsendi*, and *Rhaphiomidas maehleri* possess shorter proximal tarsomeres (state 0).

123. PULVILLI: (0) absent; (1) present (length = 3; CI = 0.33; RI = 0.77). Martin (1968) observed that the pulvilli are absent in all Leptogastrinae and a few other species of Asilidae and concluded that the lack of pulvilli is a plesiomorphic character. Pulvilli are found here to be absent in all Leptogastrinae as well as *Ablautus coquilletti*, *Acnephalum cylindricum*, and *Sisyrnodytes* sp. (Gamka) (all Willistonininae) (state 0). Among the outgroup taxa, pulvilli are present in all species (state 1).

124. NUMBER OF DORSAL LONGITUDINAL RIDGES ON PULVILLI: (0) one; (1) two (length = 2; CI = 0.50; RI = 0.90). Bequaert (1961) and later Yeates and Irwin (1996) discussed the number of dorsal longitudinal ridges on the pulvilli in Asiloidea and found that all Apioceridae and Mydidae possess only a single ridge whereas Asilidae and other Asiloidea possess two. A single ridge is found here in *Megapoda labiata* and *Pseudorus distendens* (Dasypogoninae) as well as all Apioceridae and Mydidae (state 0). All remaining taxa possess two ridges (state 1). All species lacking pulvilli (see character 123) are coded as inapplicable (-).

125. SHAPE OF CLAWS: (0) abruptly angled distally; (1) fairly straight throughout (length = 4; CI = 0.25; RI = 0.70). In Asiloidea, the claws are usually abruptly angled distally (state 0), but in all Leptogastrinae; *Lestomyia fraudiger* (Dasypogoninae), and *Ablautus coquilletti*, *Acnephalum cylindricum*, and *Sisyrnodytes* sp. (Gamka) (all Willistonininae), the claws are more or less straight and only slightly angled distally (state 1). Among the outgroup taxa, the claws are always angled distally (state 0).

126. SHAPE OF TIP OF CLAWS: (0) pointed; (1) blunt (length = 3; CI = 0.33; RI = 0.33). The tip of the claws is usually pointed in Asiloidea (state 0), but *Eichoichemus pyrrhomystax* and *Megaphorus pulchrus* (Asilinae) as well as *Lamyra gulo* and *Stiphrolamyra angularis* (Laphriinae) possess claws with a blunt tip (state 1). Hull (1962), in delimiting the Ctenotini (Laphriinae), mentioned the presence of blunt claws. Among the outgroup taxa, the claws are always pointed (state 0).

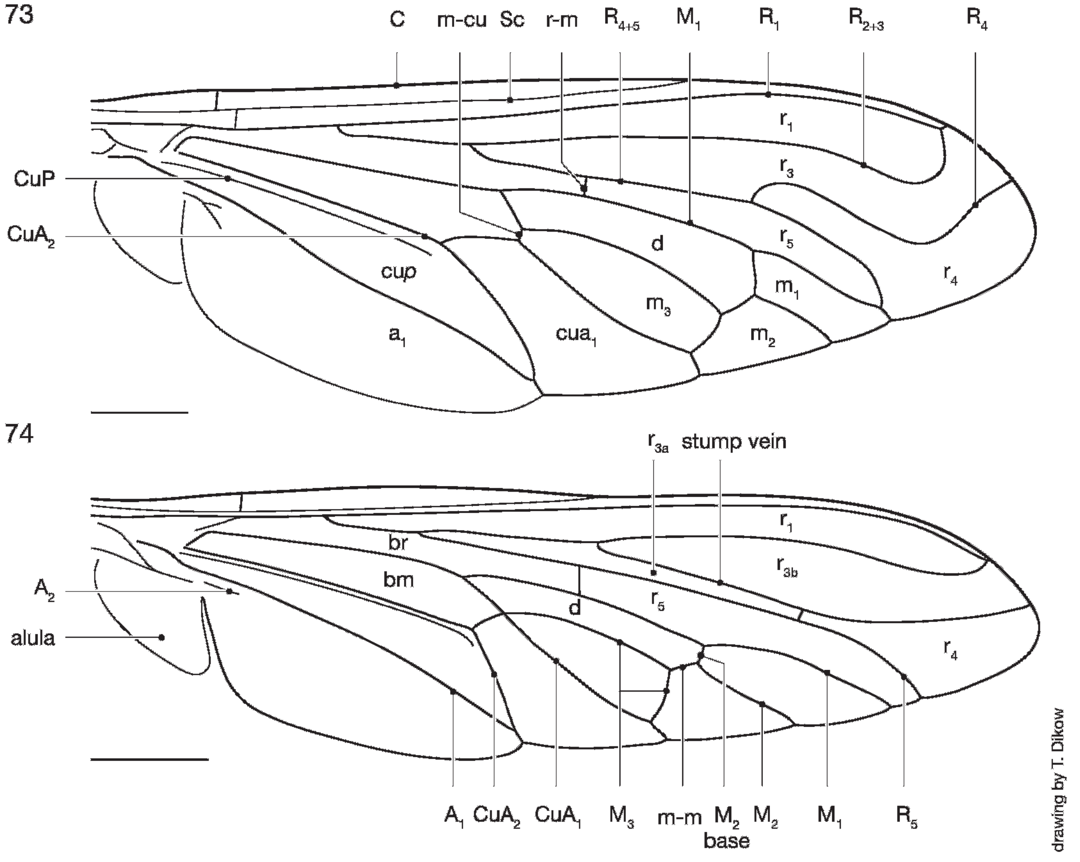
127. DEVELOPMENT OF SETIFORM EMPODIUM: (0) well developed (as long as claws); (1) reduced in length to varying degree; (2) minute or entirely absent (length = 31; CI = 0.06; RI = 0.58). In all Heterodactyla the empodium is setiform (McAlpine, 1981; Stuckenberg, 2001), and in most Asilidae it is well developed and as long as the claws (state 0). In many Brachyrhopalinae; Dasypogoninae; Leptogastrinae; Trigonomiminae; and Stenopogoninae, the empodium is reduced in length to a varying degree (state 1). In *Acronyches maya* (Leptogastrinae) and *Ablautus coquilletti* (Willistonininae) it is reduced to a minute sclerite or entirely absent (state 2). Among the outgroup taxa, in all Apioceridae, Mydidae, and Scenopinidae the empodium is minute or entirely absent (state 2, see also Yeates and Irwin, 1996). Nemestrinidae is coded as inapplicable (-) as it does not possess a setiform empodium, which is an autapomorphy for the Heterodactyla (see Introduction).

WING

Figures 73–85 illustrate a diversity of robber-fly wings and all wing veins and cells are labeled in figures 73–74.

128. ANTERIOR MARGIN OF WING IN MALES: (0) straight; (1) C bulging anteriorly (length = 5; CI = 0.20; RI = 0.00). In general, the anterior margin of the wing is straight in male and female Asilidae. In *Clephydroneura sundaica* and *Nomomyia murina* (Asilinae) as well as *Emphysomera conopsoides*, *Ommatius incurvatus*, and *Ommatius tibialis* (all Ommatiinae), the anterior margin of the wing is expanded anteriorly in males (state 1). Among the outgroup taxa, the anterior wing margin is always straight (state 0).

129. UPPER CALYPTER: (0) reduced; (1) well developed (length = 2; CI = 0.50; RI = 0.75). The upper calypter is well developed in the Apsilocephalidae, *Poecilognathus* sp. (El Hacha) (Bombyliidae), Scenopinidae, and Therevidae (state 1), but reduced in all Apioceridae, Asilidae, and Mydidae (state 0). Yeates (1994) interpreted the reduction of the upper calypter differently and stated that it is reduced only in taxa with an elongated body shape, e.g., *Leptogaster*. It is certainly further reduced in Leptogastrinae than in other Asilidae, but in all examined species of Apioceridae, Asilidae, and Mydidae it is only a small lobe more or less continuous with the

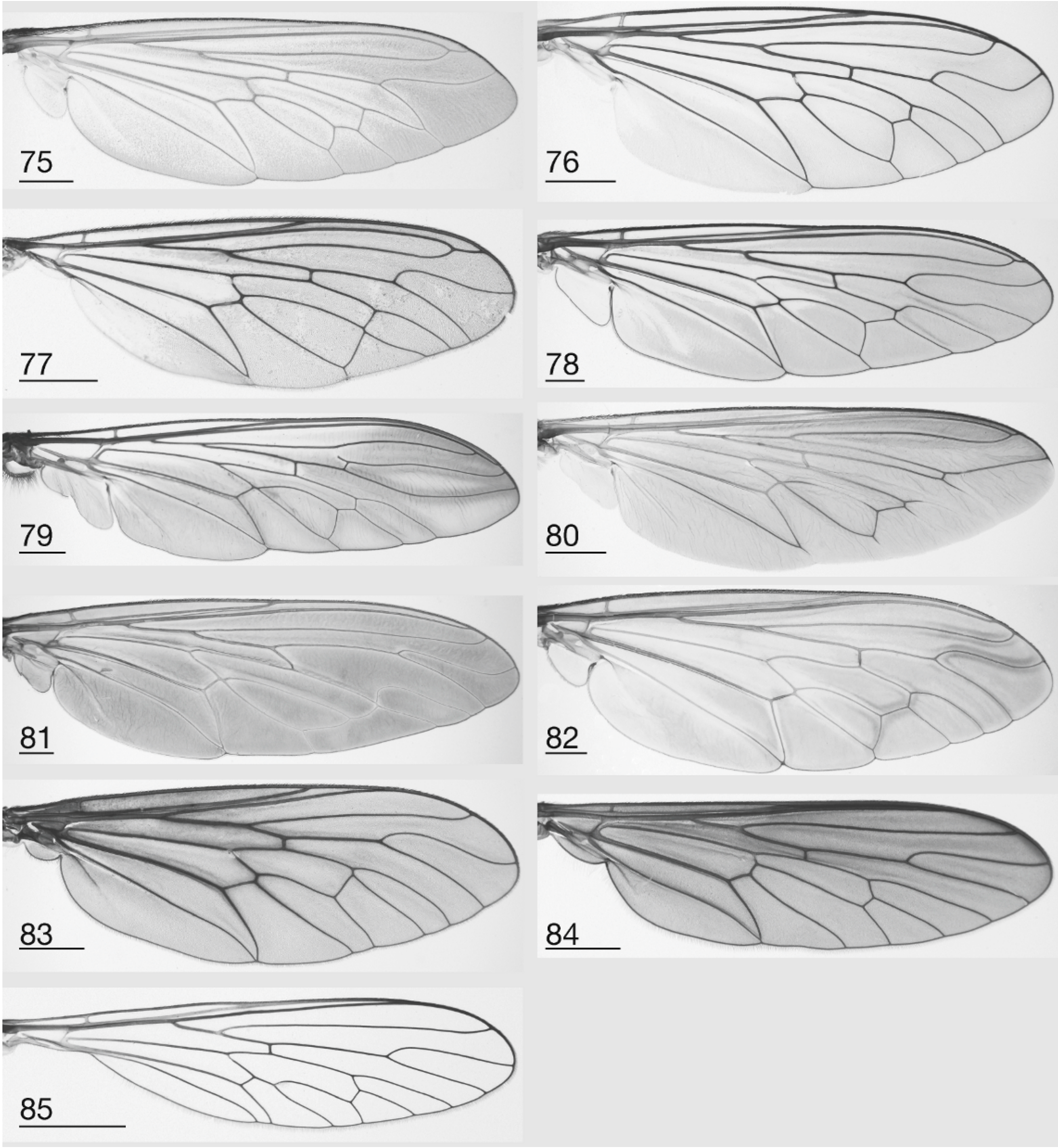


Figs. 73–74. Wings. **73.** *Hoplistomerus nobilis* (Laphriinae). **74.** *Promachus amastrus* (Asilinae). Wing veins and cells labeled; for abbreviations see character descriptions and McAlpine (1981). Scale lines = 1 mm.

thorax along the axillary cord in contrast to other outgroup taxa in which it is a distinct lobe.

130. ALULA: (0) well developed; (1) reduced in size to small lobe; (2) reduced entirely, nearly straight wing margin (length = 16; CI = 0.12; RI = 0.72). Karl (1959) and Martin (1968) discussed the reduction of the alula as an autapomorphy of the Leptogastrinae in contrast to most other species of Asilidae, which have a well-developed alula. Two different states of reduction are recognized here in that the alula can be reduced, but a small lobe is still distinct (state 1; figs. 76–77, 83–84) and the alula is completely reduced so that the posterior wing margin is nearly straight (state 2; fig. 85). State 1 is found in most Brachyrhopalinae with the exception of *Ceraturgus fasciatus*, *Chrysopogon pilosifacies*, *Codula limbipennis*, and *Dasycyrton gibbosus*, as well as *Cyrtophrys attenuatus* and *Deromyia fuscipennis* (Dasypogoninae); *Dicolonus simplex*, *Dioctria* species, *Echthodopa pubera*, *Eudioctria albius*, and *Nannodioctria* sp. (*formicaphaga*) (all Dioctriinae); *Atomosia puella*, *Cerotainia albipilosa*, and *Psilocurus modestus* (all Laphriinae); most Trigonomiminae except *Damalis* species; *Trichoura* sp. (Tierberg) and *Willistonina bilineata* (Willistoninina); and *Coleomyia setigera*. State 2 is found in all Leptogastrinae and Stichopogoninae; *Broticosia paramonovi* (Dioctriinae); *Goneccalypsis argenteoviridis* and *Loewinella nigripes* (Laphriinae); and *Oligopogon* sp. (Cape Recife). Among the outgroup taxa, the alula is partly reduced in Apsilocephalidae (state 1).

131. CELL r_1: (0) open; (1) closed, R_1 and R_{2+3} meet apically and form a stalk vein (petiolate); (2) closed, R_1 and R_{2+3} meet



Figs. 75–85. Wings of Asilidae species. **75.** *Laxenecera albicincta*; **76.** *Laphystia tolandi*; **77.** *Atomosia puella* (all Laphriinae); **78.** *Philonicus albiceps*; **79.** *Pogonioefferia pogonias*; **80.** *Megaphorus pulchrus* (all Asilinae); **81.** *Microstylum* sp. (Karkloof) (Stenopogoninae); **82.** *Dasypogon diadema* (Dasypogoninae); **83.** *Dioctria atricapillus* (Dioctriinae); **84.** *Holcocephala calva* (Trigonomiminae); **85.** *Euscelidia pulchra* (Leptogastrinae). Scale lines = 1 mm.

directly at C (length = 8; CI = 0.25; RI = 0.92). Hull (1962), Papavero (1973a), and subsequent authors widely used the development of cell r_1 for separating taxa of Asilidae, but highlighted the fact that this character has to be used with caution because a closed cell r_1 is supposed to have arisen several times independently (see Discussion). An open cell r_1, in which veins R_1 and R_{2+3} reach the wing margin separately, is present in most Asilidae (state 0; figs. 81–85). In Asilinae; *Megapoda labiata*, *Pseudorus distendens*, and *Thereutria amarac*a (all Dasypogoninae); Laphriinae except *Psilocurus modestus*; Ommatiinae; as well as Apioceridae and Mydidae cell r_1 is closed (state 1 and 2). When cell r_1 is closed, a stalk vein formed by R_1 and R_{2+3} is generally present (state 1; figs. 75, 77–80) and only in a few species of Laphriinae, i.e., *Hoplistomerus nobilis*, *Laphystia* species, *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), and *Zabrops tagax*, R_1 and R_{2+3} reach the wing margin at the same point (state 2; figs. 73, 76). Among the outgroup taxa, cell r_1 is closed in all Apioceridae and Mydidae (state 1) and open in the remaining species (state 0).

132. CELL r_4: (0) open; (1) closed (length = 1; CI = 1.00; RI = 1.00). Cell r_4 is open in all Asilidae species (state 1). Among the outgroup taxa, it is closed only in Mydidae except *Rhaphiomidas maehleri* (state 1).

133. CELL r_4 SHAPE: (0) R_4 and R_5 more or less parallel; (1) R_4 and R_5 diverging from each other; (2) R_4 and R_5 approximating each other medially; (3) R_4 and R_5 approximating each other distally (medially farthest apart); (4) R_4 and R_5 farthest apart in proximal one-third (length = 26; CI = 0.15; RI = 0.69). R_4 and R_5 run more or less parallel in many Brachyrhopalinae; *Cerotainia albipilosa* (Laphriinae); Leptogastrinae; Ommatiinae; *Holcocephala* species and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae) (state 0; figs. 84–85). Within the Asilinae, the shape of cell r_4 varies considerably and states (0–3) are found with the most common configuration being a medially approximating R_4 and R_5 (state 2; fig. 78). State 3 is illustrated in figure 79. In all remaining species of Asilidae, R_4 and R_5 diverge from each other at the wing margin (state 1; figs. 73–77, 80–83). Among the outgroup taxa, Apioceridae and Apsilocephalidae possess state 0, Mydidae and Nemestrinidae possess state 4, and the remaining taxa exhibit state 1.

134. CELL r_5: (0) open; (1) closed (length = 13; CI = 0.07; RI = 0.14). Cell r_5 is generally open among species of Asilidae (state 0, e.g.; fig. 74) and only in *Apoclea algira* (Asilinae); *Hoplistomerus nobilis*, *Hyperechia nigripennis*, *Laxenecera albicincta*, *Nusa infumata*, *Perasis transvaalensis*, *Pilica formidolosa*, *Trichardis effrena*, and *Zabrops tagax* (all Laphriinae); *Daspletis stenoura* (Stenopogoninae); *Sisyrnodytes* sp. (Gamka) (Willistonininae) cell r_5 is closed (state 1; figs. 73, 75). Among the outgroup taxa, cell r_5 is mostly open (state 0), but a few Mydidae possess a closed cell r_5 (state 1).

135. CELL m_3: (0) open; (1) closed (length = 11; CI = 0.09; RI = 0.85). Cell m_3 is closed in all Asilinae; Laphriinae; Ommatiinae; and a few other Asilidae species (state 1; figs. 73–82). Among the outgroup taxa, this cell is absent due to the reduction of vein M_3 in Bombyliidae and the species are coded as inapplicable (-), but it is open in Scenopinidae, in which vein M_2 is absent (state 0). In all remaining species it is closed (state 1).

136. CELL cu*p*: (0) open; (1) closed (length = 18; CI = 0.05; RI = 0.66). Karl (1959) used the open or closed cell cu*p* in his phylogeny of Asilidae. Cell cu*p* is closed in all Asilinae; Bathypogoninae; Laphriinae; Ommatiinae; Phellinae; Stichopogoninae; many Stenopogoninae; and most Trigonomiminae (state 1; figs. 73–82). All remaining Asilidae possess an open cell cu*p* (state 0; fig. 85). *Trigonomima* sp. (*anamaliensis*) is coded as polymorphic (state 0/1) because different individuals are observed, in which cell cu*p* is open or closed. Among the outgroup taxa, cell cu*p* is usually closed (state 1) except in *Bombylius major* (Bombyliidae) and Nemestrinidae.

137. CELL d, DISTAL END: (0) base of M_2 and m-m closing cell in nearly a single line; (1) only m-m closing cell, M_1 branching proximally; (2) only base of M_2 closing cell, M_3 branching proximally; (3) M_2 and M_3 closing cell, not aligned; (4) only base of M_2 closing cell, m-m absent (or at least highly reduced); (5) only base of M_2 closing cell, distal M_3 absent (length = 19; CI = 0.26; RI = 0.74). Cell d lies in the center of the wing in Asilidae. The branching of veins M_1 and M_3 forms the proximal angle. The distal tip is composed of veins M_1, M_2, and crossvein m-m (fig. 86). The branching between M_1 and M_2 varies in its position. State 0 is found when the branching is situated close to the distal tip of cell d and the proximal part of M_2 and crossvein m-m form nearly a straight line (figs. 83, 86). This arrangement is found in some species of Brachyrhopalinae; Dioc-

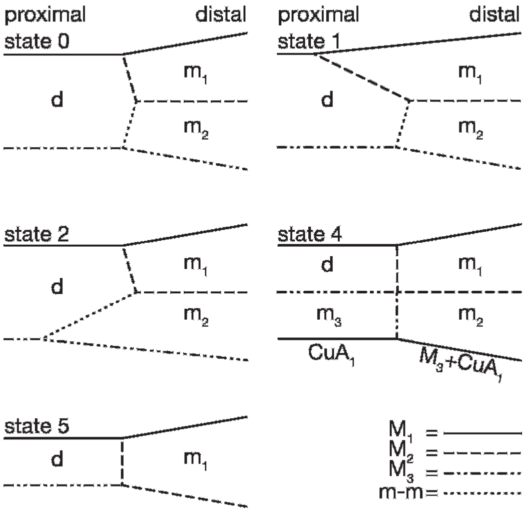


Fig. 86. Schematic drawing of closure of cell d coded in character 137. Character states, wing veins, and wing cells labeled; character state 3, which is only found in Mydidae and Nemestrinidae, not illustrated; for abbreviations see character description and McAlpine (1981); not to scale.

triinae; Leptogastrinae; Stichopogoninae; Trigonomiminae; and Willistonininae (state 0). State 1 is observed when the branching is situated more closely to the center of cell d, thus proximal part of M_2 and crossvein m-m are in an angle of about 90° (figs. 84, 86) and this arrangement is present in *Lasiocnemus lugens*, *Leptogaster* species, and *Tipulogaster glabrata* (Leptogastrinae). Laphriinae, with the exception of most Atomosiini; as well as Asilinae; Bathypogoninae; Dasypogoninae; Ommatiinae; Phellinae; Stenopogoninae except *Connomyia varipennis*; Tillobromatinae; and a few other species exhibit state 2 where M_3 branches off proximal to where M_2 originates and therefore m-m and M_2 are arranged in an angle (figs. 75–76, 78–82, 86). In the Atomosiini except *Smeryngolaphria numitor* (Laphriinae) m-m is absent or largely reduced so that the base of M_2 and part of M_3 are aligned in a straight line from anterior to posterior (state 4; figs. 77, 86; see character 150). In *Townsendia albomacula* (Stichopogoninae) and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae) the distal part of M_3 is absent and cell d is only closed by M_2 because m-m is also absent (state 5; fig. 86). Among the outgroup taxa, the Bombyliidae is coded as inapplicable (-) because vein M_3 is not present and therefore no cell d is developed. Mydidae and Nemestrinidae exhibit state 3 whereas Apioceridae and *Prorates* sp. (Escalante) exhibit state 2.

138. POSITION OF r-m WITH RESPECT TO CELL d (OR CELL dm): (0) proximal half; (1) distal half; (2) distal tip (length = 36; CI = 0.05; RI = 0.50). Yeates and Irwin (1996) used this character in the phylogenetic analysis of Apioceridae and Mydidae and established the position of r-m at the distal tip of cell d as an autapomorphy for a subordinate taxon of Mydidae. Within Asilidae and all remaining outgroup taxa the position of r-m with respect to cell d varies considerably and both states (0 and 1) are found throughout the taxa. State 0 is illustrated in figures 73–76 and 83–85 and state 1 is shown in figures 77 and 82. State 2 is here found to be present in Mydidae except *Neorhaphiomidas* sp. (Mandurah).

139. DEVELOPMENT OF DISCAL MEDIAL CELL (CELL dm): (0) absent; (1) present (length = 2; CI = 0.50; RI = 0.00). McAlpine (1981) and Yeates (1994) pointed out that with the loss of vein M_3, cell d cannot form. Vein M_3 is absent in Bombyliidae and therefore only cell dm is present in this taxon (state 1).

140. EXTENT OF C: (0) around entire wing (circumambient); (1) terminating at wing apex; (2) terminating at apices of CuA_2 and A_1; (3) terminating at apex of M2; (4) terminating at apex of M1 (length = 19; CI = 0.21; RI = 0.37). In most Asilidae and outgroup species, the costal vein C is developed around the entire wing (circumambient, state 0; figs. 74, 78–79, 81, 83–85). Different reductions of this configuration can be found in Laphriinae. In *Laxenecera albicincta*, *Nusa infumata*, and *Trichardis effrena*, C is reduced and terminates at the wing apex (state 1; fig. 75), whereas in *Hoplistomerus nobilis*, *Laphystia* species, and *Protometer* sp. (El Tuparro), it terminates at CuA_2 and A_1 (state 2; figs. 73, 76). In *Aphestia annulipes*, *Atomosia puella*, and *Cerotainia albipilosa*, C terminates at M_2 (state 2; fig. 77). Outside of Laphriinae, state 1 is found in *Megaphorus pulchrus* (fig. 80) and *Satanas gigas* (Asilinae) as well as *Sisyrnodytes* sp. (Gamka) (Willistonininae) and state 2 is found in *Afroholopogon*

peregrinus, *Dasycyrton gibbosus*, and *Rhabdogaster pedion* (Brachyrhopalinae); *Damalis* species (Trigonomiminae); and *Acnephalum cylindricum* and *Trichoura* sp. (Tierberg) (Willistonininae). Among the outgroup taxa, Scenopinidae and *Hemigephyra atra* (Therevidae) possess a costal vein terminating at the wing apex (state 1) and in the Mydidae species *Afroleptomydas* sp. (Clanwilliam), *Mitrodetus dentitarsis*, *Nemomydas brachyrhynchus*, *Neorhaphiomidas* sp. (Mandurah), and *Pseudonomoneura hirta*, C terminates at vein M_1 (state 4).

141. MICROTRICHIA ON POSTERIOR WING MARGIN: (0) arranged in a single plane; (1) arranged in two divergent planes; (2) absent (length = 26; CI = 0.07; RI = 0.46). Londt (2005b) used the development of microtrichia on the posterior wing margin as a character to separate certain Afrotropical Apocleinae genera (sensu Papavero, 1973a) following Blasdale (unpublished) who has studied the Afrotropical *Bactria* Meigen, 1820, and *Promachus* species (see Geller-Grimm, 2004, for synonymy of these genera). In most taxa examined, the microtrichia are arranged in a single plane (state 0). In a number of Asilinae; Dasypogoninae; Laphriinae; as well as *Acronyches maya* (Leptogastrinae); *Michotamia aurata* (Ommatiinae); *Phellus olgae* (Phellinae); and *Gonioscelis ventralis* and *Microstylum* sp. (Karkloof) (Stenopogoninae), the microtrichia are arranged in two divergent planes (state 1). In *Blepharotes splendidissimus* and *Satanas gigas* (Asilinae); *Obelophorus terebratus* (Phellinae); and *Sisyrnodytes* sp. (Gamka) (Willistonininae), the microtrichia on the posterior margin of the wing are reduced (state 2). Among the outgroup taxa, *Phycus frommeri* (Therevidae) exhibits state 1 and in *Mitrodetus dentitarsis* and *Neorhaphiomidas* sp. (Mandurah) (Mydidae) the microtrichia are reduced (state 2).

142. APEX OF R_{2+3}: (0) relatively straight; (1) arching sharply anteriorly in 90° angle (length = 7; CI = 0.14; RI = 0.50). Wood (1981) and later authors used the sharply arching vein R_{2+3} as a diagnostic feature to separate genera of Laphriinae from *Laphystia* and relatives (Laphystiinae sensu Papavero, 1973a). Most Asilidae exhibit a relatively straight vein R_{2+3} (state 0; figs. 74–75, 77–81, 83–85). Among the Laphriinae, *Hoplistomerus nobilis*, *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), *Trichardis effrena*, and *Zabrops tagax*; as well as Bathypogoninae; *Gonioscelis ventralis*, *Ospriocerus aeacus*, *Scleropogon subulatus*, and *Stenopogon* species (all Stenopogoninae); *Hypenetes stigmatias* (Tillobromatinae); and *Sisyrnodytes* sp. (Gamka) (Willistonininae) possess a sharply anteriorly arching vein R_{2+3} (state 1; fig. 73). Among the outgroup taxa, the R_{2+3} is relatively straight (state 0).

143. APEX OF R_4: (0) terminating anterior to wing apex; (1) terminating at wing apex; (2) terminating posterior to wing apex; (3) not reaching C (or wing margin) (length = 14; CI = 0.21; RI = 0.60). In most Asilidae species, the apex of vein R_4 reaches the wing margin anterior to the wing apex (state 0; figs. 73–84). In *Austrosaropogon nigrinus*, *Leptarthrus brevirostris*, and *Rhabdogaster pedion* (all Brachyrhopalinae); *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Molobratia teutonus*, and *Senobasis corsair* (all Dasypogoninae); *Dioctria hyalipennis*, *Dioctria rufipes*, and *Nannodioctria* sp. (*formicaphaga*) (all Dioctriinae); *Euscelidia pulchra* (Leptogastrinae); *Lasiopogon* species, *Lissoteles aquilonius*, *Stichopogon punctum*, and *Stichopogon trifasciatus* (all Stichopogoninae); and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae), R_4 reaches the wing margin at the wing apex (state 1). In Leptogastrinae except *Euscelidia pulchra* and *Pegesimallus laticornis* (Dasypogoninae), vein R_4 reaches the wing margin always posterior to the wing apex (state 2; fig. 85). Among the outgroup taxa, vein R_4 does not reach the costa or the wing margin in Mydidae except *Rhaphiomidas maehleri* (state 3).

144. SHAPE OF R_4: (0) relatively straight; (1) strongly sinuate (length = 7; CI = 0.14; RI = 0.40). Papavero (1973a) established the strongly sinuate vein R_4 (state 1) as the defining characteristic to separate Laphriinae and a number of genera related to *Laphystia* (Laphystiinae sensu Papavero, 1973a). Most species of Asilidae exhibit a relatively straight vein R_4 (state 0; figs. 74–75, 77–85). State 1 is found in the following species of Laphriinae, i.e., *Hoplistomerus nobilis*, *Laphystia* species, *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), *Stiphrolamyra angularis*, *Trichardis effrena*, and *Zabrops tagax*, as well as Bath-

ypogoninae and *Stenopogon rufibarbis* (Stenopogoninae) (figs. 73, 76). Among the outgroup taxa, R_4 is sinuate only in *Bombylius major* (Bombyliidae) (state 1).

145. R_5 APEX: (0) terminating anterior to wing apex; (1) terminating posterior to wing apex; (2) not reaching C (or wing margin) (length = 6; CI = 0.33; RI = 0.69). Woodley (1989) postulated the strongly anteriorly curved veins R_5 and M_1 that reach the wing margin anterior to the wing apex as a synapomorphy for a taxon composed of Apioceridae plus Mydidae. Within Asilidae R_5 usually reaches the wing margin posterior to the wing apex (state 1; figs. 73–78, 80–85), but in *Lochmorhynchus albicans*, *Pogonioefferia pogonias*, *Proctacanthus philadelphicus*, and *Satanas gigas* (all Asilinae) R_5 is curving anteriorly so that vein R_5 terminates anterior to the wing apex (state 0; fig. 79). Among the outgroup taxa, R_5 terminates anterior to the wing apex in Apioceridae, *Rhaphiomidas maehleri* (Mydidae), and Nemestrinidae (state 0), but in all other Mydidae species, vein R_5 does not reach the costa vein or the wing margin (state 2). In Apsilocephalidae, Bombyliidae, Scenopinidae, and Therevidae R_5 terminates posterior to the wing apex (state 1).

146. STUMP VEIN (SUPERNUMERARY CROSSVEIN) ON R_4: (0) absent; (1) present, short stump vein not reaching R_{2+3}; (2) present, long stump vein reaching base of R_{2+3} (length = 11; CI = 0.18; RI = 0.35). The wing venation in Asilidae is relatively straightforward and simple compared to, for example, Mydidae or Nemestrinidae. The short stump vein present at the base of R_4 just after departing from the common R_{4+5} in a few taxa is, however, an interesting case of the development of an additional vein not commonly present in other taxa. Oldroyd (1974b) and Londt (2005b) discussed the different configurations of this supernumerary vein in Afrotropical taxa. Hennig (1954) postulated that this vein represents R_3 and illustrated its presence in *Promachus leoninus* Loew, 1848, and related genera (Asilinae) as well as *Apiophora paulseni* Philippi, 1865 (as *Rhopalia*, Mydidae). This is only consequent as he postulated that R_3 is usually lost in Asiloidea, so that the second radial vein is R_2 and not R_{2+3} as interpreted by, for example, McAlpine (1981: fig. 4.32). Papavero (1973a) followed Hennig's view and labeled the stump vein as R_3. Most Asilidae species lack any sign of the stump vein on R_4 (state 0; figs. 73, 75–78, 81–85). It is found consistently in Asilinae, e.g., *Apoclea algira*, *Nomomyia murina*, and *Pogonioefferia pogonias*, and is also found in *Obelophorus terebratus* and *Phellus olgae* (Phellinae) and *Acnephalum cylindricum* (Willistonininae) (state 1; fig. 79). A special case is exhibited in *Eichoichemus pyrrhomystax*, *Megaphorus pulchrus*, *Philodicus tenuipes*, and *Promachus amastrus* (all Asilinae), in which the stump vein connects R_{2+3} and R_4 and forms a supernumerary crossvein thereby dividing cell r_3 into two cells r_{3a} and r_{3b} (state 2; figs. 74, 80). Among the outgroup taxa, a short stump vein is found in Apsilocephalidae, *Poecilognathus* sp. (El Hacha) (Bombyliidae), *Afroleptomydas* sp. (Clanwilliam), *Nemomydas brachyrhynchus*, *Opomydas townsendi*, and *Pseudonomoneura hirta* (all Mydidae) (state 1).

147. APEX OF M_1: (0) terminating anterior to wing apex; (1) terminating posterior to wing apex; (2) not reaching C (or wing margin) (length = 4; CI = 0.50; RI = 0.80). Woodley (1989) postulated the anteriorly curved veins R_5 and M_1 as a synapomorphy for a taxon composed of Apioceridae plus Mydidae (see character 145). In Asilidae, vein M_1 terminates posterior to the wing apex (state 1; figs. 73–85). Among the outgroup taxa, M_1 always curves anteriorly to terminate anterior to the wing apex in Apioceridae, Mydidae except *Pseudonomoneura hirta*, and Nemestrinidae (state 1). In *Satanas gigas* (Asilinae) and *Pseudonomoneura hirta* (Mydidae), vein M_1 does not reach the costa vein or the wing margin (state 2).

148. FUSION OF M_1 AND M_2: (0) separated; (1) fused (length = 2; CI = 0.50; RI = 0.85). Yeates and Irwin (1996) used the fusion of M_1 or M_1+M_2 with R_4 as a character in the phylogenetic analysis of Apioceridae and Mydidae. Here, the fusion of M_1 and M_2 itself is considered and this state is found in Mydidae except *Rhaphiomidas maehleri* and Nemestrinidae (state 1). All Asilidae species possess separated M_1 and M_2 veins (state 0; figs. 73–85).

149. DEVELOPMENT OF M_3 (DISTAL SECTION BEYOND m-m): (0) absent; (1) present (length

= 4; CI = 0.25; RI = 0.25). Yeates (1994) mentioned the reduction of vein M_3 in Bombyliidae and Scenopinidae and this is confirmed here (state 0). In *Townsendia albomacula* (Stichopogoninae) and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae), vein M_3 is also reduced beyond crossvein m-m (state 0; fig. 86). All remaining Asilidae species exhibit a well-developed vein M_3 (state 1; figs. 73–85).

150. ALIGNMENT OF BASE OF M_2 AND m-m: (0) not aligned; (1) aligned from anterior to posterior; (2) aligned from proximal to distal (nearly parallel to posterior margin of wing) (length = 4; CI = 0.50; RI = 0.71). Macquart (1838), in describing the genus *Atomosia* and later Hermann (1912) in diagnosing a taxon comprising *Atomosia* and related taxa from South America, highlighted the distinct wing venation of vein M_2 and crossvein m-m in these species. In most species of Asilidae, M_2 and m-m are not aligned in any particular way (state 0; figs. 73–76, 78–80, 82–85). In *Aphestia annulipes*, *Atomosia puella*, *Cerotainia albipilosa*, *Goneccalypsis argenteoviridis*, and *Loewinella nigripes* (all Laphriinae), M_2 and m-m are aligned from anterior to posterior (state 1; fig. 77). *Orthogonis scapularis* (Laphriinae) is coded here to be polymorphic (states 0/1) because some specimens exhibit a clear alignment of the veins (state 1) and in others, hardly any alignment is found (state 0). In *Archilestris magnificus* (Dasypogoninae); *Obelophorus terebratus* and *Phellus olgae* (Phellinae); and *Microstylum* sp. (Karkloof) (Stenopogoninae), M_2 and m-m are also aligned, but in a line from proximal to distal and running nearly parallel to the posterior wing margin (state 2; fig. 81). Among the outgroup taxa, these two veins are always unaligned (state 0).

ABDOMEN (FEMALE AND MALE)

151. SCULPTURE OF TERGITES: (0) smooth, setae with small socket only; (1) indented, setae in large grooves (length = 5; CI = 0.20; RI = 0.60). In general, the surface of the tergites is smooth and setal sockets are only barely visible under a stereomicroscope (state 0). As has been pointed out by Hermann (1912) for some South American Laphriinae, the setal sockets can be very large and distinct. This is found in *Chrysopogon pilosifacies*, *Codula limbipennis*, and *Leptarthrus brevirostris* (all Brachyrhopalinae), as well as *Aphestia annulipes*, *Atomosia puella*, *Cerotainia albipilosa*, *Goneccalypsis argenteoviridis*, *Hoplistomerus nobilis*, *Loewinella nigripes*, *Stiphrolamyra angularis*, and *Trichardis effrena* (all Laphriinae) (state 1). Among the outgroup taxa, the tergites are always smooth (state 0).

152. T1 MEDIALLY: (0) entirely sclerotized medially; (1) divided medially by membraneous area into two halves (length = 12; CI = 0.08; RI = 0.38). T1 is usually composed of a single, narrow sclerite with an entire posterior margin (state 0). A few Asilidae exhibit a medially divided tergite (state 1), which is indicated by an indentation of the posterior margin. The following species exhibit a divided T1: *Blepharotes splendidissimus*, *Eichoichemus pyrrhomystax*, *Heligmonevra laevis*, *Lochmorhynchus albicans*, *Megaphorus pulchrus*, *Myaptex brachyptera*, *Neoitamus cyanurus*, *Philodicus tenuipes*, *Proctacanthus philadelphicus*, *Promachus amastrus* (all Asilinae); as well as *Megapoda labiata* (Dasypogoninae); *Holcocephala abdominalis*, *Rhipidocephala* sp. (Harold Johnson), and *Trigonomima* sp. (*anamaliensis*) (all Trigonomiminae); and *Willistonina bilineata* (Willistonininae). Among the outgroup taxa, Bombyliidae and Scenopinidae exhibit a divided T1 (state 1).

153. T2 LENGTH: (0) wider than long or as wide as long; (1) longer than wide, less than twice as long; (2) longer than wide, more than twice as long (length = 18; CI = 0.11; RI = 0.44). Martin (1968) established the elongated second abdominal tergite in Leptogastrinae species as an autapomorphy for this taxon and it has since been used in identification keys by several authors (e.g., Wood, 1981). In most Asilidae, T2 is wider than long (state 0). In *Clephydroneura sundaica* and *Lycomya germainii* (Asilinae); *Nannocyrtopogon lestomyiformis*, *Nicocles politus*, and *Rhabdogaster pedion* (all Brachyrhopalinae); *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, and *Pegesimallus laticornis* (all Dasypogoninae); *Broticosia paramonovi*, *Dioctria hyalipennis*, *Dioctria rufipes*, and *Nannodioctria* sp. *formicaphaga* (all Dioctriinae); *Lamyra gulo* (Laphriinae); Ommatiinae except *Cophi-*

nopoda chinensis; *Plesiomma* sp. (Guanacaste) and *Stenopogon rufibarbis* (Stenopogoninae); *Tillobroma punctipennis* (Tillobromatinae); *Holcocephala calva* (Trigonomiminae); and *Oligopogon* sp. (Cape Recife), T2 is wider than long, but less than twice as long (state 1). All Leptogastrinae species exhibit state 2. Among the outgroup taxa, T2 is always wider than long (state 0).

154. T2 SHAPE DORSALLY: (0) dorsal surface smooth, without protuberance; (1) dorsal surface with proximal protuberance (length = 4; CI = 0.25; RI = 0.76). In general the dorsal surface of T2 is flat or only slightly elevated medially and declining toward the posterior margin in Asilidae (state 0). In a number of species, a proximal protuberance is evident that is distinct and easily observed (state 1). Papavero (1975) called these protuberances on T2 bullae, but these simple structures are not homologous to the bullae found in some Mydidae species, which are situated at the posterior margin of T2 and separated medially (see character 155). The following species exhibit state 1: *Ceraturgus fasciatus* (Brachyrhopalinae); *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Megapoda labiata*, *Molobratia teutonus*, *Pegesimallus laticornis*, and *Pseudorus distendens* (all Dasypogoninae); *Dioctria* species, *Echthodopa pubera*, *Eudioctria albius*, *Myelaphus melas*, and *Nannodioctria* sp. (*formicaphaga*) (all Dioctriinae). Among the outgroup taxa, all species lack dorsal protuberances on T2 (state 0).

155. BULLAE ON T2: (0) absent; (1) present (length = 1; CI = 1.00; RI = 1.00). Yeates and Irwin (1996) postulated the bullae on the lateroposterior margin of T2 as an autapomorphy of a subordinate taxon of Mydidae. It is found here in all representatives of Mydidae, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri* (state 1).

156. T2–3 DEVELOPMENT: (0) tergites square to rectangular (parallel-sided); (1) tergites forming a distinct "waist" (length = 6; CI = 0.16; RI = 0.50). In general, the abdomen is more or less parallel-sided, sometimes becoming wider toward the apex to accommodate the genitalia in Asilidae (state 0). Hennig (1973) mentioned a proximally constricted abdomen in Asilidae as an autapomorphy and attributed this character to Hull (1962; note: I am unable to find any reference to such a character in Hull's study). In some Asilidae species, namely *Brachyrhopala ruficornis* (Brachyrhopalinae); *Blepharepium cajennensis*, *Cyrtophrys attenuatus*, *Molobratia teutonus*, and *Pegesimallus laticornis* (all Dasypogoninae); *Nannodioctria* sp. (*formicaphaga*) (Dioctriinae); *Lamyra gulo* (Laphriinae); and *Emphysomera* species and *Michotamia aurata* (Ommatiinae), T2–3 are narrower than the following tergites and therefore the abdomen appears constricted proximally and waistlike (state 1). Among the outgroup taxa, the proximal abdomen is never waistlike (state 0). In some instances, it is difficult to decide whether the constriction is an artifact of a dried specimen and this is especially true in females, which have an expanded distal abdomen due to the large number of eggs held within it.

157. T3–6 DEVELOPMENT: (0) tergites entirely sclerotized; (1) tergites unsclerotized medially (length = 2; CI = 0.50; RI = 0.00). Abdominal tergites are usually sclerotized entirely (state 0), but two species of Trigonomiminae, i.e., *Rhipidocephala* sp. (Harold Johnson) and *Trigonomima* sp. (*anamaliensis*), exhibit medially unsclerotized tergites (state 1). Among the outgroup taxa, T3–6 are always well developed and sclerotized (state 0).

158. T6 SHAPE: (0) T6 the same as T5; (1) T6 cup-shaped, last visible tergite concealing remaining tergites (length = 1; CI = 1.00; RI = 1.00). The abdominal tergites are very uniform in Asilidae, in that with the exception of the tergites immediately anterior to the genitalia, they are not modified and appear very similar throughout the abdomen. T5 and T6 are no exception and are usually of the same shape although T6 might be shorter than T5 (state 0). In *Atomosia puella* and *Cerotainia albipilosa* (Laphriinae), T6 is very large, cup-shaped, and the last apparent segment concealing the following tergites and genitalia (state 1). Among the outgroup taxa, T6 has always the same shape as T5 (state 0).

159. S2 DEVELOPMENT: (0) undivided medially; (1) divided medially into two equal halves separated by fenestra (length = 1; CI = 1.00; RI = 1.00). Martin (1968) postulated the divided S2 with fenestra as an autapo-

TABLE 4

Presence/absence of marginal and medial macrosetae on abdominal tergites 2–7 in males and females of Asilinae and Laphriinae (chars. 160–165 and 186–191).

Symbols: – = no macrosetae present; • = marginal macrosetae present; △ = medial macrosetae present

	♂						♀					
Species	T2	T3	T4	T5	T6	T7	T2	T3	T4	T5	T6	T7
Afromochtherus mendax	•	•	•	•	–	–	•	•	•	•	–	–
Apoclea algira	•	•	•	•	•	–	–	–	–	–	–	–
Asilus crabroniformis	–	–	–	–	–	–	–	–	–	–	–	–
Asilus sericeus	–	–	–	–	–	–	–	–	–	–	–	–
Blepharotes splendidissimus	–	–	–	–	–	–	–	–	–	–	–	–
Clephydroneura sundaica	•	•	•	–	–	–	•	•	•	–	–	–
Clephydroneura sp. (Kepong)	•	•	–	–	–	–	•	•	•	•	–	–
Colepia rufiventris	•	•	•	–	–	–	•	•	•	–	–	–
Congomochtherus inachus	•	•	•	•	•	–	•	•	•	•	•	–
Dasophrys crenulatus	•	•	•	–	–	–	•	•	•	–	–	–
Dysmachus trigonus	•	•	•	•	•	–	•	•	•	•	•	–
Eichoichemus pyrrhomystax	•	•	–	–	–	–	•	•	•	•	–	–
Heligmonevra laevis	•	•	•	•	•	–	•	•	•	•	–	–
Lochmorhynchus albicans	–	–	–	–	–	–	–	–	–	–	–	–
Lycomya germainii	–	–	–	–	–	–	–	–	–	–	–	–
Machimus chrysitis	•	•	•	•	–	–	•	•	•	•	–	–
Machimus occidentalis	•	•	•	•	–	–	•	•	•	•	–	–
Megaphorus pulchrus	–	–	–	–	–	–	–	–	–	–	–	–
Myaptex brachyptera	•	•	•	•	•	–	•	•	•	•	•	–
Neoitamus cyanurus	•	•	•	•	–	–	•	•	•	–	–	–
Neolophonotus bimaculatus	–	–	–	–	–	–	–	–	–	–	–	–
Neomochtherus pallipes	•	•	•	•	•	–	•	•	•	•	•	–
Nomomyia murina	•	•	•	•	–	–	•	•	•	•	–	–
Philonicus albiceps	•	•	•	•	•	–	•	•	•	–	–	–
Pogonioefferia pogonias	–	–	–	–	–	–	–	–	–	–	–	–
Proctacanthus philadelphicus	–	–	–	–	–	–	–	–	–	–	–	–
Promachus amastrus	•	•	•	•	•	–	–	–	–	–	–	–
Satanas gigas	•	•	•	•	•	•	•	•	–	–	–	–
Threnia carbonaria	•	•	•	•	–	–	•	•	•	•	•	•
Tolmerus atricapillus	•	•	•	•	–	–	•	•	•	•	•	–
Zosteria rosevillensis	•	•	•	•	•	•	•	•	•	•	•	–
Andrenosoma cyrtoxys	△	△	△	△	–	–	△	△	△	△	–	–
Aphestia annulipes	△	△	△	△	△	–	△	△	△	△	△	–
Atomosia puella	△	△	△	△	–	–	△	△	–	–	–	–
Cerotainia albipilosa	–	–	–	–	–	–	–	–	–	–	–	–
Choerades bella	△	–	–	–	–	–	△	–	–	–	–	–
Dasyllis funebris	△	△	△	△	–	–	△	△	△	△	–	–
Goneccalypsis argenteoviridis	△	△	△	△	△	△	△	△	△	△	△	△
Hoplistomerus nobilis	△	△	△	△	△	–	△	△	△	△	△	–
Hyperechia nigripennis	–	–	–	–	–	–	–	–	–	–	–	–
Lampria clavipes	△	△	–	–	–	–	△	–	–	–	–	–
Lamyra gulo	△	△	△	△	–	–	△	△	△	–	–	–
Laphria aktis	–	–	–	–	–	–	△	△	–	–	–	–
Laphria flava	–	–	–	–	–	–	–	–	–	–	–	–
Laphystia aegyptiaca	△	△	△	△	△	–	△	△	△	△	△	–
Laphystia toland	△	△	△	△	△	–	△	△	△	△	△	–
Laxenecera albicincta	△	△	–	–	–	–	△	–	–	–	–	–
Loewinella nigripes	△	△	△	△	△	△	△	△	△	△	△	△
Maira aenea	△	△	△	△	–	–	△	△	△	△	–	–
Nusa infumata	△	△	△	△	△	–	△	△	△	△	△	–

TABLE 4
(Continued)

	♂						♀					
Species	T2	T3	T4	T5	T6	T7	T2	T3	T4	T5	T6	T7
Orthogonis scapularis	△	△	△	△	–	–	△	△	△	△	–	–
Perasis transvaalensis	–	–	–	–	–	–	–	–	–	–	–	–
Pilica formidolosa	△	△	△	△	–	–	△	△	△	△	–	–
Proagonistes praeceps	△	△	–	–	–	–	△	△	△	△	–	–
Protometer sp. (El Tuparro)	△	△	△	△	–	–	△	△	△	△	△	–
Psilocurus modestus	△	△	△	–	–	–	△	△	△	△	△	–
Smeryngolaphria numitor	△	△	△	△	–	–	△	△	△	△	–	–
Stiphrolamyra angularis	△	△	△	–	–	–	△	△	△	△	–	–
Trichardis effrena	△	△	△	△	△	–	△	△	△	△	△	–
Zabrops tagax	△	–	–	–	–	–	△	–	–	–	–	–

morphy for his Leptogastridae. State 1 is found here in all Leptogastrinae species, but not in any other Asilidae. The fenestrae, small unsclerotized parts of the cuticle, are situated medially on the elongated second abdominal segment. It is important to highlight the observation that S2 also appears to be divided proximally in, for example, *Ommatius* or *Damalis*, but this state is not considered homologous to the state found in Leptogastrinae. The problem lies in the difficulty to distinguish between S1 and S2. The unsclerotized area in *Damalis* could be interpreted as the intersegmental membrane between S1 and S2 and not as a subdivision of S2. Among the outgroup taxa, S2 is never subdivided (state 0).

Female Abdomen

Note: *Broticosia paramonovi* (Dioctriinae), *Emphysomera conopsoides* (Ommatiinae), *Ancylorhynchus fulvicollis* (Stenopogoninae), and *Nemomydas brachyrhynchus* (Mydidae) are represented by male specimens only and could not be coded for the female abdominal characters. Only previously dissected specimens of *Megapoda labiata* (Dasypogoninae) where available for study and characters 166–174 and 181–185 could not be coded for this species. *Neorhaphiomidas* sp. (Mandurah) (Mydidae) and *Prorates* sp. (Escalante) (Scenopinidae) are not coded for characters 175–182. In some instances reference is made to illustrations of species represented in this study published previously by Theodor (1976) who studied the internal female genitalia in detail.

160. Lateral macrosetae on T2: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 7; CI = 0.28; RI = 0.88). The presence of lateral marginal macrosetae, also often called discal setae, on the abdominal tergites has been widely used in the identification of Asilinae species in which these macrosetae are often well developed. Many Laphriinae species also have lateral macrosetae on the abdominal tergites, but these setae are situated medially and not on the posterior margin of the tergites, therefore, being interpreted as nonhomologous to the marginal setae in Asilinae. Table 4 summarizes the presence/absence of marginal setae (state 1) and medial setae (state 2) in Asilinae and Laphriinae. *Daspletis stenoura* (Stenopogoninae) exhibits also marginal setae on T2. Among the outgroup taxa, neither marginal nor medial setae are developed (state 0).

161. Lateral macrosetae on T3: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 8; CI = 0.25; RI = 0.84). See character 160 and table 4.

162. Lateral macrosetae on T4: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 9; CI = 0.22; RI = 0.82). See character 160 and table 4. State 1 is also found in *Emphysomera pallidapex*, *Afroestricus chiastoneurus*, and *Ommatius tibialis* (all Ommatiinae).

163. Lateral macrosetae on T5: (0) absent; (1) marginal (m l) setae present; (2)

medial setae present (length = 15; CI = 0.13; RI = 0.60). See character 160 and table 4. State 1 is also found in *Emphysomera pallidapex*, *Afroestricus chiastoneurus*, and *Ommatius tibialis* (all Ommatiinae).

164. LATERAL MACROSETAE ON T6: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 12; CI = 0.16; RI = 0.44). See character 160 and table 4. State 1 is also found in *Emphysomera pallidapex*, *Afroestricus chiastoneurus*, and *Ommatius tibialis* (all Ommatiinae).

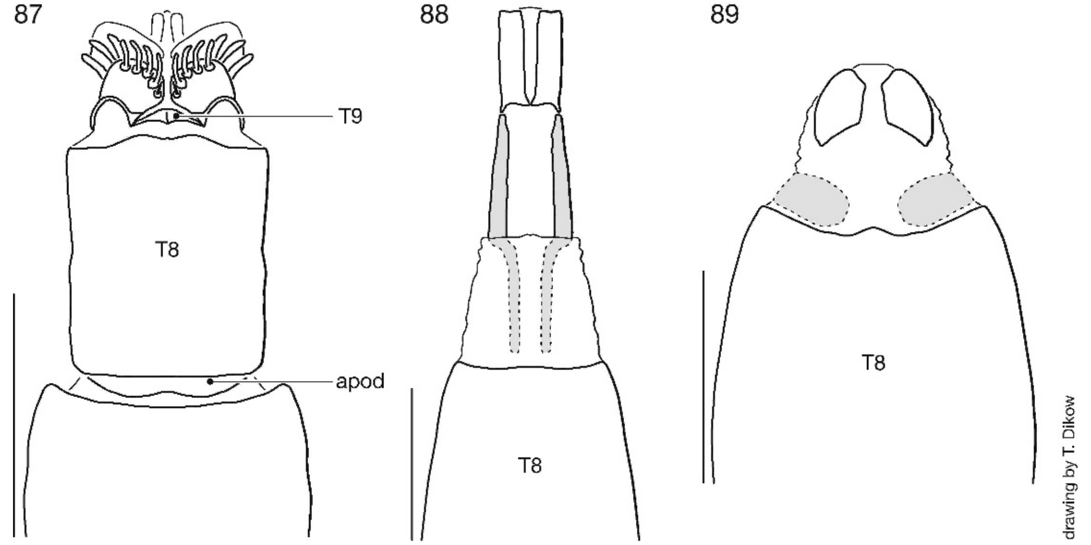
165. LATERAL MACROSETAE ON T7: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 4; CI = 0.50; RI = 0.50). See character 160 and table 4. State 1 is also found in *Emphysomera pallidapex*, *Afroestricus chiastoneurus*, and *Ommatius tibialis* (all Ommatiinae).

166. SEGMENT 7: (0) S7 and T7 normally developed; (1) S7 and T7 distinctly shortened; (2) S7 and T7 elongated; (3) only S7 reduced in size (length = 3; CI = 1.00; RI = 1.00). The abdominal segments are usually of the same size and in some instances become slightly shorter only toward the apex of the abdomen. Only the segments that are directly involved in oviposition (see character 167) are altered in their proportions. In a few species, however, segment 7 is morphologically different from the following segments. In *Aphestia annulipes*, *Atomosia puella*, and *Cerotainia albipilosa* (all Laphriinae) segment 7 is much shorter than segment 8 (state 1) and in *Leptarthrus brevirostris* (Brachyrhopalinae) segment 7 is elongated (state 2). In *Dicolonus simplex* (Dioctriinae) S7 is reduced in size whereas T7 is normally developed (state 3). Among the outgroup taxa, segment 7 is always normally developed (state 0).

167. SEGMENTS COMPRISING OVIPOSITOR: (0) 8th and following; (1) 7th and following (length = 3; CI = 0.33; RI = 0.60). The specialized abdominal segments that are associated with the oviposition of eggs are generally referred to as the ovipositor. The ovipositor of Diptera is not homologous to the "true" ovipositor found in other Endopterygota (e.g., Mickoleit, 1973; McAlpine, 1981). In general, the ovipositor comprises segments 8 and 9 (state 0), but in *Leptarthrus brevirostris* (Brachyrhopalinae); *Aphestia annulipes*, *Atomosia puella*, and *Cerotainia albipilosa* (all Laphriinae); and *Obelophorus terebratus* and *Phellus olgae* (Phellinae), segment 7 is specialized and involved in oviposition (state 1). Among the outgroup taxa, segments 8 and following comprise the ovipositor (state 0).

168. DIRECTION OF SETAE ON T8: (0) posteriorly; (1) anteriorly; (2) erect (length = 29; CI = 0.06; RI = 0.65). T8 is generally modified and part of the ovipositor (see character 167). The setation of T8 varies among Asilidae species with respect to the orientation of the setae. All species of Dioctriinae; Laphriinae; Leptogastrinae; Ommatiinae; Trigonomiminae; and a few other species exhibit state 0 in that the setae are directed posteriorly in the same direction as setae on proximal tergites. In *Dasycyrton gibbosus*, *Holopogon priscus*, and *Leptarthrus brevirostris* (all Brachyrhopalinae); *Dasypogon diadema*, *Diogmites grossus*, *Pegesimallus laticornis*, *Saropogon dispar*, and *Thereutria amaraca* (all Dasypogoninae); *Gonioscelis ventralis* (Stenopogoninae); *Stichopogon punctum* (Stichopogoninae); *Lycostommyia albifacies* (Tillobromatinae); and *Acnephalum cylindricum* (Willistonininae), the setae are directed anteriorly (state 1). Many Asilinae; Bathypogoninae; Brachyrhopalinae; Phellinae; Stenopogoninae; Tillobromatinae; Willistonininae; and *Oligopogon* sp. (Cape Recife) possess erect setae, which are directed perpendicular to the surface (state 2). In some instances, states (1) and (2) are difficult to distinguish. Among the outgroup taxa, state 0 is found in Apsilocephalidae, Bombyliidae, Nemestrinidae, Scenopinidae, and Therevidae and only within Apioceridae and Mydidae are states (1) and (2) present.

169. T8 ANTERIOR RECTANGULAR PROJECTION: (0) absent, no apodeme present; (1) present, rectangular apodeme, entirely fused to T8; (2) present, rectangular apodeme, dissociated from T8; (3) present, cylindrical apodeme, fused to T8 (length = 20; CI = 0.15; RI = 0.61). The anterior margin of T8 is generally simple with no particular appendages or projections (state 0). When macerated in KOH, a narrow projection, which is situated ventral of the intersegmental membrane, and fused entirely to T8 can be found in all Bathypogoninae; Tillobromatinae; Willistonininae; and a number of



Figs. 87–89. Female posterior part of abdomen in dorsal view with tergites labeled. **87.** *Hypenetes stigmatias* (Tillobromatinae). **88.** *Dasyllis funebris* (Laphriinae), T10 grey. **89.** *Acronyches maya* (Leptogastrinae), lightly sclerotized T10 grey. Apod = anterior apodeme of T8; vestiture omitted. Scale lines = 1 mm.

Brachyrhopalinae; Dasypogoninae; and Stenopogoninae (state 1; fig. 87). *Senobasis corsair* (Dasypogoninae) exhibits a projection as well, but it is not fused to T8 (state 2). Among the outgroup taxa, *Bombylius major* (Bombyliidae) and *Hemigephyra atra* (Therevidae) exhibit a smaller, cylindrical apodeme that is fused to T8 (state 3). Most Apioceridae and Mydidae species, with the exception of *Mydas clavatus* and *Rhaphiomidas maehleri*, which lack a projection, exhibit state 1.

170. SHAPE OF S8: (0) platelike, slightly emarginate mediodistally; (1) platelike, with median area elongated; (2) proximally platelike, hypogynial valves forming keel distally; (3) keellike throughout; (4) platelike, hypogynial valves extending; (5) platelike, distal margin medially membranous; (6) platelike, hypogynial valves separated (surrounded by membrane); (7) platelike, divided into two halves; (8) S8 modified to form part of sand chamber (length = 33; CI = 0.24; RI = 0.77). The shape of the ovipositor varies considerably in Asilidae as different oviposition sites are used by different species. *Leptogaster cylindrica* (Leptogastrinae) and *Holcocephala calva* (Trigonomiminae) perch on vegetation and drop their eggs to the ground whereas *Pogonioefferia pogonias* places the eggs between the leaves of grass stems and *Laphria flava* deposits eggs in old tree trunks. S8 is modified to accommodate these different oviposition mechanisms and figure 90 illustrates the different configurations of S8 that are here coded as character states. A simple platelike S8 with slight emarginations (state 0) is found in Leptogastrinae, with the exception of *Acronyches maya* (state 6); Ommatiinae; Trigonomiminae, with the exception of *Rhipidocephala* sp. (Harold Johnson) (state 5); some Laphriinae and most of the outgroup taxa (state 0; figs. 96, 98). State 1 is exhibited in *Leptarthrus brevirostris* (Brachyrhopalinae) and the following Laphriinae: Andrenosomatini, Ctenotini, Laphriini, *Nusa infumata*, *Orthogonis scapularis*, and *Smeryngolaphria numitor* (fig. 94). State 2 is found in *Chrysopogon pilosifacies* and *Codula limbipennis* (Brachyrhopalinae) and the following Asilinae species: *Afromochtherus mendax*, *Asilus* species, *Apoclea algira*, *Blepharotes splendidissimus*, *Colepia rufiventris*, *Congomochtherus inachus*, *Heligmonevra laevis*, *Lycomya germainii*, *Megaphorus pulchrus*, *Neoitamus cyanurus*, *Neomochtherus pallipes*, *Nomomyia murina*,

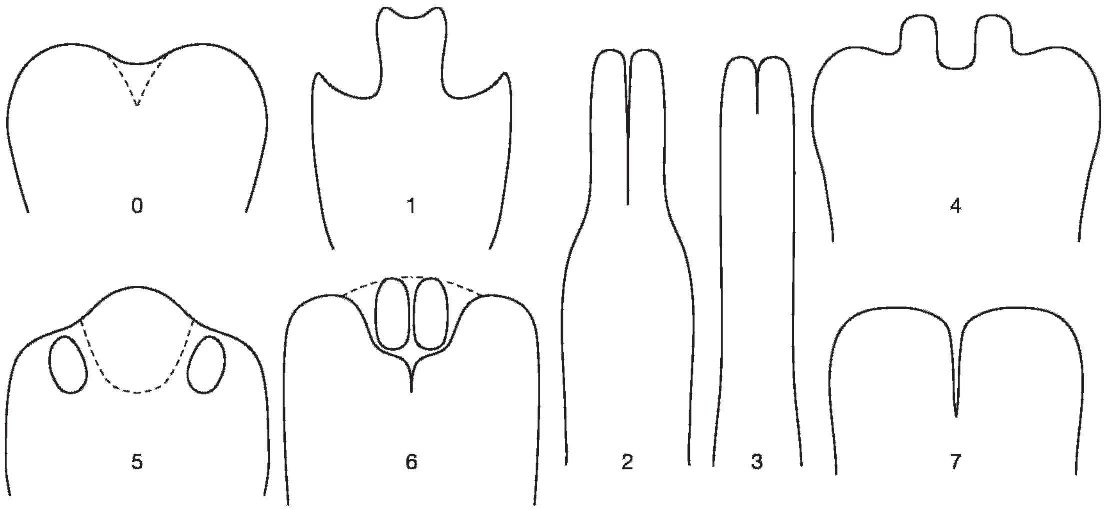
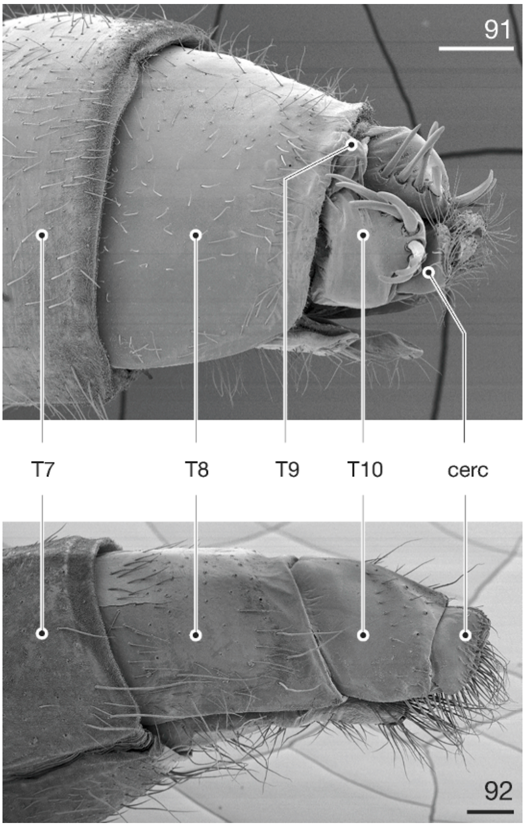


Fig. 90. Schematic illustration of shape of female S8 in ventral view as coded in character 170. Numbers refer to character states; state 8, which is only found in *Bombylius major* (Bombyliidae), is illustrated in Yeates (1994); vestiture omitted; not to scale.

Philodicus tenuipes, *Philonicus albiceps*, *Proctacanthus philadelphicus*, *Promachus amastrus*, *Satanas gigas*, and *Zosteria rosevillensis* (figs. 92, 95). All remaining Asilinae together with *Pseudorus distendens* (Dasypogoninae) and *Obelophorus terebratus* and *Phellus olgae* (Phellinae) possess an ovipositor that is keellike throughout (state 3; fig. 93). A platelike S8 with extending hypogynial valves (state 4) is found in all Bathypogoninae; Tillobromatinae; and in the majority of species of Brachyrhopalinae; Dasypogoninae; Dioctriinae; Stenopogoninae; and Willistonininae. All Stichopogoninae; *Threnia carbonaria* (Asilinae); *Cophura brevicornis* and *Nicocles politus* (Brachyrhopalinae); *Dasypogon diadema*, *Diogmites grossus*, and *Thereutria amaraca* (all Dasypogoninae) possess a platelike S8 in which the hypogynial valves are separated and surrounded by membrane (state 6; fig. 97). *Connomyia varipennis* (Stenopogoninae); *Apiocera painteri* (Apioceridae), and Therevidae have a platelike S8 that is divided into two halves (state 7). *Bombylius major* (Bombyliidae) has a modified ovipositor to form a sand chamber (see Yeates, 1994) and is coded here as state 8.

171. T9 SHAPE (WHEN DISTINGUISHABLE): (0) small, triangular sclerite; (1) wide, rectangular sclerite without median protuberance; (2) wide, rectangular sclerite with median protuberance (length = 2; CI = 1.00; RI = 1.00). Yeates (1994) pointed out that in Apioceridae and Mydidae T9 bears a dorsal spine whereas other Asiloidea have a smooth dorsal surface. T9 and T10 are fused in many Asiloidea (see character 173) making it difficult to examine the shape of T9. All taxa with a fused T9 and T10 are coded as inapplicable (-). For all Asilidae in which both sclerites are distinguishable, T9 is small and triangular (state 0; figs. 87, 91). Among the outgroup taxa, state 1 is found in *Bombylius major* (Bombyliidae), Nemestrinidae, and *Phycus frommeri* (Therevidae) and state 2 is only found in Apioceridae and Mydidae.

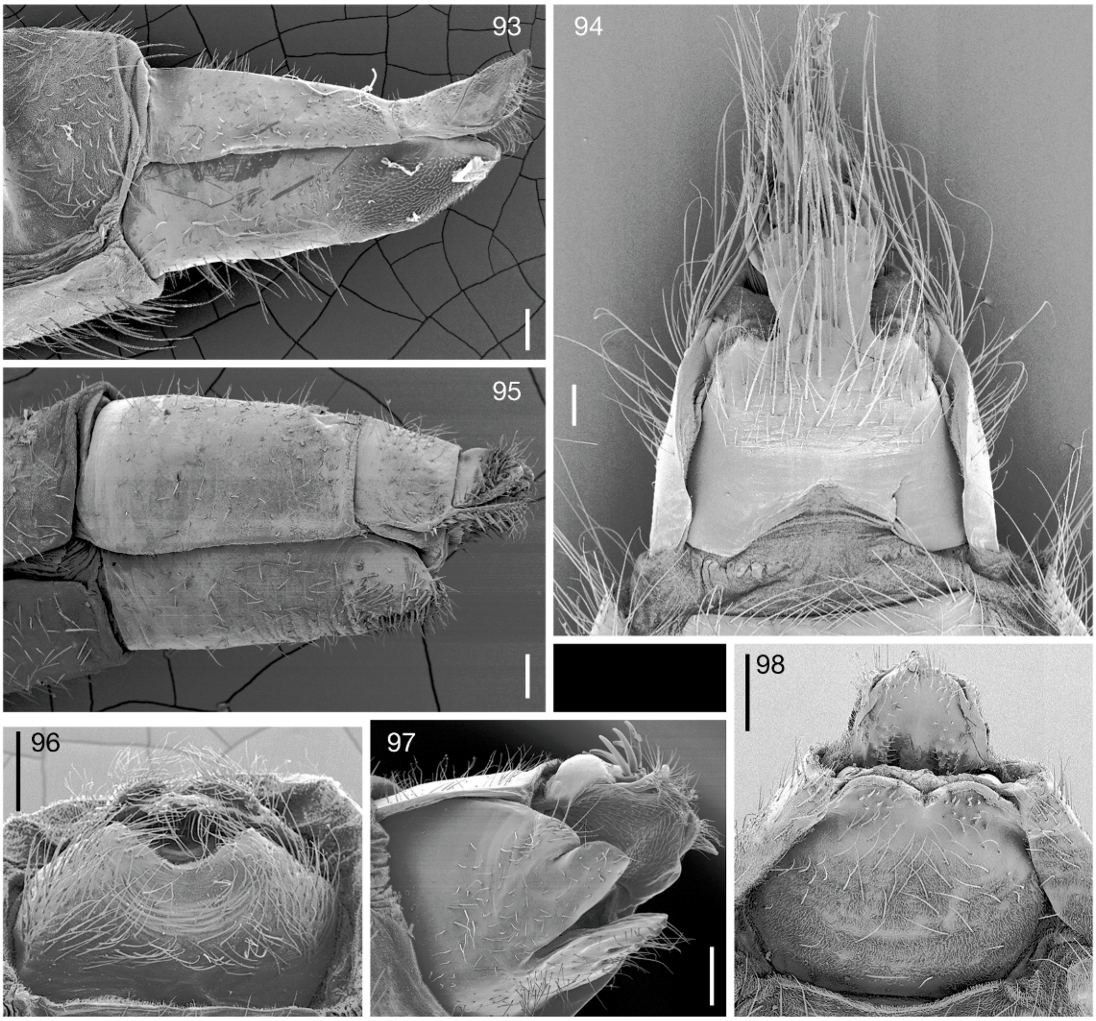
172. T10 SHAPE: (0) single sclerite; (1) tergite partly divided posteromedially; (2) tergite divided into two heavily sclerotized acanthophorite plates; (3) tergite divided into two heavily sclerotized sclerites that are far apart; (4) tergite divided into two slightly sclerotized sclerites; (5) T10 lost or fused to cerci (length = 21; CI = 0.23; RI = 0.82). Hull (1962), Oldroyd (1964), and Hennig (1976) observed the division of T9 into two sclerites called acanthophorite plates that bear generally strong spurs used to excavate soil for oviposition. Hardy (1944) was



Figs. 91–92. SEM micrographs of female ovipositor in lateral view with morphological features labeled. **91.** *Lasiopogon cinctus* (Stichopogoninae). **92.** *Promachus amastrus* (Asilinae). For abbreviations see Materials and Methods. Scale lines = 200 μm.

ambiguous in his description and mentioned both T9 and T10 as bearing the spurs although he also indicated that the sclerites appear fused in many instances. It has been shown by Adisoemarto and Wood (1975), Irwin (1976), McAlpine (1981) and subsequent authors that it is actually T10 that is divided. T9 is often reduced to a small sclerite and sometimes even fused to T10 so that both are indistinguishable. The reduction of T9 can probably be attributed to the transformation of S9 into the furca (see character 184). A single, separate sclerite T10 is found only in the majority of species of Asilinae; Dioctriinae; and Ommatiinae (state 0; figs. 93, 95); all remaining Asilidae possess a modified T10. A partly posteromedially divided T10 is found in *Megaphorus pulchrus*, *Nomomyia murina*, *Promachus amastrus*, and *Zosteria rosevillensis* (all Asilinae) (state 1; fig. 92). A divided T10 with two heavily sclerotized acanthophorite plates is found in all Bathypogoninae; Brachyrhopalinae; Dasypogoninae except *Senobasis corsair*; Phellinae; Stenopogoninae; Stichopogoninae; Tillobromatinae; Willistonininae; and *Oligopogon* sp. (Cape Recife) (state 2; figs. 87, 91, 97). Species of Andrenosomatini (Laphriinae) exhibit state 3 in which two separate heavily sclerotized sclerites are positioned far apart from each other (fig. 88). In Leptogastrinae; *Emphysomera pallidapex* (Ommatiinae); as well as *Holcocephala* species and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae), T10 is visible only as two weakly sclerotized sclerites that are positioned far apart (state 4; fig. 89). Karl (1959) referred to a personal communication by E. Hennig who found that the 9th abdominal segment is absent in Leptogastrinae. This conclusion could be attributed to the difficulty of distinguishing the weakly sclerotized plates forming T10 in Leptogastrinae. T10 is either entirely reduced or fused to the cerci so that it is indistinguishable in most species of Laphriinae as well as *Damalis* species (Trigonomiminae) (state 5). Among the outgroup taxa, either a simple T10 is developed in Apsilocephalidae, *Poecilognathus* sp. (El Hacha) (Bombyliidae), and *Hemigephyra atra* (Therevidae) (state 0), or acanthophorite plates are developed as in Apioceridae, *Bombylius major* (Bombyliidae), Mydidae except *Mydas clavatus*, Scenopinidae, and *Phycus frommeri* (Therevidae) (state 2).

173. Fusion of T9 and T10: (0) not fused; (1) partly fused; (2) entirely fused, sclerites not distinguishable (length = 12; CI = 0.16; RI = 0.83). An entirely separated T9 and T10 is found only in *Chrysopogon pilosifacies*, *Codula limbipennis*, *Cophura brevicornis*, and *Nicocles politus* (all Brachyrhopalinae) as well as *Blepharepium cajennensis* and *Neodiogmites melanogaster* (Dasypogoninae) (state 0). A partly fused T9 and T10 is found in most Brachyrhopalinae and Dasypogoninae; Phellinae; Stenopogoninae; Tillobromatinae; Willistonininae; and *Oligopogon* sp. (Cape Recife) (state 1; fig. 87). The two tergites are entirely fused or at least not



Figs. 93–98. SEM micrographs of female ovipositor in lateral and ventral view. **93.** *Dysmachus trigonus* (Asilinae), lateral. **94.** *Laphria flava* (Laphriinae), ventral. **95.** *Philonicus albiceps* (Asilinae), lateral. **96.** *Dioctria atricapillus* (Dioctriinae), ventral. **97.** *Lasiopogon cinctus* (Stichopogoninae), ventral. 98. *Euscelidia pallasii* (Wiedemann, 1818) (Leptogastrinae), ventral. Scale lines = 200 μm.

distinguishable, which could also be due to the reduction of T9, in all Asilinae; Bathypogoninae; *Leptarthrus brevirostris* (Brachyrhopalinae); *Senobasis corsair* and *Molobratia teutonus* (Dasypogoninae); Dioctriinae; Laphriinae; Leptogastrinae; Ommatiinae; and Trigonomiminae (state 2; fig. 92). Among the outgroup taxa, Nemestrinidae exhibit state 0, *Bombylius major* (Bombyliidae) state 1, and Apioceridae, Apsilocephalidae, *Poecilognathus* sp. (El Hacha) (Bombyliidae), Mydidae, Scenopinidae, and Therevidae state 2.

174. Spurs on ovipositor: (0) absent; (1) acanthophorite spurs on T10; (2) spurs on cerci (length = 16; CI = 0.12; RI = 0.81). Hardy (1927a, 1944), Hull (1962), and Papavero (1973a) discussed the presence of spurs on the modified T10 within Asilidae and Asiloidea. Many species of Asilidae lack spurs on T10 no matter how this tergite is modified (see also character 172). Even when

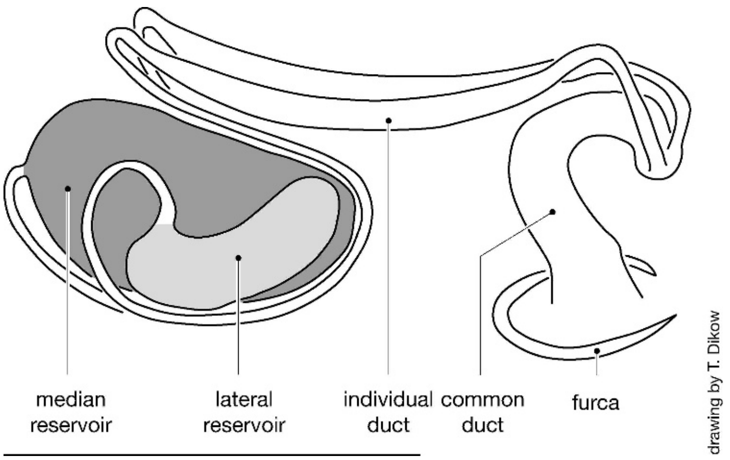


Fig. 99. Female spermathecae of *Lasiocnemus lugens* (Leptogastrinae) in lateral view. Morphological features labeled; spermathecal reservoirs grey; second lateral spermathecal duct and reservoir, in this view situated ventral to median reservoir, omitted. Scale line = 0.5 mm.

T10 is divided into two acanthophorite plates, the large, movable spurs are not always present (note: I use the term spurs instead of spines as spurs have been defined by Torre-Bueno [Nichols, 1989] as moveable structures connected to the cuticula by a joint whereas spines are not connected by a joint). Spurs are absent in most Asilinae; Dioctriinae; Laphriinae; Leptogastrinae; Ommatiinae; Trigonomiminae; and a few other species (state 0; figs. 88–89, 92, 93). Acanthophorite spurs are present in all Bathypogoninae; most Brachyrhopalinae and Dasypogoninae; Phellinae; Stenopogoninae; Tillobromatinae; Willistonininae; and *Oligopogon* sp. (Cape Recife) (state 1; figs. 87, 91, 97). *Apoclea algira*, *Philodicus tenuipes*, *Philonicus albiceps*, *Proctacanthus philadelphicus*, *Satanas gigas*, and *Zosteria rosevillensis* (all Asilinae) possess spurs on the cerci that are probably used in the same way as acanthophorite spurs (state 2; fig. 95). Hull (1962) and Papavero (1973a) stated that these cercal spurs are situated on T10 or acanthophorite plates, respectively, but there is no evidence for this hypothesis as T10 is clearly differentiated from the cerci in these species (fig. 95). Among the outgroup taxa, all taxa with acanthophorite plates also possess spurs (state 1, see character 172).

175. NUMBER OF SPERMATHECAE: (0) three; (1) two; (2) one (length = 6; CI = 0.33; RI = 0.20). The number of spermathecae varies little in Asilidae and with the exception of *Myaptex brachyptera* and *Proctacanthus philadelphicus* (Asilinae), which possess only two spermathecae (state 1), robber flies have three spermathecae (state 0). Among the outgroup taxa, *Afroleptomydas* sp. (Clanwilliam), *Nemomydas brachyrhynchus*, and *Pseudonomoneura hirta* (Mydidae), Nemestrinidae, and *Hemigephyra atra* (Therevidae) possess only two spermathecae (state 1) and *Mitrodetus dentitarsis* (Mydidae) has only a single spermatheca (state 2).

176. DEVELOPMENT OF SPERMATHECAE: (0) all equally large spermathecae; (1) median spermatheca larger than lateral ones; (2) median spermatheca smaller than lateral ones (length = 4; CI = 0.50; RI = 0.00). The development of each of the spermathecal reservoirs varies little in robber flies with the exception of Leptogastrinae. Here, *Euscelidia pulchra* and *Lasiocnemus lugens* possess smaller lateral spermathecae in comparison to the median one (state 1; fig. 99) and *Beameromyia bifida* possesses a smaller median spermathecal reservoir (state 2). Among the outgroup taxa, *Opomydas townsendi* (Mydidae) also possesses reduced lateral spermathecae (state 1).

177. LENGTH OF COMMON SPERMATHECAL DUCT: (0) short, not extending beyond tip of furca; (1) long, extending beyond tip of furca (length = 12; CI = 0.08; RI = 0.47). Theodor (1976) and Yeates (1994) discussed the

variation in length of the common spermathecal duct in Asilidae. Most assassin flies possess a short common spermathecal duct that does not extend beyond the tip of the furca anteriorly (state 0). The following species exhibit a long common duct: *Apoclea algira* (see fig. 399 in Theodor, 1976: 164), *Colepia rufiventris*, *Neoitamus cyanurus*, *Neolophonotus bimaculatus*, *Philodicus tenuipes*, *Promachus amastrus*, and *Threnia carbonaria* (all Asilinae); *Brachyrhopala ruficornis*, *Cabasa pulchella*, *Codula limbipennis*, and *Chrysopogon pilosifacies* (all Brachyrhopalinae); *Laphystia* species, *Nusa infumata*, *Perasis transvaalensis*, and *Protometer* sp. (El Tuparro) (all Laphriinae); *Tipulogaster glabrata*, *Leptogaster species*, and *Lasiocnemus lugens* (fig. 99) (all Leptogastrinae); *Cophinopoda chinensis* (Ommatiinae); and *Plesiomma* sp. (Guanacaste) (Stenopogoninae) (state 1; fig. 99). Among the outgroup taxa, all species possess a short common spermathecal duct (state 0).

178. Length of individual spermathecal ducts: (0) short; (1) long (length = 9; CI = 0.11; RI = 0.60). The length of the individual spermathecal ducts from the common duct to the reservoir varies considerably within Asilidae. A short duct is found in *Apoclea algira* (see fig. 399 in Theodor, 1976: 164), *Colepia rufiventris*, *Neolophonotus bimaculatus*, *Philodicus tenuipes*, and *Threnia carbonaria* (all Asilinae); *Blepharepium cajennensis*, *Diogmites grossus*, and *Neodiogmites melanogaster* (all Dasypogoninae); *Andrenosoma cyrtoxys*, *Dasyllis funebris*, and *Pilica formidolosa* (all Laphriinae); Leptogastrinae except *Acronyches maya* (fig. 99); and some Mydidae species (state 0). All remaining species possess a long spermathecal duct (state 1).

179. Ejection apparatus: (0) absent; (1) present (length = 8; CI = 0.12; RI = 0.22). Theodor (1976) illustrated the spermathecae of many Asilidae species in detail and discussed the development of an ejection apparatus at the base of the spermathecal duct. Within Asilinae the ejection apparatus can be absent, and this is found in the following species (state 0): *Apoclea algira* (see fig. 399 in Theodor, 1976: 164), *Dasophrys crenulatus*, *Neolophonotus bimaculatus*, *Philodicus tenuipes*, *Promachus amastrus*, and *Zosteria rosevillensis*. It has to be pointed out that it is difficult to observe the ejection apparatus with a stereomicroscope and I rely in some instances on Theodor's (1976) drawings and comments of congeneric species to interpret the presence/absence of the ejection apparatus. Among the outgroup taxa, it is absent in *Mitrodetus dentitarsis*, *Pseudonomoneura hirta*, *Rhaphiomidas maehleri* (Mydidae), and Nemestrinidae (state 0) and present in all other species (state 1).

180. Development of spermathecal reservoir: (0) reservoir not differentiated from spermathecal ducts; (1) reservoir formed by more or less expanded ducts to sac-shaped reservoir; (2) reservoir formed by more or less expanded and coiled ducts; (3) reservoir spherical (length = 46; CI = 0.06; RI = 0.60). The shape of the spermathecal reservoir varies considerably in Asilidae and Asiloidea in general (see illustrations in Theodor, 1976; Yeates, 1994). I attempt to code this character in a meaningful and discrete way so that no overlap between the character states is possible (see fig. 100). Forty-three Asilidae species have an unmodified reservoir that is basically the same width as the spermathecal ducts (state 0). Reservoirs composed by more or less expanded ducts that might be slightly curved are found in all Leptogastrinae and Ommatiinae; many Asilinae and Dasypogoninae; and a few other species (state 1). Coiled ducts of varying degree of expansion can be found in most Laphriinae; Stenopogoninae; and a few other taxa (state 2). An entirely spherical reservoir is present in some Asilinae; Stenopogoninae; and Tillobromatinae (state 3). Among the outgroup taxa, species possess either spherical reservoirs (Apsilocephalidae, *Bombylius major* (Bombyliidae), Nemestrinidae, Therevidae, state 3) or an unmodified reservoir that is as wide as the spermathecal duct (most Mydidae, state 0).

181. Sclerotization of spermathecal reservoir: (0) not sclerotized; (1) weakly sclerotized; (2) heavily sclerotized (length = 42; CI = 0.04; RI = 0.42). Yeates (1994) used the sclerotization of the spermathecal reservoir as a character in the Bombyliidae phylogeny and mentioned that it varies considerably within Asilidae. In fact, all three characters states are found in Asilidae and

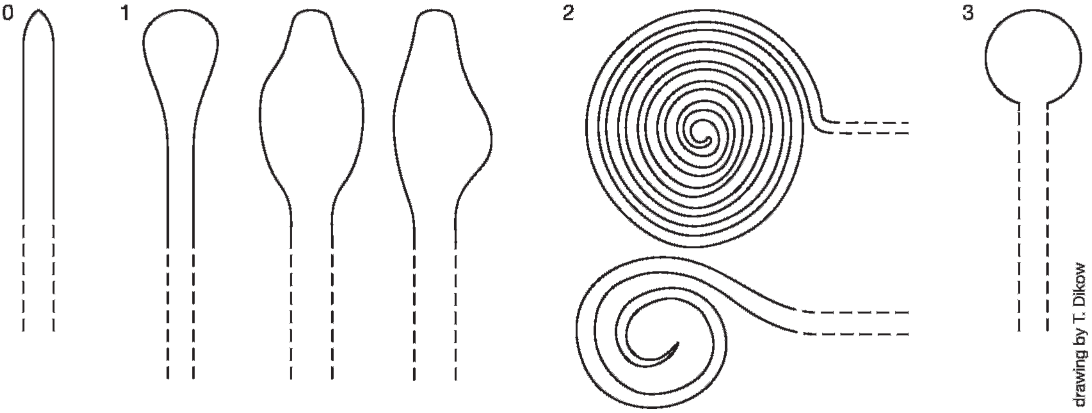


Fig. 100. Schematic illustration of female spermathecal reservoirs as coded in character 180. Solid lines = reservoir; dotted lines = spermathecal duct; numbers refer to character states; not to scale.

every subfamily taxon has representatives with unsclerotized, weakly sclerotized or heavily sclerotized spermathecae. Among the outgroup taxa, all character states are found as well.

182. LENGTH SPERMATHECAE: (0) occupying at most posterior three segments; (1) occupying more than the posterior three segments (length = 14; CI = 0.07; RI = 0.51). In general, the spermathecae occupy only the posterior two abdominal segments (state 0), but in a few Asilidae species the spermathecae are longer and occupy large extents of the abdomen (state 1). These species are: several Brachyrhopalinae; some Dasypogoninae and Dioctriinae; *Nusa infumata* (Laphriinae); many Stenopogoninae; a few Stichopogoninae; *Tillobroma punctipennis* (Tillobromatinae); and all Trigonomiminae (state 1). Among the outgroup taxa, the spermathecae only occupy at most the posterior three segments (state 0).

183. MEDIAN SCLERITE AT POSTERIOR END OF FURCA (REMNANT OF T9?): (0) absent; (1) present (length = 6; CI = 0.16; RI = 0.79). Theodor (1976: 5; fig. 1) illustrated a median sclerite at the posterior end of the furca, but did not label or discuss it. This sclerite is easily observed when present and connects the furca to T10 (see figs. 342, 349, 399 in Theodor, 1976). It is present in Asilinae, with the exception of *Blepharotes splendidissimus*, *Colepia rufiventris*, *Heligmonevra laevis*, *Lycomya germainii*, *Neoitamus cyanurus*, *Neolophonotus bimaculatus*, *Nomomyia murina*, *Pogonioefferia pogonias*, *Satanas gigas*, *Threnia carbonaria*, and *Zosteria rosevillensis*; as well as all Andrenosomatini (Laphriinae) (state 1). Judging by the position of this sclerite and its connection of S9 (furca) and T10 it could be interpreted as the remnant of T9. Among the outgroup taxa, the median sclerite is always absent (state 0).

184. DEVELOPMENT OF FURCA (S9): (0) single sclerite; (1) divided anteriorly into two lateral sclerites (length = 13; CI = 0.07; RI = 0.29). Theodor (1976) and Yeates (1994) observed that the furca in Asilidae can be composed of a single sclerite or be divided anteriorly into two sclerites. The majority of Asilidae species possesses an undivided furca (state 0; fig. 99). A divided furca is found in *Dioctria* species, *Eudioctria albius*, *Echthodopa pubera*, and *Nannodioctria* sp. (*formicaphaga*) (all Dioctriinae); *Cerotainia albipilosa*, *Goneccalypsis argenteoviridis*, and *Loewinella nigripes* (all Laphriinae); *Acronyches maya*, *Beameromyia bifida*, and *Leptogaster cylindrica* (see fig. 8 in Theodor, 1976: 16) (all Leptogastrinae); *Lasiopogon aldrichii* (Stichopogoninae); *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae); and *Trichoura* sp. (Tierberg) (Willistonininae) (state 1). Among the outgroup taxa, *Opomydas townsendi* and *Rhaphiomidas maehleri* (Mydidae) and *Hemigephyra atra* (Therevidae) possess a divided furca (state 1).

185. FURCAL APODEME: (0) absent; (1) present, long platelike apodeme; (2) present, short platelike apodeme; (3) present, two

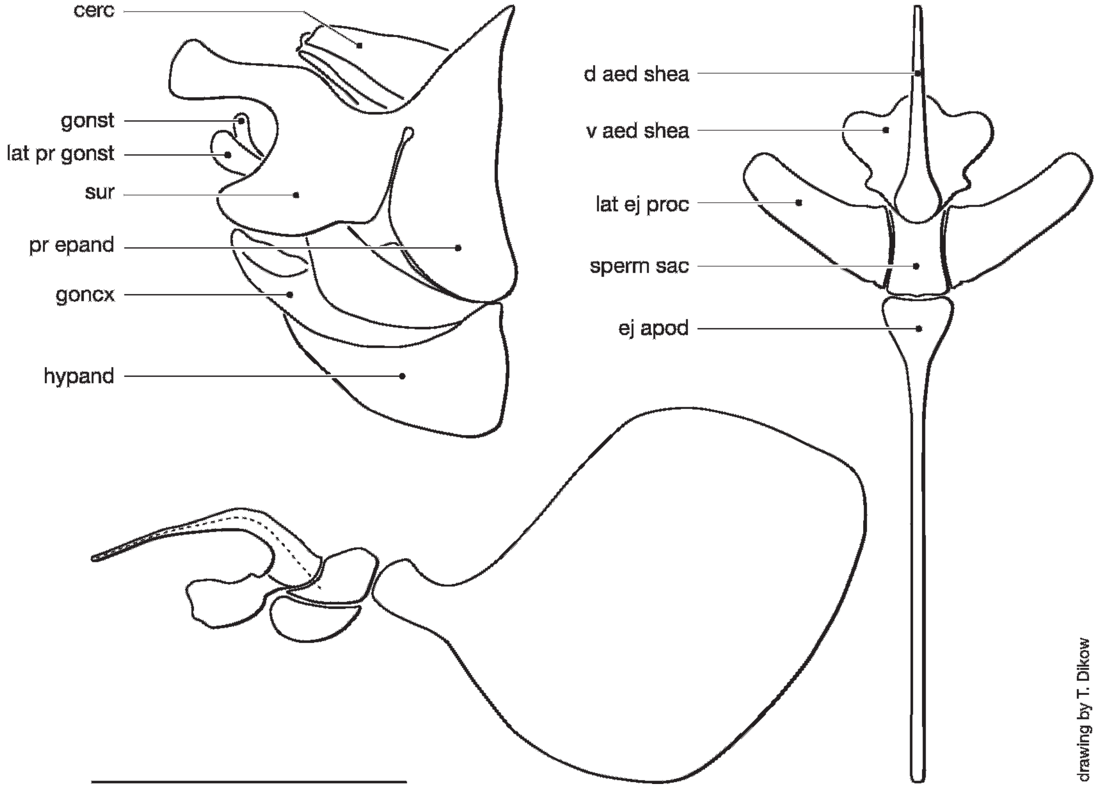


Fig. 101. Male hypopygium and aedeagus of *Lasiocnemus lugens* (Leptogastrinae). Hypopygium in lateral view and aedeagus in dorsal and lateral view. Morphological features labeled; vestiture omitted; abbreviations see Materials and Methods. Scale line = 1 mm.

lateral projections forming divided apodeme (length = 30; CI = 0.10; RI = 0.74). Reichardt (1929) and Theodor (1976) discussed and illustrated the furca of several species pointing out that the development of the anterior furcal apodeme (termed *Gabel* by Reichardt) varies within Asilidae. All Dioctriinae and Leptogastrinae; most Dasypogoninae and Laphriinae; and a few other species lack a furcal apodeme (state 0, see figs. 8, 23, 39, 184, 217 in Theodor, 1976). A long, narrow platelike apodeme is found in all Asilinae; Bathypogoninae; Andrenosomatini (Laphriinae); *Cophinopoda chinensis* and *Ommatius* species (Ommatiinae); Phellinae; *Damalis* species (Trigonomiminae); and a few other species (state 1, see figs. 228, 342, 349, 357, 399 in Theodor, 1976). A short, platelike apodeme is present in many Brachyrhopalinae; Stenopogoninae; Stichopogoninae; Tillobromatinae; Trigonomiminae; Willistoninae; and a few other species (state 2, see figs. 143, 154 in Theodor, 1976). A medially divided apodeme that appears bifid is present in *Cabasa pulchella* (Brachyrhopalinae) as well as *Connomyia varipennis*, *Creolestes nigribarbis*, and *Microstylum* sp. (Karkloof) (all Stenopogoninae) (state 3). Among the outgroup taxa, Apsilocephalidae possess state 2 and states 0, 1, and 3 are found in representatives of the Mydidae.

MALE ABDOMEN

Figures 101–102 illustrate the male hypopygial features referred to in the following section. In some instances, reference is made to illustrations of species represented in the present study published by Theodor (1976) who studied the external and internal male terminalia in detail.

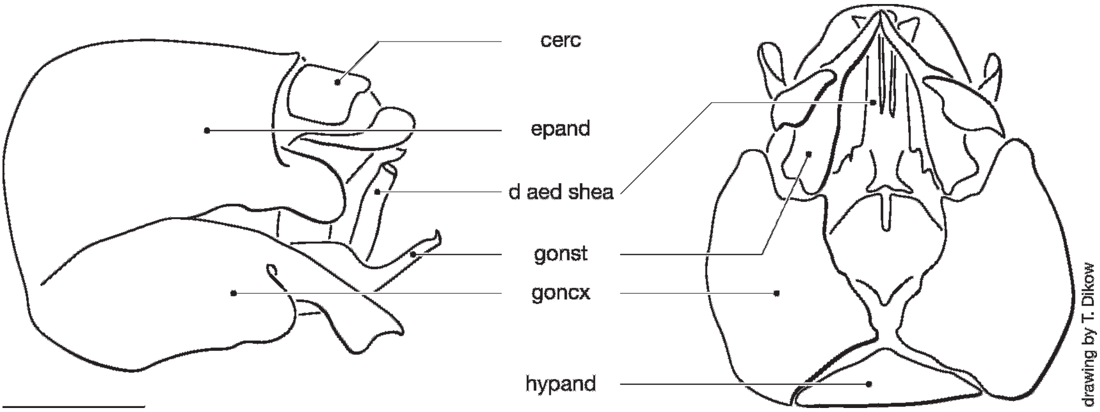


Fig. 102. Hypopygium of *Lamyra gulo* (Laphriinae) in lateral and ventral view. Morphological features labeled; vestiture omitted; abbreviations see Materials and Methods. Scale line = 1 mm.

186. Lateral macrosetae on T2: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 10; CI = 0.20; RI = 0.83). See character 160 and table 4. State 1 is also found in *Pegesimallus laticornis* (Dasypogoninae); *Daspletis stenoura* (Stenopogoninae); and *Oligopogon* sp. (Cape Recife). Among the outgroup taxa, lateral macrosetae are never present (state 0).

187. Lateral macrosetae on T3: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 10; CI = 0.20; RI = 0.82). See character 160 and table 4. State 1 is also found in *Ommatius tibialis* (Ommatiinae); *Daspletis stenoura* (Stenopogoninae); and *Oligopogon* sp. (Cape Recife).

188. Lateral macrosetae on T4: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 12; CI = 0.16; RI = 0.75). See character 160 and table 4. State 1 is also found in *Ommatius tibialis* (Ommatiinae); *Daspletis stenoura* (Stenopogoninae); and *Oligopogon* sp. (Cape Recife).

189. Lateral macrosetae on T5: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 16; CI = 0.12; RI = 0.62). See character 160 and table 4. State 1 is also found in *Afroestricus chiastoneurus* and *Ommatius tibialis* (Ommatiinae); *Daspletis stenoura* (Stenopogoninae); and *Oligopogon* sp. (Cape Recife).

190. Lateral macrosetae on T6: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 15; CI = 0.13; RI = 0.31). See character 160 and table 4. State 1 is also found in *Afroestricus chiastoneurus* and *Ommatius tibialis* (Ommatiinae) and *Oligopogon* sp. (Cape Recife).

191. Lateral macrosetae on T7: (0) absent; (1) marginal (m l) setae present; (2) medial setae present (length = 5; CI = 0.40; RI = 0.40). See character 160 and table 4. State 1 is also found in *Afroestricus chiastoneurus* and *Ommatius tibialis* (Ommatiinae) and *Oligopogon* sp. (Cape Recife).

192. Anterior margins of T3–8: (0) straight, no apodemes; (1) two lateral apodemes (length = 1; CI = 1.00; RI = 1.00). Yeates and Irwin (1996) established the presence of two lateral apodemes on the anterior margin of the male T3–8 as an autapomorphy of a subordinate taxon of Mydidae. Two lateral apodemes (state 1) are found here in Mydidae species, with the exception of *Neorhaphiomidas* sp. (Mandurah) and *Rhaphiomidas maehleri*, and an entire anterior margin in all other taxa (state 0).

193. Abdominal segments: (0) T1–T8 and S1–S8 well developed; (1) T1–T7 and S1–S7 well developed, T8 + S8 reduced to ring of sclerites; (2) T1–T7 well developed, T8 entirely lost; (3) T1–T6 and S1–S6 well developed, T7–T8 and S7 reduced, S8 well developed; (4) T1–T8 and S1–S7 well developed, S8 reduced; (5) T1–T7 and S1–S8 well developed, T8 reduced to narrow sclerite; (6) T1–T6 and S1–S6 well developed, T7–T8 and S7–S8 reduced to ring of sclerites (length = 28; CI = 0.21; RI = 0.68). The reduction of

TABLE 5

Development of abdominal tergites and sternites of segments 6–8 in males of species of Laphriinae (character 193)

Symbols: • = sclerites developed normally; △ = sclerites reduced to narrow sclerite

Species	T6	S6	T7	S7	T8	S8	state
Andrenosoma cyrtoxys	•	•	•	•	△	•	5
Aphestia annulipes	•	•	•	•	△	△	1
Atomosia puella	•	•	△	△	△	△	6
Cerotainia albipilosa	•	•	△	△	△	△	6
Choerades bella	•	•	•	•	△	•	5
Dasyllis funebris	•	•	•	•	△	•	5
Goneccalypsis argenteoviridis	•	•	•	•	△	△	1
Hoplistomerus nobilis	•	•	△	△	△	•	4
Hyperechia nigripennis	•	•	•	•	△	•	5
Loewinella nigripes	•	•	•	•	△	△	1
Lamyra gulo	•	•	△	△	△	•	4
Lampria clavipes	•	•	•	•	△	•	5
Laphria aktis	•	•	•	•	△	△	1
Laphria flava	•	•	•	•	△	△	1
Laphystia aegyptiaca	•	•	△	△	△	•	4
Laphystia tolandi	•	•	△	△	△	•	4
Laxenecera albicincta	•	•	△	△	△	•	4
Maira aenea	•	•	•	•	△	•	5
Nusa infumata	•	•	•	•	△	•	5
Orthogonis scapularis	•	•	•	•	△	•	5
Perasis transvaalensis	•	•	△	△	△	•	4
Pilica formidolosa	•	•	•	•	△	•	5
Proagonistes praeceps	•	•	•	•	△	•	5
Protometer sp. (El Tuparro)	•	•	△	△	△	•	4
Psilocurus modestus	•	•	△	△	△	•	4
Smeryngolaphria numitor	•	•	•	•	△	•	5
Stiphrolamyra angularis	•	•	△	△	△	•	4
Trichardis effrena	•	•	△	△	△	•	4
Zabrops tagax	•	•	△	△	△	•	4

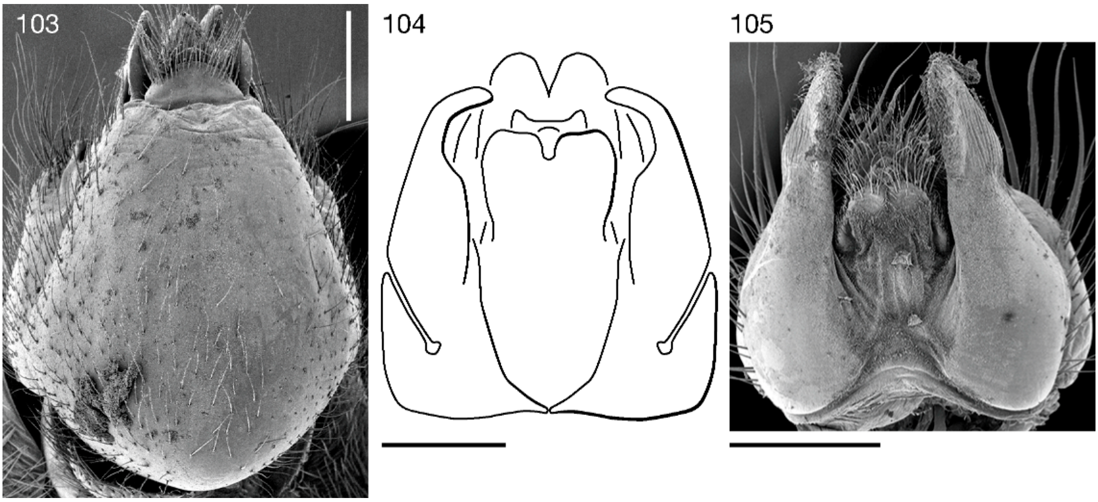
tergites or sternites just anterior to the male terminalia can be found in many Asilidae species. Sixty-nine out of 158 species possess tergites or sternites that are reduced at least to some extent. Hermann (1920) based his Prytaninae (unavailable name: Sabrosky, 1999; Dikow, 2004) on the reduction of the 6th abdominal segment. The different character states are found widely within Asilidae, but in all Asilinae; Bathypogoninae; Leptogastrinae; Ommatiinae; Phellinae; and Tillobromatinae; abdominal segments 1–8 are well developed (state 0). State 0 is also found in most Brachyrhopalinae; Stenopogoninae except *Daspletis stenoura*; and Willistonininae except *Sisyrnodytes* sp. (Gamka). State 1 is found in many Dasypogoninae; *Lasiopogon* species (Stichopogoninae); *Damalis* species (Trigonomiminae); and a few other species. T8 seems to be entirely lost in *Rhipidocephala* sp. (Harold Johnson) and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae) (state 2). The highest degree of reduction is found within Laphriinae where character states (3), (5), and (6) are exclusively found and the character state distribution for these species is summarized in table 5. State 4 is found in a few Brachyrhopalinae and Dasypogoninae; Dioctriinae except *Broticosia paramonovi*; Stichopogoninae except *Lasiopogon* species; and *Holcocephala* species (Trigonomiminae). Among the outgroup taxa, *Poecilognathus* sp. (El Hacha) (Bombyliidae) and Nemestrinidae possess state 1 whereas *Mydas clavatus*, *Nemomydas brachyrhynchus*, *Neorhaphiomidas* sp. (Mandurah), *Opomydas townsendi*, and *Pseudonomoneura hirta* (all Mydidae) possess state 5.

194. Shape of S8: (0) simple, rectangular sclerite or reduced to narrow sclerite; (1) distal margin with protuberances; (2) distal margin with flaplike sclerite (length = 5; CI = 0.40; RI = 0.00). Reichardt (1929) described and illustrated an elongated and setose S8 in *Tolmerus atricapillus* (as Machimus). This is in contrast to most other Asilidae species in which S8 is simple and no distal projections are developed (state 0). In the present analysis projections are found only in a few species of Asilinae. *Lochmorhynchus albicans*, *Machimus chrysitis*, and *Tolmerus atricapillus* possess a projection of S8 (state 1), which is well connected to the remaining part of S8. *Afromochtherus mendax*, *Heligmonevra laevis*, and *Zosteria rosevillensis* possess a projection on S8, but here it is not visible in dried specimens and can be examined only when the abdomen is macerated in KOH because it is joined to the sclerite by a piece of lightly sclerotized cuticle and can be flipped underneath S8 (state 2). Among the outgroup taxa, S8 is always simple (state 0). Species in which S8 is entirely lost are coded as inapplicable (-) (see character 193).

195. Rotation of hypopygium: (0) not rotated; (1) rotated by 90°–180° (length = 18; CI = 0.05; RI = 0.73). The rotation of the hypopygium within Asilidae and particularly in Laphriinae, where it is most widespread, has been observed by Snodgrass (1902), Reichardt (1929), Karl (1959), and subsequent authors. Here, only the rotation of more than 90° is considered as a rotation of a few degrees may result from the preservation method of individual specimens. The direction of the rotation is not considered. Dasypogoninae, with the exception of *Diogmites grossus*, *Saropogon dispar*, and *Thereutria amaraca*; Laphriinae except *Perasis transvaalensis*; many Stenopogoninae; Tillobromatinae; *Damalis* species (Trigonomiminae); and a few other Asilidae species possess rotated hypopygia (state 1). Among the outgroup taxa, *Bombylius major* (Bombyliidae) possesses a rotated hypopygium (state 1) whereas all remaining species exhibit unrotated hypopygia (state 0).

196. Direction of hypopygium: (0) pointing posteriorly; (1) pointing dorsally (length = 4; CI = 0.25; RI = 0.00). The hypopygium is generally positioned in line with the abdominal segments (state 0). In a few species of Asilinae, the hypopygium is positioned perpendicular to the abdomen and held upright (state 1; fig. 3). This was observed by Karl (1959) for *Erax* Scopoli, 1763 who stated that the gonocoxites are angled proximally and therefore pushing the remaining hypopygium dorsad. Species exhibiting state 1 are *Clephydroneura sundaica*, *Eichoichemus pyrrhomystax*, *Neoitamus cyanurus*, and *Pogonioefferia pogonias* (all Asilinae). Among the outgroup taxa, the hypopygium is always pointing posteriorly (state 0).

197. Development of epandrium: (0) a single sclerite, fused more or less entirely medially; (1) separated medially and joining proximally; (2) separated medially and far apart proximally (length = 24; CI = 0.08; RI = 0.70). Reichardt (1929), Hardy (1948), Karl (1959), Papavero (1973a), Theodor (1976), and Sinclair et al. (1994) observed the different development of the epandrium, which may be entirely fused medially to form a single sclerite (state 0; figs. 102–103), or both epandrial halves may be separated medially (state 1; figs. 104, 113; state 2; fig. 105). All three character states are found widely within Asilidae and the outgroup taxa. A single epandrium is found in *Austrosaropogon nigrinus*, *Brachyrhopala ruficornis*, *Cabasa pulchella*, *Chrysopogon pilosifacies*, *Codula limbipennis*, *Heteropogon manicatus*, and *Nannocyrtopogon lestomyiformis* (all Brachyrhopalinae); *Cyrtophrys attenuatus*, *Dasypogon diadema*, *Deromyia fuscipennis*, *Lestomyia fraudiger*, *Megapoda labiata*, *Molobratia teutonus*, *Pegesimallus laticornis*, *Pseudorus distendens*, and *Senobasis corsair* (all Dasypogoninae); *Dicolonus simplex*, *Dioctria species*, *Eudioctria albius*, and *Nannodioctria* sp. (*formicaphaga*) (all Dioctriinae); Laphriinae; *Connomyia varipennis* (Stenopogoninae); *Lissoteles aquilonius*, *Stichopogon species*, and *Townsendia albomacula* (all Stichopogoninae); and *Sisyrnodytes* sp. (Gamka) (Willistonininae) (state 0; fig. 103). *Holopogon priscus* (Brachyrhopalinae); *Cophinopoda chinensis*, *Ommatius incurvatus*, and *Ommatius tibialis* (all Ommatiinae); and *Willistonina bilineata* (Willistonininae) possess a medially divided epandrium, but the epandrial halves are set far apart from each



Figs. 103–105. SEM micrographs and drawing of male hypopygia in dorsal view. **103.** *Hoplistomerus nobilis* (Laphriinae). **104.** *Euscelidia pulchra* (Leptogastrinae). **105.** *Damalis monochaetes* (Trigonomiminae). Scale lines = 0.5 mm.

other and do not join proximally (state 2; fig. 105). The highest morphological diversity of epandrial development is found within Trigonomiminae in that *Damalis annulata* and *Damalis* sp. (Palatupana) possess a single epandrium (state 0), *Rhipidocephala* sp. (Harold Johnson) and *Trigonomima* sp. (*anamaliensis*) possess a medially divided epandrium (state 1), and *Damalis monochaetes* and *Holcocephala* species possess a medially divided epandrium in which the epandrial halves are set far apart (state 2; fig. 105). Among the outgroup taxa, Apioceridae, Mydidae, with the exception of *Afroleptomydas* sp. (Clanwilliam) and *Opomydas townsendi*, and Scenopinidae possess a medially divided epandrium (state 1) and all remaining species possess a single epandrial sclerite (state 0).

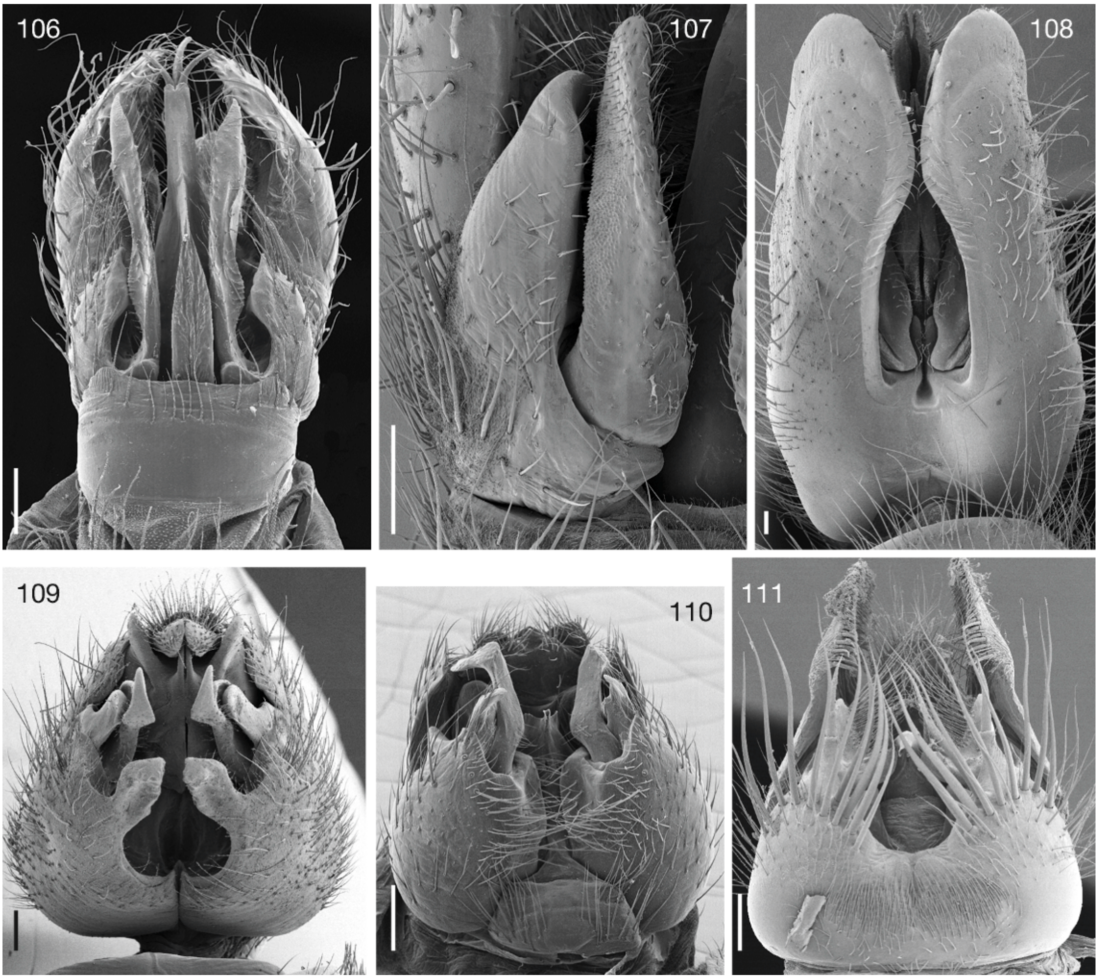
198. SURSTYLUS ON EPANDRIUM: (0) absent; (1) present, distal two-thirds of epandrium form a secondary, movable lobate; (2) present, small, movable epandrial lobes connected to subepandrial sclerites (length = 2; CI = 1.00; RI = 1.00). Karl (1959) and Martin (1968) discussed the division of the epandrium into a fixed, proximal sclerite and a movable, distal surstylus in many species of Leptogastrinae (sensu Martin). Surstyli are found within Eremoneura in a number of Empidoidea taxa and all Cyclorrhapha (e.g., Cumming et al., 1995; Sinclair and Cumming, 2006) and the homology of the structure found in Asilidae and in Eremoneura is not established (Griffiths, 1994). However, Emden and Hennig (1970: 341) and Torre-Bueno (Nichols, 1989: 735) define surstyli as "secondary lobate differentiations of epandria" and this accurately describes the structure found in Leptogastrinae (sensu Martin) (state 1, 101). Emden and Hennig (1970) studied *Dioctria cothurnata* Meigen, 1820 (Dioctriinae) and labeled a small, distal lobe of the epandrium as a surstylus. A similar, nonmovable distal projection of the epandrium is also evident in many Laphriinae, e.g., *Lamyra gulo* (fig. 102), and even in Mydidae (*Mydas clavatus*). Adisoemarto and Wood (1975) used the development of the surstylus in their phylogenetic analysis of Dioctriinae as a character, but upon close examination it is evident that the structures described are not the same that Emden and Hennig (1970) labeled as such and are rather lateral projections of the subepandrial sclerite (see character 211) and not part of the epandrium. Therefore, these structures are not considered homologous to the state found in Leptogastrinae (sensu Martin) as was also emphasized by Karl (1959). Sinclair et al. (1994) reviewed the surstylus found in Apsilocephalidae and this structure is not

homologous to the surstylus found in Leptogastrinae (sensu Martin) as it is connected to the subepandrial sclerite (state 2). Ovtshinnikova (1989) established that the surstyli in Leptogastrinae (sensu Martin) are moved by the tergosternal muscle M51, which is connected to the lateral parts of the gonocoxites and the distal part of the epandrium in Asiloidea (Ovtshinnikova and Yeates, 1998). Griffiths (1994), therefore, concluded that surstyli in Leptogastrinae (sensu Martin) are not appendages (= styli) musculated from the epandrium itself and therefore should not be called surstyli. For lack of a better term, I use surstyli in the following sense: secondary, movable lobate differentiations of epandria (state 1; figs. 101, 104). These surstyli are found in Leptogastrinae, with the exception of *Acronyches maya*. Among the outgroup taxa, surstyli are absent (state 0) except for Apsilocephalidae (state 2).

199. HYPANDRIUM SHAPE: (0) well developed, rectangular or square sclerite; (1) well developed, triangular sclerite; (2) reduced or not differentiated (length = 36; CI = 0.05; RI = 0.67). Karl (1959) used the rectangular shape and the reduction of the hypandrium as characters in his phylogenetic study on Asilidae. Papavero (1973a) discussed the shape of the hypandrium in several taxa and postulated that a free, triangular hypandrium is the plesiomorphic state in Asilidae. The different shapes are divided here into three states as these seem to be easily delineated. A well-developed, rectangular or square hypandrium is found in Asilinae except *Congomochtherus inachus; Psilocurus modestus* and *Zabrops tagax* (Laphriinae); *Leptogaster arida* and *Tipulogaster glabrata* (Leptogastrinae); Ommatiinae except *Michotamia aurata*; and a few species of Brachyrhopalinae; Dasypogoninae; Dioctriinae; and Stenopogoninae (state 0; figs. 106, 110, 113). A triangular hypandrium is illustrated in fig. 102 (state 1). The hypandrium can be reduced or is at least not differentiated from the gonocoxites (see character 200), which is found in many species of Laphriinae; *Acronyches maya*, *Beameromyia bifida*, and *Euscelidia pulchra* (all Leptogastrinae); Stichopogoninae except *Lasiopogon* species; Trigonomiminae except *Rhipidocephala* sp. (Harold Johnson); and *Trichoura* sp. (Tierberg) (Willistonininae) (state 2; figs. 108–109). All remaining species possess a well-developed, triangular hypandrium. Among the outgroup taxa, all three states are found.

200. GONOCOXITES FUSION WHEN HYPANDRIUM REDUCED: (0) not fused medially; (1) fused proximomedially (length = 4; CI = 0.25; RI = 0.72). Snodgrass (1902), Cole (1927), and Reichardt (1929) labeled the dorsal part of the rotated hypopygium of species of *Laphria* and *Dasyllis* as S9 (= hypandrium) and therefore postulated that the gonocoxites are absent. Karl (1959), however, showed that the dorsal structures in *Laphria* are in fact the gonocoxites, postulating that the hypandrium is reduced and that the gonocoxites are sometimes fused medially. This hypothesis is followed here when coding the development of the hypandrium. Thirty-five Asilidae species possess a reduced hypandrium and in most of these species the gonocoxites are not fused medially (state 0). In Andrenosomatini except *Hyperechia nigripennis* as well as *Hoplistomerus nobilis*, *Laphriini*, *Laphystia aegyptiaca*, and *Stiphrolamyra angularis* (all Laphriinae) the hypandrium is reduced and the gonocoxites are fused proximomedially (state 1; figs. 108–109). Among the outgroup taxa, no species with a reduced hypandrium possesses medially fused gonocoxites. All species with a well-developed hypandrium (see character 199) are coded as inapplicable (-).

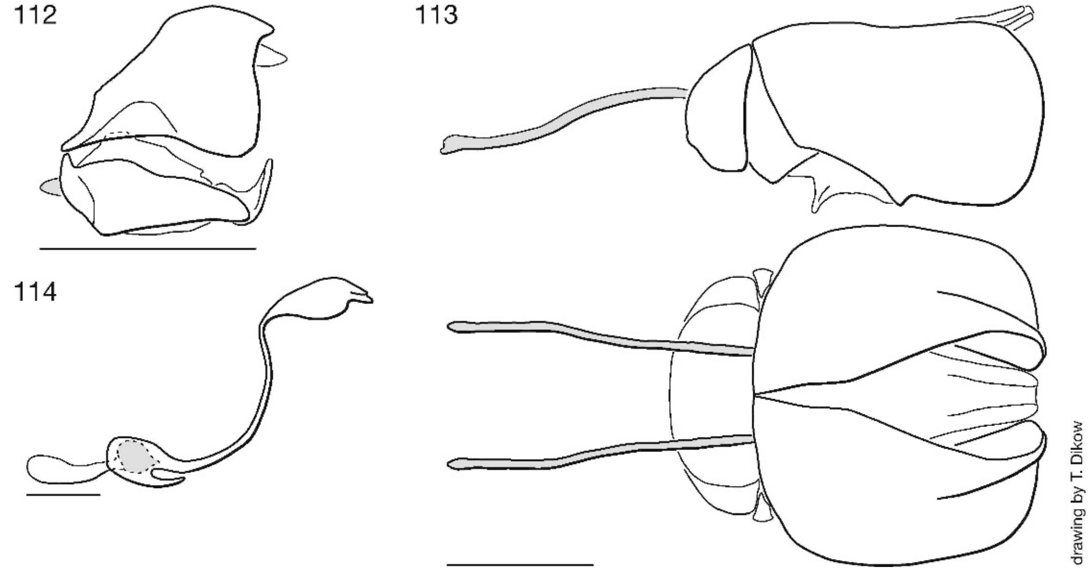
201. HYPANDRIUM AND EPANDRIUM: (0) not approximating, separated by gonocoxites; (1) approximating, but not fused proximally; (2) fused at least partially; (3) fused, connected by narrow sclerites proximally (length = 16; CI = 0.18; RI = 0.83). Both Yeates (1994) and Sinclair et al. (1994) independently observed the proximal connection of the epandrium and hypandrium in some species of Asilidae and postulated this character as a possible autapomorphy of robber flies. Separated epandria and hypandria are found in *Ceraturgus fasciatus*, *Dasycyrton gibbosus*, and *Heteropogon manicatus* (all Brachyrhopalinae); Dioctriinae; Laphriinae except *Stiphrolamyra angularis*; *Connomyia varipennis* (Stenopogoninae); and *Acnephalum cylindricum* and *Sisyrnodytes* sp. (Gamka) (Willistonininae) (state 0; fig. 102). Epandrium and hypandrium are approximat-



Figs. 106–111. SEM micrographs of male hypopygia in ventral view. **106.** *Dysmachus trigonus* (Asilinae). **107.** *Philonicus albiceps* (Asilinae), detail of gonocoxite and gonostyli. **108.** *Laphria flava* (Laphriinae). **109.** *Hoplistomerus nobilis* (Laphriinae). **110.** *Dioctria atricapillus* (Dioctriinae). **111.** *Damalis monochaetes* (Trigonomiminae). Scale lines = 200 μm.

ing and fused at least partly in *Neolophonotus bimaculatus* (Asilinae); *Holopogon priscus* and *Leptarthrus brevirostris* (Brachyrhopalinae); *Cyrtophrys attenuatus*, *Deromyia fuscipennis*, *Megapoda labiata*, *Pegesimallus laticornis*, *Pseudorus distendens*, and *Senobasis corsair* (all Dasypogoninae); *Beameromyia bifida* and *Euscelidia pulchra* (Leptogastrinae); *Damalis* sp. (Palatupana), *Holcocephala* species, and *Trigonomima* sp. (*anamaliensis*) (all Trigonomiminae); and *Trichoura* sp. (Tierberg) (Willistonininae) (state 2; fig. 101). A proximal sclerite originating from the epandrium connecting to the hypandrium is found in *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae) (state 3; fig. 112). In all species of Bathypogoninae; Ommatiinae; Phellinae; and Tillobromatinae; and the remaining species not mentioned above, the epandrium and hypandrium approximate, but are not fused (state 1). Among the outgroup taxa, the epandrium and hypandrium are always separated by the gonocoxites (state 0).

202. HYPANDRIUM AND GONOCOXITES: (0) gonocoxites entirely free; (1) gonocoxites fused to hypandrium; (2) gonocoxite-hypandrial complex (length = 23; CI = 0.08; RI =



Figs. 112–114. Hypopygia and aedeagus. **112.** *Stichopogon trifasciatus* (Stichopogoninae), hypopygium lateral, gonocoxal apodeme grey. **113.** *Philodicus tenuipes* (Asilinae), hypopygium lateral and dorsal, gonocoxal apodeme grey. **114.** *Philodicus tenuipes*, aedeagus lateral, sperm sac grey. Vestiture omitted. Scale lines = 1 mm.

0.73). In general, the gonocoxites are free or only proximally associated with the hypandrium so that they can be moved in a vertical plane. Martin (1968) found that in most species of Leptogastrinae the gonocoxites and hypandrium are fused. A distinct suture is evident between the two parts in lateral view and this is found in all species of Asilinae; most Brachyrhopalinae; Dasypogoninae; with the exception of *Saropogon dispar* and *Thereutria amaraca*; Dioctriinae except *Eudioctria albius*; *Hoplistomerus nobilis*, *Laxenecera albicincta*, *Nusa infumata*, and *Trichardis effrena* (all Laphriinae); *Emphysomera* species and *Michotamia aurata* (Ommatiinae); Stenopogoninae, with the exception of *Gonioscelis ventralis* and *Prolepsis tristis*; and Tillobromatinae except *Lycostommyia albifacies* (state 0; figs. 101, 110, 113). The fusion of the hypandrium and gonocoxites is not uncommon among Asilidae species and is found in all Bathypogoninae; most Laphriinae; *Lasiocnemus lugens*, *Leptogaster* species, and *Tipulogaster glabrata* (all Leptogastrinae); *Cophinopoda chinensis* and *Ommatius* species (Ommatiinae); Phellinae; Stichopogoninae; *Rhipidocephala* sp. (Harold Johnson) (Trigonomiminae); and a few other species not mentioned above (state 1; figs. 101, 108–109, 112). In some species, no suture is visible and this state is here referred to as a gonocoxite-hypandrial complex, which is found in *Acronyches maya*, *Beameromyia bifida*, and *Euscelidia pulchra* (all Leptogastrinae); most Trigonomiminae; and *Trichoura* sp. (Tierberg) (Willistonininae) (state 2; fig. 111). It is important to verify whether hypandrium and gonocoxite are fused or whether one or the other is simply reduced (see character 200). Karl (1959) postulated that the hypandrium is more often reduced than the gonocoxites. The presence of gonostyli is an indicator that gonocoxite and hypandrium are fused. Among the outgroup taxa, it is assumed that the gonocoxite and hypandrium are fused into a gonocoxite-hypandrial complex in Mydidae species, with the exception of *Opomydas townsendi* (state 2). In Mydidae, the gonostyli are reduced (see character 205) and there is no evidence to support fusion over reduction or vice versa. Therevidae possess entirely free gonocoxites (state 0) whereas in Apioceridae, Apsilocephalidae, Bombyliidae, and Scenopinidae, the gonocoxites are fused to the hypandrium (state 1).

Nemestrinidae possess a gonocoxite-hypandrial complex (state 2).

203. Epandrium and gonocoxites: (0) gonocoxites or gonocoxite-hypandrial complex entirely free; (1) gonocoxites or gonocoxite-hypandrial complex partially fused to epandrium (length = 12; CI = 0.08; RI = 0.52). In a similar way to the fusion of gonocoxite and hypandrium, the epandrium can also be fused to the gonocoxite in addition to the usual proximal connection found in most species. The vertical movement of the gonocoxite is reduced due to the fusion of both sclerites. Fused epandrium and gonocoxite or a gonocoxite-hypandrial complex are found in *Hoplistomerus nobilis*, *Lamyra gulo*, *Laphria species*, *Laxenecera albicincta*, *Maira aenea*, *Nusa infumata*, *Perasis transvaalensis*, *Smeryngolaphria numitor*, *Stiphrolamyra angularis*, and *Trichardis effrena* (all Laphriinae); Leptogastrinae except *Acronyches maya*; *Ommatius tibialis* and *Ommatius incurvatus* (Ommatiinae); *Gonioscelis ventralis* (Stenopogoninae); *Holcocephala* species and *Trigonomima* sp. (*anamaliensis*) (Trigonomiminae); and *Acnephalum cylindricum* (Willistonininae) (state 1; figs. 101–102). All remaining Asilidae and outgroup taxa possess free gonocoxites (state 0; figs. 112–113).

204. Gonocoxal apodeme: (0) absent; (1) present, short, at most only slightly extending hypopygium proximally; (2) present, long, extending well into abdominal segment 8 (length = 20; CI = 0.10; RI = 0.66). Sinclair et al. (1994) and Cannings (2002) discussed the different development of gonocoxal apodemes in Asiloidea and Stichopogoninae, respectively. Most species of Asilidae possess a gonocoxal apodeme (state 1; figs. 112–113) and it is absent only in *Pogonioefferia pogonias* (Asilinae); *Austrosaropogon nigrinus*, *Codula limbipennis*, *Dasycyrton gibbosus*, and *Rhabdogaster pedion* (all Brachyrhopalinae); *Dasypogon diadema*, *Deromyia fuscipennis*, and *Pegesimallus angularis* (all Dasypogoninae); Laphriinae, with the exception of *Aphestia annulipes*, *Perasis transvaalensis*, *Smeryngolaphria numitor*, and *Stiphrolamyra angularis*; Leptogastrinae except *Acronyches maya*; *Damalis* species (Trigonomiminae); and *Acnephalum cylindricum* (Willistonininae) (state 0). In *Apoclea algira*, *Megaphorus pulchrus*, *Philodicus tenuipes*, and *Promachus amastrus* (all Asilinae), the gonocoxal apodeme is very long and extending well into abdominal segment 8 (state 2; fig. 113). Among the outgroup taxa, a short gonocoxal apodeme is present in Apioceridae, Mydidae, with the exception of *Afroleptomydas* sp. (Clanwilliam), *Nemomydas brachyrhynchus*, and *Pseudonomoneura hirta*, and Therevidae (state 1), and Scenopinidae possess an elongated gonocoxal apodeme (state 2).

205. Development of gonostyli: (0) absent; (1) present (length = 1; CI = 1.00; RI = 1.00). Karl (1959) found that *Dissmeryngodes nigripes* (Macquart, 1838) (referred to as junior synonym *Atomosia dispar* Walker, 1850, Laphriinae) is the only robber fly he studied that lacks gonostyli. Martin (1968) mentioned additional Atomosiini genera, i.e., *Atomosia*, *Atomosiella* Wilcox, 1937, *Atoniomyia* Hermann, 1912, *Eumecosoma* Schiner, 1866, and *Cerotainia*, lacking gonostyli. In the present analysis, all Asilidae possess gonostyli (state 1; figs. 101–102, 106–107, 109–110). Yeates and Irwin (1996) established the lack of gonostyli as an autapomorphy of Mydidae, which was also found by Karl (1959) in *Mitrodetus dentitarsis*, and all mydas flies sampled here lack gonostyli (state 0). All remaining outgroup taxa possess gonostyli (state 1).

206. Gonostyli position on gonocoxites: (0) proximal; (1) medial; (2) distal (length = 30; CI = 0.06; RI = 0.50). Karl (1959) and Papavero (1973a) discussed the position of gonostyli on the gonocoxites and concluded that a distal position is plesiomorphic. The position of the gonostyli is variable within Asilidae and a distal position is most common (state 2; figs. 101–102, 109–110, 112). The gonostyli are proximal in most Asilinae, with the exception of *Blepharotes splendidissimus*, *Heligmonevra laevis*, *Megaphorus pulchrus*, *Neoitamus cyanurus*, *Nomomyia murina*, and *Threnia carbonaria* (state 0; figs. 106–107). The gonostyli are situated medially in *Cyrtopogon* species and *Nannocyrtopogon lestomyiformis* (Brachyrhopalinae); *Blepharepium cajennensis*, *Dasypogon diadema*, *Megapoda labiata*, and *Pseudorus distendens* (all Dasypogoninae); *Emphysomera* species (Ommatiinae); *Atomosia puella*, *Cerotainia albipilosa*, *Laphria species*,

Laxenecera albicincta, *Orthogonis scapularis*, *Perasis transvaalensis*, and *Stiphrolamyra angularis* (all Laphriinae); *Phellus olgae* (Phellinae); *Ancylorhynchus fulvicollis*, *Prolepsis tristis*, and *Stenopogon rufibarbis* (Stenopogoninae); *Hypenetes stigmatias* and *Lycostommyia albifacies* (Tillobromatinae); *Damalis monochaetes* (Trigonomiminae); and *Ablautus coquilletti* and *Willistonina bilineata* (Willistonininae) (state 1; fig. 111). Among the outgroup taxa, Apioceridae possess gonostyli medially on the gonocoxites (state 1) and the remaining species possess distal gonostyli (state 2). Mydidae is coded as inapplicable (-) as mydas flies lack gonostyli (see character 205).

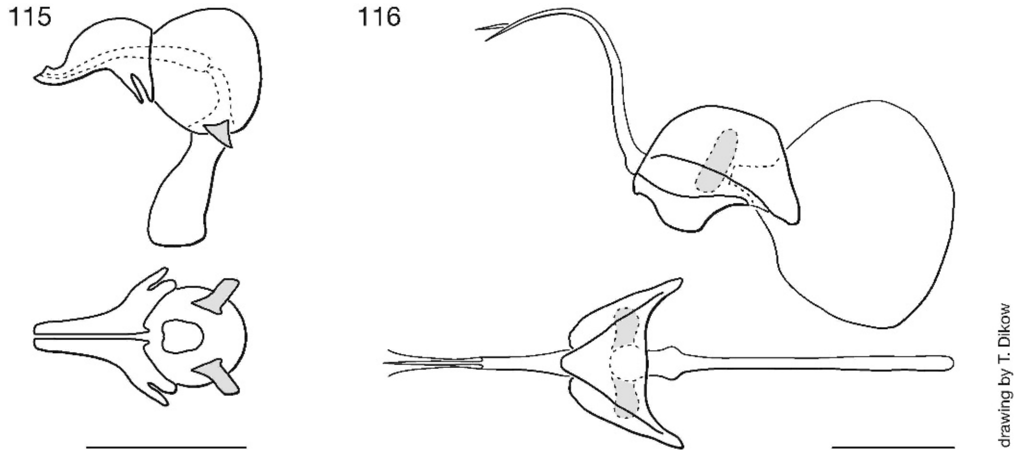
207. LATERAL PROCESSES OF GONOSTYLI: (0) absent; (1) present (length = 1; CI = 1.00; RI = 1.00). Martin (1968) observed lateral processes of the gonostyli in all Leptogastrinae. Later, Theodor (1976: figs. 20, 21) illustrated median processes in the species of Leptogastrinae he examined and showed a large process medially to the gonostylus that appears to be movable. The lateral processes are smaller or similar in size to the gonostyli and in my interpretation are actually situated laterally to the gonostyli as was postulated by Martin (1968). Lateral processes of gonostyli are found only to be present in Leptogastrinae except *Acronyches maya* (state 1; fig. 101). Among the outgroup taxa, lateral processes of gonostyli are absent (state 0) and Mydidae is coded as inapplicable (-) as all species lack gonostyli (see character 205).

208. SUBEPANDRIAL SCLERITE SHAPE: (0) no modifications; (1) with protuberances medially (length = 9; CI = 0.11; RI = 0.11). Karl (1959) illustrated comblike setae at the posterior tip of the subepandrial sclerite in *Stichopogon scaliger* Loew, 1847 (Stichopogoninae). Cannings (2002) discussed the setation of the subepandrial sclerite in species of *Lasiopogon* (Stichopogoninae) and as it is found that within Asilidae, different protuberances and setae can be found on this sclerite (see characters 208–211). In general, robber flies possess a smooth sclerite without special protuberances (state 0), but *Colepia rufiventris* and *Lycomya germainii* (Asilinae); *Psilocurus modestus* (Laphriinae); *Stenopogon sabaudus* (Stenopogoninae); *Hypenetes stigmatias* and *Tillobroma punctipennis* (Tillobromatinae); and *Holcocephala* species (Trigonomiminae), possess medial protuberances on the subepandrial sclerite (state 1). Among the outgroup taxa, *Bombylius major* (Bombyliidae) and *Neorhaphiomidas* sp. (Mandurah) (Mydidae) also possess medial protuberances (state 1).

209. SUBEPANDRIAL SCLERITE DISTAL MARGIN: (0) simple, straight margin; (1) distal projections; (2) short, stout macrosetae (length = 12; CI = 0.16; RI = 0.52). The distal margin of the subepandrial sclerite is usually simple and straight (state 0). Distal projections are present in *Afromochtherus mendax*, *Apoclea algira*, *Clephydroneura species*, *Colepia rufiventris*, *Heligmonevra laevis*, *Machimus occidentalis*, *Neoitamus cyanurus*, *Neomochtherus pallipes*, *Philodicus tenuipes*, *Pogonioefferia pogonias*, *Zosteria rosevillensis*, and *Threnia carbonaria* (all Asilinae); *Dasypogon diadema* (Dasypogoninae); *Aphestia annulipes* and *Pilica formidolosa* (Laphriinae); *Daspletis stenoura* (Stenopogoninae); and *Lycostommyia albifacies* (Tillobromatinae) (state 1). Short, stout macrosetae are found in *Lissoteles aquilonius* and *Stichopogon* species (Stichopogoninae) (state 2), and have been observed before by Karl (1959) in *Stichopogon scaliger*. Among the outgroup taxa, only Nemestrinidae possesses distal projections (state 1).

210. SUBEPANDRIAL SCLERITE SETATION: (0) absent or only a few weak setae; (1) short, stout macrosetae (length = 1; CI = 1.00; RI = 1.00). Cole (1927) and Cannings (2002) found short, stout macrosetae on the subepandrial sclerite surface only in species of *Lasiopogon* (state 1) and this is confirmed here and no other Asilidae species possesses these setae (state 0). Among the outgroup taxa, these setae are always absent (state 0).

211. SUBEPANDRIAL SCLERITE LATERAL PROTUBERANCES: (0) absent; (1) present (length = 13; CI = 0.07; RI = 0.42). Karl (1959) described the subepandrial sclerite (referred to as *ventrale Lamelle des Analkegels*) and its platelike appearance in Asilidae. Adisoemarto and Wood (1975) discussed the presence of protuberances of the subepandrial sclerite within the Dioctriinae (referred to as surstyli, see character 198). In most species of Asilidae, the lateral margin of the subepandrial sclerite is smooth without any



Figs. 115–116. Aedeagi. **115.** *Afroholopogon peregrinus* (Brachyrhopalinae), lateral and ventral. **116.** *Pilica formidolosa* (Laphriinae), lateral and dorsal. Lateral ejaculatory process grey. Scale lines = 0.5 mm.

protuberances (state 0). In *Threnia carbonaria* (Asilinae); *Ceraturgus fasciatus* and *Cyrtopogon* species (Brachyrhopalinae); *Saropogon* species (Dasypogoninae); Dioctriinae except *Echthodopa pubera*; *Cophinopoda chinensis*, *Emphysomera conopsoides*, *Ommatius incurvatus*, and *Ommatius tibialis* (all Ommatiinae); *Creolestes nigribarbis*, *Microstylum* sp. (Karkloof), and *Prolepsis tristis* (all Stenopogoninae); lateral protuberances are present (state 1). Among the outgroup taxa, *Mitrodetus dentitarsis* (Mydidae) also possesses lateral protuberances (state 1).

212. Fusion of cerci: (0) not fused (two distinct sclerites); (1) fused to a single sclerite (length = 18; CI = 0.05; RI = 0.32). The fusion of the cerci was observed by Karl (1959) and used as a character in Stichopogoninae by Cannings (2002). The two cerci are generally distinct and only join proximally in Asilidae (state 0). In *Ceraturgus fasciatus*, *Chrysopogon pilosifacies*, *Cyrtopogon rattus*, *Holopogon priscus*, and *Nannocyrtopogon lestomyiformis* (all Brachyrhopalinae); *Cyrtophrys attenuatus*, *Dasypogon diadema*, *Lestomyia fraudiger*, *Megapoda labiata*, and *Pegesimallus laticornis* (all Dasypogoninae); *Psilocurus modestus*, *Protometer* sp. (El Tuparro), and *Zabrops tagax* (all Laphriinae); *Ancylorhynchus fulvicollis*, *Creolestes nigribarbis*, *Ospriocerus aeacus*, *Prolepsis tristis*, and *Scylaticus costalis* (all Stenopogoninae); *Stichopogon* species (Stichopogoninae); Tillobromatinae; *Damalis* sp. (Palatupana) (Trigonomiminae); and *Coleomyia setigera*, the two cerci are fused to a single sclerite medially (state 1). Among the outgroup taxa, the cerci are never fused (state 0).

213. Lateral ejaculatory process: (0) absent; (1) present, small triangular sclerite; (2) present, large cylindrical sclerite; (3) present, wide rectangular sclerite (length = 33; CI = 0.09; RI = 0.73). Karl (1959) observed the absence of lateral ejaculatory processes in Asilinae and Ommatiinae (referred to as *Querapodeme*). They are found here to be absent in Asilinae; *Deromyia fuscipennis*, *Megapoda labiata*, *Pegesimallus laticornis*, and *Pseudorus distendens* (all Dasypogoninae); *Echthodopa pubera* (Dioctriinae); Ommatiinae; Stichopogoninae except *Lasiopogon* species; and *Oligopogon* sp. (Cape Recife) (state 1; fig. 114). When the lateral ejaculatory process is present, it can be of different shape with a small triangular sclerite most commonly represented (state 1; fig. 115). A large, cylindrical process is present in Bathypogoninae; Laphriinae, with the exception of *Atomosia puella*, *Perasis transvaalensis*, and *Psilocurus modestus*; Leptogastrinae; *Phellus olgae* (Phellinae); *Lycostommyia albifacies* (Tillobromatinae); *Damalis monochaetes* (Trigonomiminae); and a few Brachyrhopalinae; Dasypogoninae; and Stenopogoninae (state 2; fig. 101). A wide

rectangular sclerite is present in *Brachyrhopala ruficornis* and *Cabasa pulchella* (Brachyrhopalinae); *Aphestia annulipes*, *Choerades bella*, *Lamyra gulo*, and *Laphria flava* (all Laphriinae); and *Acnephalum cylindricum* and *Sisyrnodytes* sp. (Gamka) (Willistonininae) (state 3). Among the outgroup taxa, states (0), (1), and (2) are present.

214. FUNCTIONAL AEDEAGAL PRONGS: (0) one prong; (1) two prongs; (2) three prongs (length = 11; CI = 0.18; RI = 0.81). Reichardt (1929), Karl (1959), and Theodor (1976) studied the aedeagus of many Asilidae in detail and emphasized the difference in number of functional aedeagal prongs as openings of the ductus ejaculatorius. A single prong is found in most Asilidae species, i.e., all Brachyrhopalinae; Dasypogoninae; Dioctriinae; Leptogastrinae; Ommatiinae; Phellinae; Stenopogoninae; Stichopogoninae; Tillobromatinae; and Willistonininae (state 0; figs. 101, 110–111). Two prongs are found only in *Myaptex brachyptera* and *Proctacanthus philadelphicus* (Asilinae) (state 1). Three prongs are found in Asilinae, with the exception of *Blepharotes splendidissimus*, *Colepia rufiventris*, *Dasophrys crenulatus*, *Lycomya germainii*, *Neoitamus cyanurus*, *Neolophonotus bimaculatus*, *Nomomyia murina*, *Satanas gigas*, *Threnia carbonaria*, and *Zosteria rosevillensis*; Laphriinae, with the exception of *Laphystia* species, *Perasis transvaalensis*, *Protometer* sp. (El Tuparro), and *Zabrops tagax* (state 2; figs. 102, 106, 114). Among Trigonomiminae, *Damalis* species and *Rhipidocephala* sp. (Harold Johnson) possess a single prong (state 0; fig. 111) whereas *Holcocephala* species and *Trigonomima* sp. (*anamaliensis*) possess three prongs (state 2). Among the outgroup taxa, *Afroleptomydas* sp. (Clanwilliam) (Mydidae) is the only species that possesses two aedeagal prongs and all remaining species possess only a single prong (state 0).

215. DORSAL AEDEAGAL SHEATH LENGTH: (0) short, sperm sac entirely free; (1) long, sperm sac entirely covered (length = 13; CI = 0.07; RI = 0.85). The dorsal aedeagal sheath is usually short and does not cover the sperm sac (state 0; figs 101, 115). In Asilinae except *Neoitamus cyanurus*; *Deromyia fuscipennis*, *Megapoda labiata*, and *Pseudorus distendens* (Dasypogoninae); *Echthodopa pubera* (Dioctriinae); Laphriinae, with the exception of Atomosiini sensu stricto and *Maira aenea*; Ommatiinae; and Stichopogoninae except *Lasiopogon* species, the dorsal aedeagal sheath is long and covers the sperm sac entirely dorsally (state 1; fig. 114; see also figs. 229, 293, 358, 399 in Theodor, 1976). Among the outgroup taxa, Mydidae except *Pseudonomoneura hirta*, Nemestrinidae, Scenopinidae, and Therevidae possess a long dorsal aedeagal sheath (state 1).

216. HYPANDRIUM POSTERIOR MARGIN: (0) simple, no distinct projections; (1) long median projection (length = 6; CI = 0.16; RI = 0.28). The distal margin of the hypandrium can be of different shape and some southern African species as well as a few other species possess a long median projection (state 1). Karl (1959) called this projection *brettartiges Gebilde*. *Afroholopogon* peregrinus (see figs. 45, 47 in Londt, 2005a: 247) and *Rhabdogaster pedion* (see figs. 83, 85 in Londt, 2006a: 307, Brachyrhopalinae); *Broticosia paramonovi* (Dioctriinae); *Creolestes nigribarbis*, *Daspletis stenoura* (see figs. 22, 24 in Londt, 1983: 296), and *Microstylum* sp. (Karkloof) (all Stenopogoninae); *Lycostommyia albifacies* (see figs. 56, 58 in Londt, 1992: 70; Tillobromatinae); and *Sisyrnodytes* sp. (Gamka) (Willistonininae) possess this process of unknown function (state 1) whereas all remaining Asilidae species lack a median process (state 0). Among the outgroup taxa, the posterior margin of the hypandrium is always simple (state 0).

217. VENTRAL MEDIAN MARGIN OF DORSAL AEDEAGAL SHEATH: (0) weakly sclerotized, appearing incompletely closed; (1) strongly sclerotized, appearing entirely closed (length = 12; CI = 0.08; RI = 0.85). Sinclair et al. (1994) discussed the incompletely closed ventral median margin of the dorsal aedeagal sheath as supporting the homology of the aedeagal sheath in all Brachycera as it is found in different taxa of Brachycera. In Asilidae, the dorsal aedeagal sheath is completely closed in Asilinae except *Threnia carbonaria*; *Pegesimallus laticornis* (Dasypogoninae); *Echthodopa pubera* (Dioctriinae); Laphriinae except *Laphystia* species; Leptogastrinae except *Acronyches maya*; Ommatiinae; Stichopogoninae; and Trigonomiminae,

with the exception of *Damalis annulata* and *Damalis monochaetes* (state 1; figs. 114, 116). State 0 is illustrated in figure 115. Among the outgroup taxa, only Apsilocephalidae, Bombyliidae, *Pseudonomoneura hirta* (Mydidae), and Nemestrinidae exhibit an incompletely closed dorsal aedeagal sheath (state 0).

218. Sperm sac: (0) appearing weakly sclerotized; (1) appearing more or less heavily sclerotized (length = 30; CI = 0.03; RI = 0.57). The sperm sac is always sclerotized in Asilidae, but it appears that some species have a less sclerotized sperm sac compared to other species. The majority of Asilinae; Dasypogoninae; Dioctriinae; Laphriinae; Leptogastrinae; Ommatiinae; Phellinae; and Stenopogoninae and a few Brachyrhopalinae and Willistonininae exhibit a heavily sclerotized sperm sac (state 1) whereas all remaining species exhibit a weakly sclerotized sperm sac (state 0). Among the outgroup taxa, only Apsilocephalidae, *Opomydas townsendi* and *Pseudonomoneura hirta* (Mydidae), and Nemestrinidae exhibit a weakly sclerotized sperm sac (state 0).

219. Lateral ejaculatory process and ventral aedeagal sheath: (0) lateral ejaculatory processes directed laterally or anteriorly, not surrounded by ventral aedeagal sheath; (1) lateral ejaculatory processes directed posteriorly and surrounded by ventral aedeagal sheath (length = 6; CI = 0.16; RI = 0.80). When lateral ejaculatory processes are present (see character 213) they can be free or surrounded by the ventral aedeagal sheath. A free process is most commonly found within Asilidae (state 0; figs. 101, 115). Species of Laphriinae vary in their development and, with the exception of Atomosiini sensu stricto, *Laphria aktis*, and *Perasis transvaalensis*, Laphriinae exhibit state 1 (fig. 116). Among the outgroup taxa, *Mitrodetus dentitarsis* (Mydidae), Scenopinidae, and Therevidae possess state 1 whereas all remaining species possess state 0. All species lacking a lateral ejaculatory process are coded as inapplicable (-).

220. Shape of ejaculatory apodeme: (0) single plate of varying diameter and shape (two lateral surfaces only): (1) triangular in anterior view (two lateral and one dorsal surface); (2) diamond-shaped in anterior view (four lateral surfaces) (length = 9; CI = 0.22; RI = 0.41). Reichardt (1929) and Theodor (1976) illustrated the musculature of the ejaculatory apodeme connecting to the dorsal aedeagal sheath. The apodeme itself can be of different shape and is most commonly a single plate of varying diameter, which has two lateral surfaces and is positioned vertically in the hypopygium or abdominal segment 8 (state 0; figs. 101, 114–117). A triangular apodeme with two lateral and one dorsal surface is found in *Blepharepium cajennensis* (Dasypogoninae); Phellinae; Stichopogoninae except *Lasiopogon cinctus*; and *Willistonina bilineata* (Willistonininae) (state 1; fig. 117). A diamond-shaped apodeme with four lateral surfaces is found in *Megapoda labiata* (Dasypogoninae) and *Nusa infumata* and *Smeryngolaphria numitor* (Laphriinae) (state 2; fig. 117). Among the outgroup taxa, most species possess a single plate (state 0) and only Nemestrinidae possess a triangular ejaculatory apodeme (state 1).

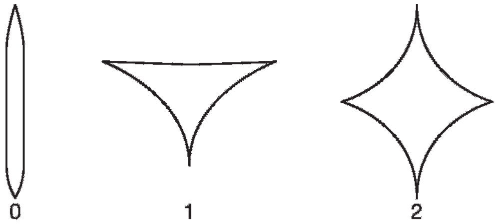


Fig. 117. Schematic drawing of ejaculatory apodemes in posterior view as coded in character 220 with character states indicated. Not to scale.

Characters Not Considered

Many characters and character complexes show a high degree of morphological variation within Asilidae, such as pruinosity on the thorax and abdomen, setal arrangement on legs, wing microtrichia covering, shape and appendages of the aedeagus, and shape of gonostyli in males. Such characters are not included here as their development is often associated with species-specific differences that are very difficult to homologize across taxa. Only features for which character states are consistently applicable across the entire Asilidae are included.

Fisher (1986) postulated a field of sensilla situated laterally on the cerci in female Andrenosomatini as an autapomorphy for this taxon. This character is not included here as it would have been necessary to take scanning electron micrographs of the ovipositor of every female specimen to identify it correctly. The value of this character is not in doubt, however. Fisher (personal commun.) studied a number of Asilinae species with respect to the presence of a crop (absent in Asilinae but present in Apocleinae sensu Papavero (1973a) and Geller-Grimm (2004)). As this character is observable only in freshly killed or specially preserved specimens, it could not be included here as the vast majority of specimens are dry-mounted, many of them considerably old.

The musculature of the male terminalia has been shown to contain characters that can be useful in delimiting taxa (Ovtshinnikova, 1989; Ovtshinnikova and Yeates, 1998), e.g., support for a clade Apioceridae, Asilidae, and Mydidae is provided by the presence of muscle M33 in these three taxa. Despite the usefulness of this character complex, no musculature is examined due to the different preservation conditions of the many specimens examined and the exemplar approach employed here.

Theodor (1976) and Yeates (1994) discussed a number of characters of the female spermathecae that are only observable under high magnification in a compound microscope, e.g., sclerotized tubules on spermathecal duct, and these characters are not considered as no slide mounts of spermathecae are prepared.

RESULTS

The equally weighted parsimony analysis of the character matrix in appendix 1 resulted in 720 most parsimonious cladograms of 2760 steps (CI = 0.13; RI = 0.68); one of the most parsimonious cladograms is illustrated in figure 118. The strict consensus topology, in which 37 nodes are collapsed, has a length of 2965 steps (CI = 0.12; RI = 0.65; fig. 119). The initial search of 300 RAS+TBR resulted in 20 trees of 2761 steps length. The following 1500 iterations of the parsimony ratchet (Nixon, 1999) found 710 trees of 2760 steps length and the 1500 rounds of tree drifting (Goloboff, 1999) added another 10 trees of the same length. Increasing the number of ratchet or tree-drifting iterations did not find any shorter trees nor did it increase the number of most parsimonious trees. Farris et al. (1996) and Goloboff and Farris (2001) highlighted the fact that it is not necessary to find all most parsimonious topologies for large data sets. As can be seen in the strict consensus topology (fig. 119) the majority of collapsed branches concerns the phylogenetic relationships within the Asilinae. Finding additional optimal trees of 2760 steps will therefore likely be uninformative for the higher-level relationships of Asilidae. The search for Bremer support and relative Bremer support resulted in 2785 suboptimal trees of 1–8 steps longer than the most parsimonious trees of 2760 steps. Although search algorithms are implemented to find primarily most parsimonious trees the present procedure exhaustively searched the tree space for suboptimal topologies so that the calculation of Bremer support is as accurate as possible. These support measures are indicated in figure 119.

Asilidae is corroborated as monophyletic with the following autapomorphies: labella fused to prementum at least ventrally (character 23; fig. 31), hypopharynx heavily sclerotized (30; figs. 39–40), hypopharynx with dorsal seta-like spicules (33; figs. 42–43), labrum short, at most half as long as labium (34; fig. 31), cibarium trapezoidal (36; figs. 46–47). Additional apomorphic character states, which are also present in some outgroup taxa or not all robber flies, under unambiguous optimization are: vertex sharply depressed (3; fig. 28), prementum circular in cross section (18), labella with rounded tip (24; fig. 31), hypopharynx as long as labium (31; fig. 31), cibarium with median longitudinal ridge (38; figs. 46–47), postpronotal lobes extending medially (72; fig. 64), anterior anepisternal setae erect (78), prothoracic tibiae with at least three setae anteroventrally (105), macrosetae and regular setae on median surface of metathoracic trochanter (114).

Under fast optimization the following additional apomorphic character states are optimized at the root of Asilidae: cross

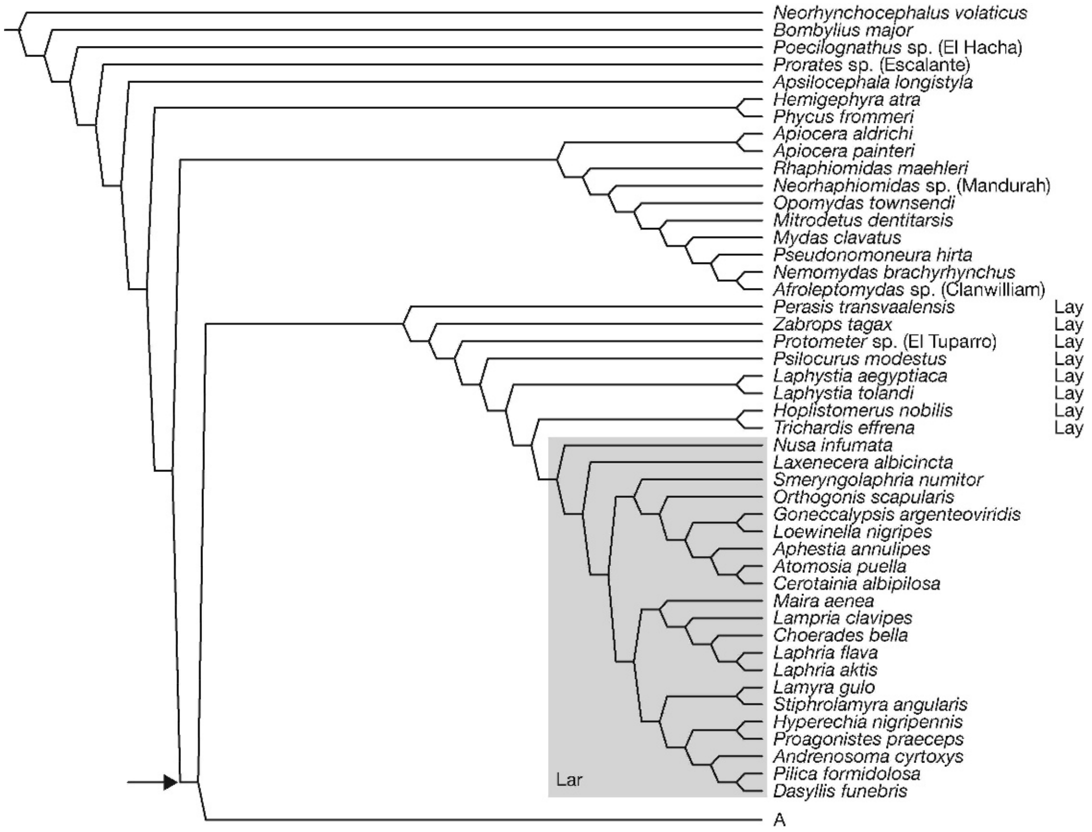


Fig. 118. (above and right) One of the 720 most parsimonious trees obtained from parsimony analysis of 158 Asilidae species and 17 outgroup taxa of the character matrix of appendix 1 (length = 2760; CI = 0.13; RI = 0.68). Arrow indicates root of Asilidae; assignment of genera to subfamily taxa sensu Geller-Grimm (2004) on right; monophyletic taxa in grey boxes (abbreviations: Apo = Apocleinae; Asi = Asilinae; Das = Dasypogoninae; Dio = Dioctriinae; Lep = Leptogastrinae; Lar = Laphriinae; Lay = Laphystiinae; Omm = Ommatiinae; Ste = Stenopogoninae; Sti = Stichopogoninae; Tri = Trigonomiminae).

section of prementum proximally circular (18), dorsoposterior margin of cibarium with one transverse ridge connecting cornua (35; fig. 47), ocellar setae composed of macrosetae and regular setae (62), setae on posterior meron + metanepisternum composed of only regular setae (no macrosetae) (85). One character (23, labella fused to prementum at least ventrally), which is an autapomorphy under unambiguous optimization, becomes only an apomorphic character under fast optimization.

Under slow optimization the following additional apomorphic character states are optimized at the root of Asilidae: facial swelling extending over entire face (4), mystax present (6), stipites fused to postgenae (15; figs. 33–34), cross section of prementum proximally circular (18), sclerotized hypopharynx parallel-sided throughout, only distal tip suddenly pointed (32; figs. 39–40), antennae positioned in dorsal half of head (51; figs. 26–29), ocellar setae composed of macrosetae and regular setae (62), katatergal setae composed of macrosetae and regular setae (83), no protuberance developed on anterior surface of metathoracic coxa (113).

Comparing the placement of genera in the most recent subfamilial classification of Asilidae summarized by Geller-Grimm (2004) to the present phylogenetic hypothesis, it is evident that not all higher-level taxa as

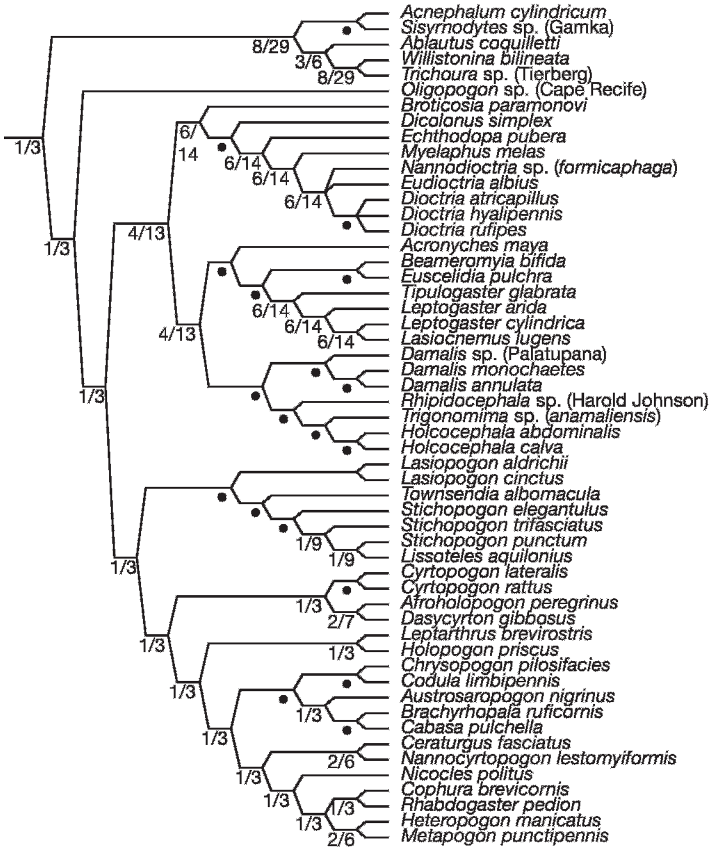


Fig. 119. (left and above) Strict consensus topology of 720 most parsimonious trees obtained from parsimony analysis of 158 Asilidae species and 17 outgroup taxa of the character matrix of appendix 1 (length = 2965; CI = 0.12; RI = 0.65). Bremer support/relative Bremer support below branches. Support of ≥8/100 is indicated with filled circle. Arrow indicates root of Asilidae.

previously delimited are monophyletic. Thus changes in the assignment of certain genera are necessary. The only taxa recovered as monophyletic are Laphriinae; Leptogastrinae; Ommatiinae; Stichopogoninae; and Trigonomiminae. Dioctriinae is recovered as monophyletic, but *Myelaphus melas*, which was assigned to Stenopogoninae: Ceraturgini by Artigas and Papavero (1991) and Geller-Grimm (2004), groups within Dioctriinae as postulated previously by Hull (1962) and Adisoemarto and Wood (1975). Apocleinae and Asilinae are paraphyletic with respect to each other and Laphystiinae is paraphyletic with respect to Laphriinae. Dasypogoninae and Stenopogoninae are non-monophyletic and representatives form several clades in phylogenetically unrelated positions in the cladogram. Many tribal taxa are recovered as monophyletic although the delimitation of a number of them has to be changed and genera transferred to recognize only monophyletic taxa. The taxon Apioceridae + Mydidae is the sister group to Asilidae (see Discussion).

A Revised, Higher-Level Classification of Asilidae

Since the first theoretical contributions by Hennig (1950, 1966), only monophyletic taxa, i.e., taxa including all descendents, extant and extinct, of their most recent common ancestor, are recognized in phylogenetic systematics. Evolutionary taxonomists, in contrast, use anagenesis in addition to cladogenesis in deriving classifications. The result is the delimitation of taxa that do not entail every descendent of the most recent common ancestor (e.g., Mayr, 1974, 1981). It is not evident from the introduction to the two most comprehensive classifications on Asilidae by Hull (1962) and Papavero (1973a) whether they propose a cladistic or evolutionary classification. Both studies, as outlined in the introduction, are not cladistic in nature, although both authors labeled their diagrams of relationships as phylogenetic, i.e., "A provisional philogenetic [sic] arrangement of the Asilidae" (Hull, 1962: text-fig. 35) and "Hypothetical phylogeny of the subfamilies of Asilidae" (Papavero, 1973a: fig. 1). Both authors first postulated a classification from which they then deduced a phylogeny. In cladistics, by contrast, the phylogeny is postulated first, and only then is a phylogenetic classification derived, so that only monophyletic taxa are recognized. Griffiths (1974), Hennig (1975), Farris (1979), Gaffney (1979), and many later authors emphasized that "the most important biological reference system is a phylogeny and that a classification that mirrors a phylogenetic hypothesis (however transitory) is the most useful for systematists and nonsystematists" (Gaffney, 1979: 104). Wheeler (1995: 31) stated,

> Ultimately, however, it is the primary product of taxonomy that proves most useful to taxonomists and biologists in general: the predictive classification, based on cladistic hypotheses. Such phylogenetic classifications combine the best of descriptive taxonomy and phylogenetic analysis providing the historical perspective essential to a biology that is truly evolutionary.

The present study is the most comprehensive phylogenetic analysis of Asilidae to date and there is no other choice than to also use the phylogenetic branching pattern to establish a new, monophyletic, revised classification. Admittedly, translating a phylogeny into a monophyletic classification is straightforward, but it is certainly subjective in the sense that one cannot (1) recognize every monophyletic taxon with a name and (2) objectively decide whether to call a certain taxon a tribal taxon or subfamily taxon. The only objective consideration is that when one recognizes a group of species as a taxon, one also has to recognize its sister taxon at the same rank no matter its position in the cladogram.

Unfortunately, at this stage it is impossible to write a useful dichotomous or matrix-based identification key that would place all genera of Asilidae into subordinate taxa. The desire of dipterists to have this tool is understandable, but since only 140 out of 537 genera are represented in the present analysis, no meaningful key can be written. However, table 7 summarizes the character distribution of 24 easily observed characters that can aid in placing yet unstudied genera and species. The provided diagnoses of all taxa including autapomorphies and additional apomorphic character states, which are also found in other phylogenetically unrelated robber flies, should also be consulted. Table 3 indicates the respective lengths of the proximal tarsomeres that appear to be diagnostic for at least some taxa, and so should be consulted as well.

The following discussion, also summarized in figures 120–121 and table 6, provides an overview of the taxa (subfamily and tribe) recognized in the revised classification. A numbering system is employed to indicate the subordination of taxa and the following information for each taxon is provided: autapomorphies, additional apomorphic character states that are diagnostic, and remarks with respect to the use of the family-group name by previous authors. One of the 720 most parsimonious cladograms is selected to illustrate the character optimization and character distribution (figs. 122–126) although the delimitation of taxa is based on the strict consensus topology (fig. 119) as it is the summary of all equally parsimonious hypotheses. Taxa that only contain a single genus are indicated as well, although the diagnosis is based only on the single included species.

This newly revised phylogenetic classification recognizes 14 subfamilial taxa based on already published family-group names summarized in Sabrosky (1999) and Dikow (2004). The status of some of the taxa is revised, but no new family-group names are described. It should be highlighted that a

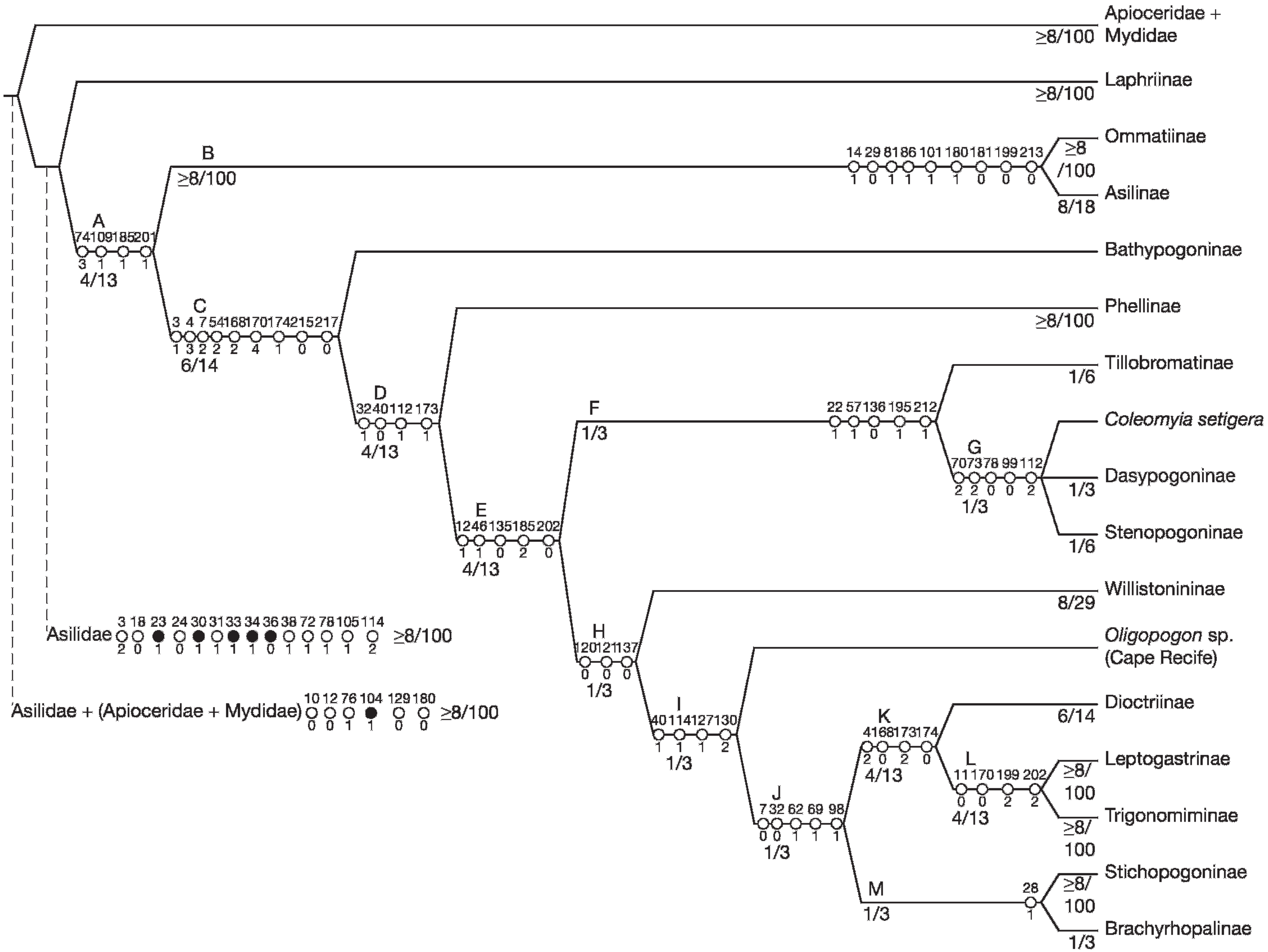


Fig. 120. Summary of relationships of subfamily taxa based on strict consensus topology of figure 119 and revised classification of table 6. Character state optimization and distribution for higher-level clades mapped onto cladogram with character number above circle and character state below circle; filled circle = autapomorphy; open circle = reversal or homoplasy; clade names above branches; Bremer support/relative Bremer support below branches.


Apioceridae + Mydidae
Perasis transvaalensis
Zabrops tagax
Protometer sp. (El Tuparro)
Psilocurus modestus
Laphystiini
Hoplistomerini
Nusa infumata
Laxenecera albicincta
Atomosiini
Laphriini
Ctenotini
Andrenosomatini
Ommatiinae
Blepharotes splendidissimus
Lycomyini
Apocleini
Asilini
Neomochtherini
Philonicini
Congomochtherus inachus
Lochmorhynchus albicans
Dasophrys crenulatus
Heligmonevra laevis
Tolmerus atricapillus
Machimus occidentalis
Machimus chrysitis
Satanas gigas
Zosteria rosevillensis
Nomomyia murina
Proctacanthus philadelphicus
Myaptex brachyptera
Pogonioefferia pogonias
Eichoichemus pyrrhomystax
Neolophonotus bimaculatus
Dysmachus trigonus
Clephydroneura sundaica
Clephydroneura sp. (Kepong)
Colepia rufiventris
Neoitamus cyanurus
Threnia carbonaria
Bathypogoninae
Phellinae
Tillobromatinae
Coleomyia setigera
Lestomyia fraudiger
Dasypogonini
Saropogonini
Thereutriini
Archilestris magnificus
Lastauracini
Diogmites grossus
Blepharepiini
Molobratiini
Megapodini: Senobasina
Megapodini: Cyrtophryina
Megapodini: Lagodiina
Megapodini: Megapodina
Enigmomorphini
Ancylorhynchus fulvicollis
Scylaticus costalis
Plesiommatini
Stenopogonini
Willistonininae
Oligopogon sp. (Cape Recife)
Broticosia paramonovi
Dicolonus simplex
Echthodopini
Myelaphus melas
Dioctriini
Acronychini
Leptogastrini
Xenomyzini
Trigonomimini
Lasiopogon cinctus
Lasiopogon aldrichii
Townsendia albomacula
Stichopogonini
Cyrtopogonini
Leptarthrus brevirostris
Holopogon priscus
Chrysopogonini
Brachyrhopalini
Ceraturgini
Nicocles politus
Cophura brevicornis
Rhabdogaster pedion
Heteropogon manicatus
Metapogon punctipennis
A
B
C
D
E
F
G
H
I
J
K
L
M
c
c
† *Araripogon axelrodi*
† New Jersey amber species

number of higher-level taxa actually contain the same genera as postulated by previous authors; for example, the present delimitation of Laphriinae comprises all genera that Papavero (1973a) and Geller-Grimm (2004) placed in Laphriinae and Laphystiinae. The phylogenetic hypothesis could also have been divided into three higher-level taxa, i.e., Asilinae (including Ommatiinae, = taxon B), Laphriinae, and Dasypogoninae (= taxon C), which would be the same arrangement as postulated by Macquart in 1838. However, I did not choose to propose this classification as taxon C would be (1) morphologically very heterogeneous, (2) the large leftover group that is not easily diagnosable, and (3) the majority of generic and species diversity that, in my view, would not be investigated as thoroughly as the easily delimited Asilinae or Laphriinae.

1. LAPHRIINAE

Laphriinae Macquart, 1838. Type genus *Laphria* Meigen, 1803. Species represented: 29. Figures 120–122.

Autapomorphies: None. Additional apomorphic character states: Dorsal margin of postocciput with triangular projection (42; fig. 50), apical "seta-like" sensory element situated apically in cavity on stylus (57; fig. 57), dorsal margin of prosternum with distinct flangelike projection (75; fig. 66), metkatepisternum large and visible between mesothoracic and metathoracic coxae (ventral view) (100), setae present on lateral metathoracic coxae (112), cell r_1 closed, R_1 and R_{2+3} meet at costa (131; figs. 73, 76), R_{2+3} apex arching sharply anteriorly in 90° angle (142; fig. 73), R_4 strongly sinuate (144; fig. 73), female T10 lost or fused to cerci (172), male abdominal segments 1–6 well developed, T7–8 and S7 reduced while S8 is well developed (193). Laphriinae is the oldest available family-group name within this clade and includes all genera, which had been previously assigned to Laphriinae and Laphystiinae by Papavero (1973a) and Geller-Grimm (2004).

1.1. LAPHYSTIINI HENDEL, 1936, NEW STATUS.

Type genus: *Laphystia* Loew, 1847. Genera included: *Laphystia*. Autapomorphies: None. Additional apomorphic character states: Stylus of antenna composed of two elements (58), female common spermathecal duct long and extending beyond tip of furca (177), male ventral median margin of dorsal aedeagal sheath weakly sclerotized (217), male sperm sac appearing weakly sclerotized (218). The taxon Laphystiinae sensu Papavero (1973a) is not recovered as monophyletic in the present analysis and only the two included species of *Laphystia* form a clade that is here recognized as a tribal taxon.

1.2. ATOMOSIINI LYNCH ARRIBALZAGA, 1882.

Type genus *Atomosia* Macquart, 1838. Genera included: *Aphestia*, *Atomosia*, *Cerotainia*, *Goneccalypsis*, *Loewinella*, *Orthogonis*, *Smeryngolaphria*. Autapomorphies: None. Additional apomorphic character states: Postpedicel cylindrical (same diameter throughout) (54), apical "seta-like" sensory element positioned subapically laterally on postpedicel (57), fringe of parallel setae present ventrally on metathoracic femora and tibiae (118), metathoracic tibiae straight (not arched) (119). The Atomosiini is considered here to contain also the Dasytrichini, i.e., *Orthogonis* and Smeryngolaphria, which is not recovered as monophyletic. The diagnostic characters mentioned above are sufficient to recognize Atomosiini and the fact that *Orthogonis scapularis* shares an autapomorphy with the Atomosiini sensu previous authors exemplifies their close phylogenetic relationship. Atomosiini except *Smeryngolaphria* are characterized by an autapomorphy, i.e., cell d is closed at the distal end only by the base of M_2 and crossvein m-m is absent or at least highly reduced (137), and additional apomorphic character states (14: 0, 40: 2, 86: 0, 203: 0). The Atomosiini sensu previous authors are

←

Fig. 121. Summary of relationships of tribal taxa based on strict consensus topology of figure 119 and phylogenetic placement of the two oldest fossil Asilidae. Clade names as in figure 120.

TABLE 6

Revised classification of Asilidae and list of recognized family-group taxa.

Placement of genera in each taxon is based on the present phylogenetic hypothesis

Subfamily taxon: Tribal taxon	Genera
Asilinae: Apocleini	*Apoclea* Macquart, 1838, *Megaphorus* Bigot, 1857, *Philodicus* Loew, 1847, *Promachus* Loew, 1848
Asilinae: Asilini	*Asilus* Linnaeus, 1758
Asilinae: Lycomyini	*Lycomya* Bigot, 1857
Asilinae: Machimini	*Machimus* Loew, 1849
Asilinae: Neomochtherini	*Afromochtherus* Lehr, 1996, *Neomochtherus* Osten-Sacken, 1878
Asilinae: Philonicini	*Philonicus* Loew, 1849
Asilinae: unplaced	*Blepharotes* Duncan, 1840, *Clephydroneura* Becker, 1925, *Colepia* Daniels, 1987, *Congomochtherus* Oldroyd, 1970, *Dasophrys* Loew, 1858, *Dysmachus* Loew, 1860, *Eichoichemus* Bigot, 1857, *Heligmonevra* Bigot, 1858, *Lochmorhynchus* Engel, 1930, *Myaptex* Hull, 1962, *Neoitamus* Osten-Sacken, 1878, *Neolophonotus* Engel, 1925 (see Londt (2004) for synonymy of genus), *Nomomyia* Artigas, 1970, *Pogonioefferia* Artigas and Papavero, 1997, *Proctacanthus* Macquart, 1838, *Satanas* Jacobson, 1908, *Threnia* Schiner, 1868, *Tolmerus* Loew, 1849, *Zosteria* Daniels, 1987
Bathypogoninae	*Bathypogon* Loew, 1851
Brachyrhopalinae: Brachyrhopalini	*Austrosaropogon* Hardy, 1934, *Brachyrhopala* Macquart, 1847, *Cabasa* Walker, 1851
Brachyrhopalinae: Ceraturgini	*Ceraturgus* Wiedemann, 1824, *Nannocyrtopogon* Wilcox and Martin, 1936
Brachyrhopalinae: Chrysopogonini	*Chrysopogon* von Röder, 1881, *Codula* Macquart, 1850
Brachyrhopalinae: Cyrtopogonini	*Afroholopogon* Londt, 1994, *Cyrtopogon* Loew, 1847, *Dasycyrton* Philippi, 1865
Brachyrhopalinae: unplaced	*Cophura* Osten-Sacken, 1887, *Heteropogon* Loew, 1847, *Holopogon* Loew, 1847, *Leptarthrus* Stephens, 1829, *Metapogon* Coquillett, 1904, *Nicocles* Jaennicke, 1867, *Rhabdogaster* Loew, 1858
Dasypogoninae: Blepharepiini	*Blepharepium* Rondani, 1848
Dasypogoninae: Dasypogonini	*Dasypogon* Meigen, 1803
Dasypogoninae: Lastauracini	*Neodiogmites* Carrera, 1949
Dasypogoninae: Megapodini: Cyrtophryina	*Cyrtophrys* Loew, 1851, *Deromyia* Philippi, 1865
Dasypogoninae: Megapodini: Lagodiina	*Pegesimallus* Loew, 1858
Dasypogoninae: Megapodini: Megapodina	*Megapoda* Macquart, 1834, *Pseudorus* Walker, 1851
Dasypogoninae: Megapodini: Senobasina	*Senobasis* Macquart, 1838
Dasypogoninae: Molobratiini	*Molobratia* Hull, 1958
Dasypogoninae: Saropogonini	*Saropogon* Loew, 1847
Dasypogoninae: Thereutriini	*Thereutria* Loew, 1851
Dasypogoninae: unplaced	*Archilestris* Loew, 1874, *Diogmites* Loew, 1866, *Lestomyia* Williston, 1884
Dioctriinae: Dioctriini	*Dioctria* Meigen, 1803, *Eudioctria* Wilcox and Martin, 1941, *Nannodioctria* Wilcox and Martin, 1942
Dioctriinae: Echthodopini	*Echthodopa* Loew, 1866
Dioctriinae: unplaced	*Broticosia* Hull, 1957, *Dicolonus* Loew, 1866, *Myelaphus* Bigot, 1882
Laphriinae: Andrenosomatini	*Andrenosoma* Rondani, 1865, *Dasyllis* Loew, 1851, *Hyperechia* Schiner, 1866, *Pilica* Curran, 1931, *Proagonistes* Loew, 1858
Laphriinae: Atomosiini	*Aphestia* Schiner, 1866, *Atomosia* Macquart, 1838, *Cerotainia* Schiner, 1868, *Goneccalypsis* Hermann, 1912, *Loewinella* Hermann, 1912, *Orthogonis* Hermann, 1914, *Smeryngolaphria* Hermann, 1912
Laphriinae: Ctenotini	*Lamyra* Loew, 1851, *Stiphrolamyra* Engel, 1928
Laphriinae: Hoplistomerini	*Hoplistomerus* Macquart, 1838, *Trichardis* Hermann, 1906
Laphriinae: Laphriini	*Choerades* Walker, 1851, *Lampria* Macquart, 1838, *Laphria* Meigen, 1803, *Maira* Schiner, 1866

TABLE 6
(Continued)

Subfamily taxon: Tribal taxon	Genera
Laphriinae: Laphystiini	*Laphystia* Loew, 1847
Laphriinae: unplaced	*Laxenecera* Macquart, 1838, *Nusa* Walker, 1851, *Perasis* Hermann, 1906, *Protometer* Artigas, Papavero, and Costa 1995, *Psilocurus* Loew, 1874, *Zabrops* Hull, 1957
Leptogastrinae: Acronychini	*Acronyches* Williston, 1908
Leptogastrinae: Leptogastrini	*Beameromyia* Martin, 1957, *Euscelidia* Westwood, 1850, *Lasiocnemus* (Loew, 1851), *Leptogaster* Meigen, 1803, *Tipulogaster* Cockerell, 1913
Ommatiinae	*Afroestricus* Scarbrough, 2005, *Cophinopoda* Hull, 1958, *Emphysomera* Schiner, 1866, *Michotamia* Macquart, 1838, *Ommatius* Wiedemann, 1821
Phellinae	*Obelophorus* Schiner, 1868, *Phellus* Walker, 1851
Stenopogoninae: Enigmomorphini	*Connomyia* Londt, 1992, *Creolestes* Hull, 1962, *Daspletis* Loew, 1859, *Microstylum* Macquart, 1838, *Prolepsis* Walker, 1851
Stenopogoninae: Plesiommatini	*Plesiomma* Macquart, 1838
Stenopogoninae: Stenopogonini	*Gonioscelis* Schiner, 1866, *Ospriocerus* Loew, 1866, *Scleropogon* Loew, 1866, *Stenopogon* Loew, 1847
Stenopogoninae: unplaced	*Ancylorhynchus* Berthold, 1827, *Scylaticus* Loew, 1858
Stichopogoninae: Stichopogonini	*Lissoteles* Bezzi, 1910, *Stichopogon* Loew, 1847
Stichopogoninae: unplaced	*Lasiopogon* Loew, 1847, *Townsendia* Williston, 1895
Tillobromatinae	*Hypenetes* Loew, 1858, *Lycostommyia* Oldroyd, 1980, *Tillobroma* (Hull, 1962)
Trigonomiminae: Trigonomimini	*Holcocephala* Jaennicke, 1867, *Rhipidocephala* Hermann, 1926, *Trigonomima* Enderlein, 1914
Trigonomiminae: Xenomyzini	*Damalis* Fabricius, 1805
Willistonininae	*Ablautus* Loew, 1866, *Acnephalum* Macquart, 1838, *Sisyrnodytes* Loew, 1856, *Trichoura* Londt, 1994, *Willistonina* Back, 1909
incertae sedis	*Coleomyia* Wilcox and Martin, 1935, *Oligopogon* Loew, 1847

characterized by an autapomorphy, i.e., anatergal setae are formed by short and stout macrosetae (82), and additional apomorphic character states (23: 2, 25: 1, 95: 1, 100: 0, 102: 3, 109: 1, 141: 0, 151: 1, 170: 0, 193: 1, 215: 0, 219: 0). The clade *Goneccalypsis* + *Loewinella* is characterized by three autapomorphies, i.e., two short, stout, erect macrosetae are present on the anterior mesonotum (87), females and males possess medial setae on T7 (165, 191), and additional apomorphic character states (50: 1, 70: 0, 130: 2, 184: 1). The clade *Aphestia* + (*Atomosia* + *Cerotainia*) possesses two autapomorphies, i.e., costa terminates at M_2 (140; fig. 77), females with segment 7 distinctly shortened (166), and additional apomorphic character states (167: 1, 199: 1). *Aphestia* is characterized by a single autapomorphy, i.e., fringe of parallel setae is only present on metathoracic tibiae (118). The clade *Atomosia* + *Cerotainia* possesses two autapomorphies, i.e., T6 is cup-shaped and the last visible tergite conceals the remaining tergites (158), male T7–8 and S7–8 are reduced to ring of sclerites (193), and additional apomorphic character states (83: 1, 130: 1, 162: 0, 163: 0, 206: 1).

1.3. HOPLISTOMERINI ENDERLEIN, 1936.

Type genus *Hoplistomerus* Macquart, 1838. Genera included: *Hoplistomerus*, *Trichardis*. Autapomorphies: None. Additional apomorphic character states: Macrosetae and setae on the postpronotum (73), postsutural dorsocentral setae absent (94), scutal setae possess a large socket (95), short and stout cone-shaped macrosetae present on metathoracic femora (116), R_{2+3} apex arching sharply anteriorly in 90° angle (142; fig. 73), abdominal tergites indented and setae possess large sockets (151). *Trichardis* is assigned to this taxon for the first time.

1.4. LAPHRIINI MACQUART, 1838.

Genera included: *Choerades*, *Lampria*, *Laphria*, *Maira*. Autapomorphies: Face with circular and dorsoventrally flattened setae laterally in males and females (45), medial setae on posterior scutum present, appressed to surface and directed posteriorly (96). Additional apomorphic character states: Prementum laterally compressed proximally (18;

TABLE 7

Comparative identification matrix for the 14 subfamily taxa based on the present phylogenetic hypothesis

Symbols: • = present in all species; △ = present in majority of species; # = present in a few species; – = absent. See also table 3 for respective lengths of proximal tarsomeres

	maxillary stipites divided (fig. 33)	tentorial pits antero-medially v (fig. 26)	all ommatidia same size	frons sharply diverging (fig. 27)	macrosetae on lateral frons	postpedicel cylindrical (fig. 52)	setae anteriorly on stylus	lateral eye margin sinuate (fig. 60)	median occipital sclerite setae (fig. 51)	prosternum with flange dorsally (fig. 66)	metkatepisternum visible (ventral)	postmetacoxal bridge sclerotized	dorso-ventrally flattened setae on legs	straight spine on pro tibia (fig. 71)	blunt protuberance on met coxa	pulvilli absent	alula reduced in size (figs 83–85)	cell r_1 closed (figs 73–74)	cell *cup* open (fig. 85)	R_{2+3} arching 90° (figs 73, 75)	R_4 sinuate (figs 73, 75)	short stump vein on R_4 (fig. 79)	T2 more than twice as long as wide	ovipositor 7^{th} and following segments
Taxon	14	44	46	48	49	54	59	64	65	75	100	102	103	106	113	123	130	131	136	142	144	146	153	167
Asilinae	#	–	#	–	△	–	–	–	–	–	–	–	–	–	–	–	–	•	–	–	–	#	–	–
Bathypogoninae	•	–	–	–	•	–	–	–	–	–	–	–	–	–	•	–	–	–	–	•	•	–	–	–
Brachyrhopalinae	#	–	–	–	–	△	–	–	#	–	–	#	–	#	#	–	△	–	△	–	–	–	–	#
Dasypogoninae	–	–	#	–	#	#	–	–	△	–	#	–	–	△	–	–	#	#	#	–	–	–	–	–
Dioctriinae	•	–	△	–	#	△	–	–	–	#	–	–	–	–	–	–	△	–	△	–	–	–	–	–
Laphriinae	#	–	#	–	#	#	–	–	–	•	△	#	–	–	–	–	#	△	–	#	#	–	–	#
Leptogastrinae	–	–	–	–	–	△	–	–	–	△	#	–	–	–	–	•	•	–	#	–	–	–	•	–
Ommatiinae	–	–	–	–	–	–	•	–	–	–	–	•	–	–	–	–	–	•	–	–	–	–	–	–
Phellinae	#	–	–	–	–	#	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	•	–	•
Stenopogoninae	#	–	•	–	△	△	–	–	#	–	–	–	–	–	#	–	–	–	#	△	#	–	–	–
Stichopogoninae	•	–	–	•	–	#	–	•	–	△	–	–	–	–	#	–	•	–	–	–	–	–	–	–
Tillobromatinae	–	–	#	–	–	#	–	–	#	#	–	–	–	–	△	–	–	–	•	#	–	–	–	–
Trigonomiminae	–	•	–	–	–	#	–	–	–	•	–	#	–	–	–	–	△	–	#	–	–	–	–	–
Willistonininae	#	–	–	#	△	–	–	–	#	–	–	–	△	–	#	#	#	–	#	–	–	#	–	–

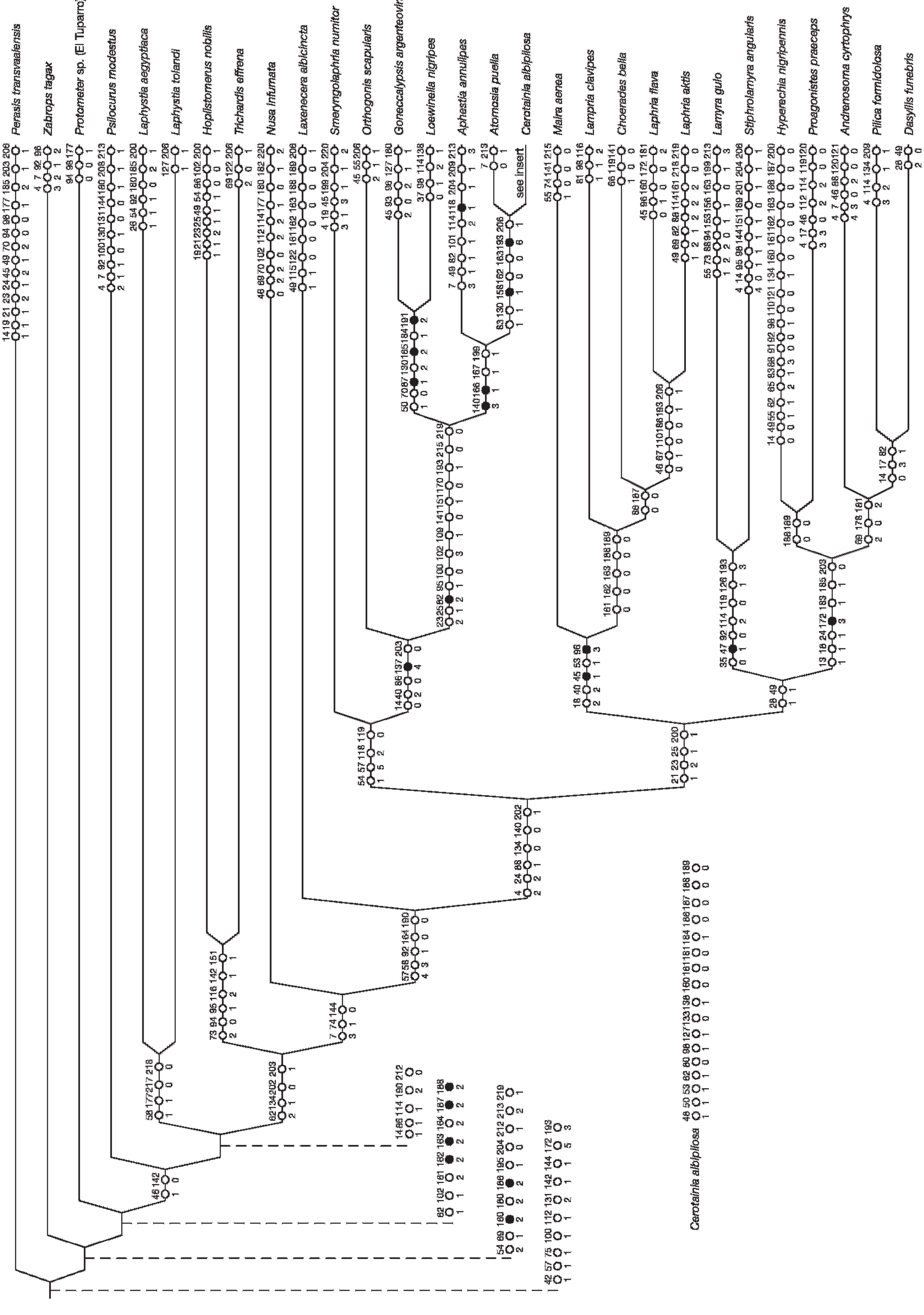


Fig. 122. Clade Laphriinae of figure 120 with character state optimization and distribution mapped onto cladogram. Character number above circle and character state below circle; filled circle = autapomorphy; open circle = reversal or homoplasy.

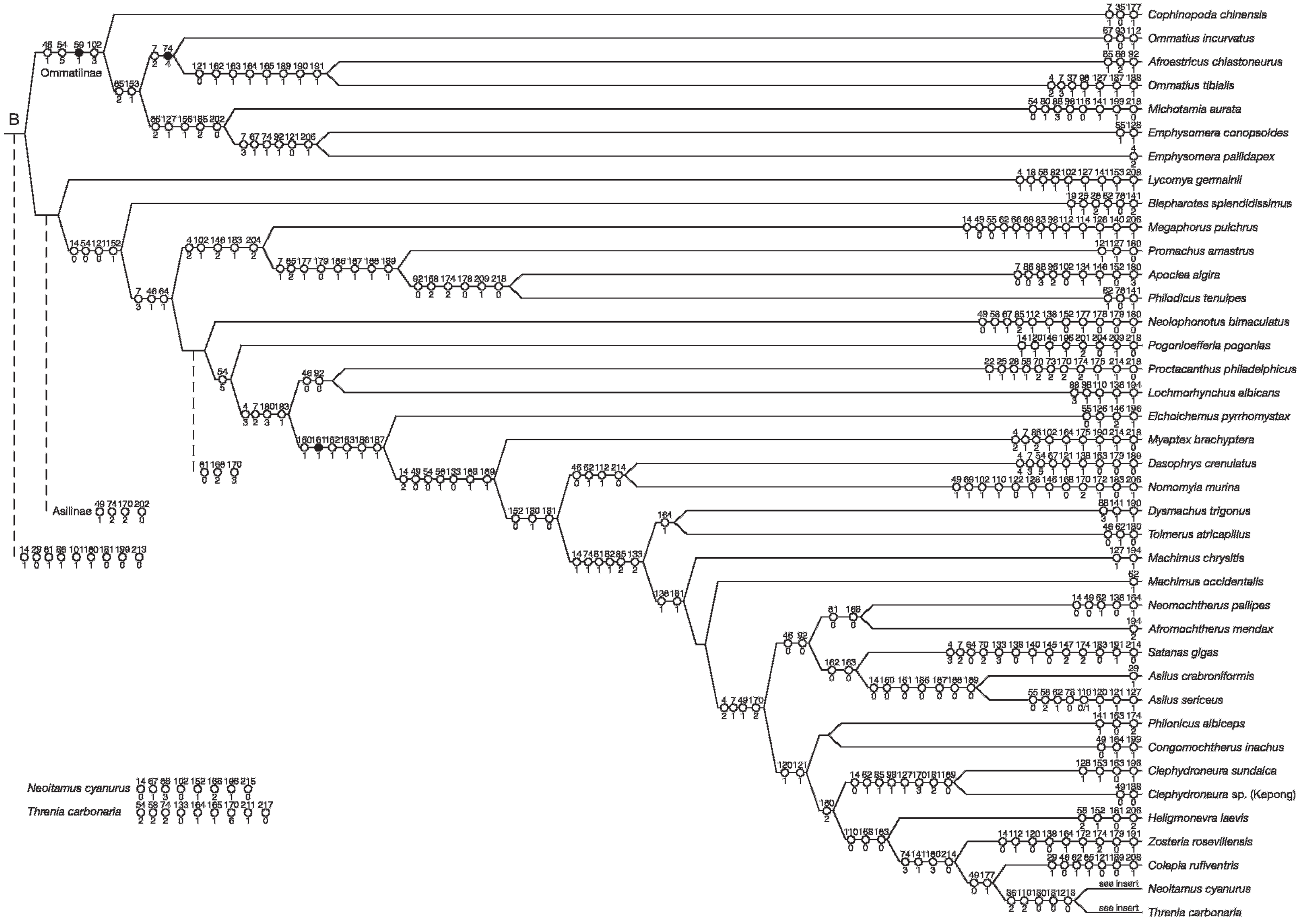


Fig. 123. Clade B (Asilinae + Ommatiinae) of figure 120 with character state optimization and distribution mapped onto cladogram. Character number above circle and character state below circle; filled circle = autapomorphy; open circle = reversal or homoplasy.

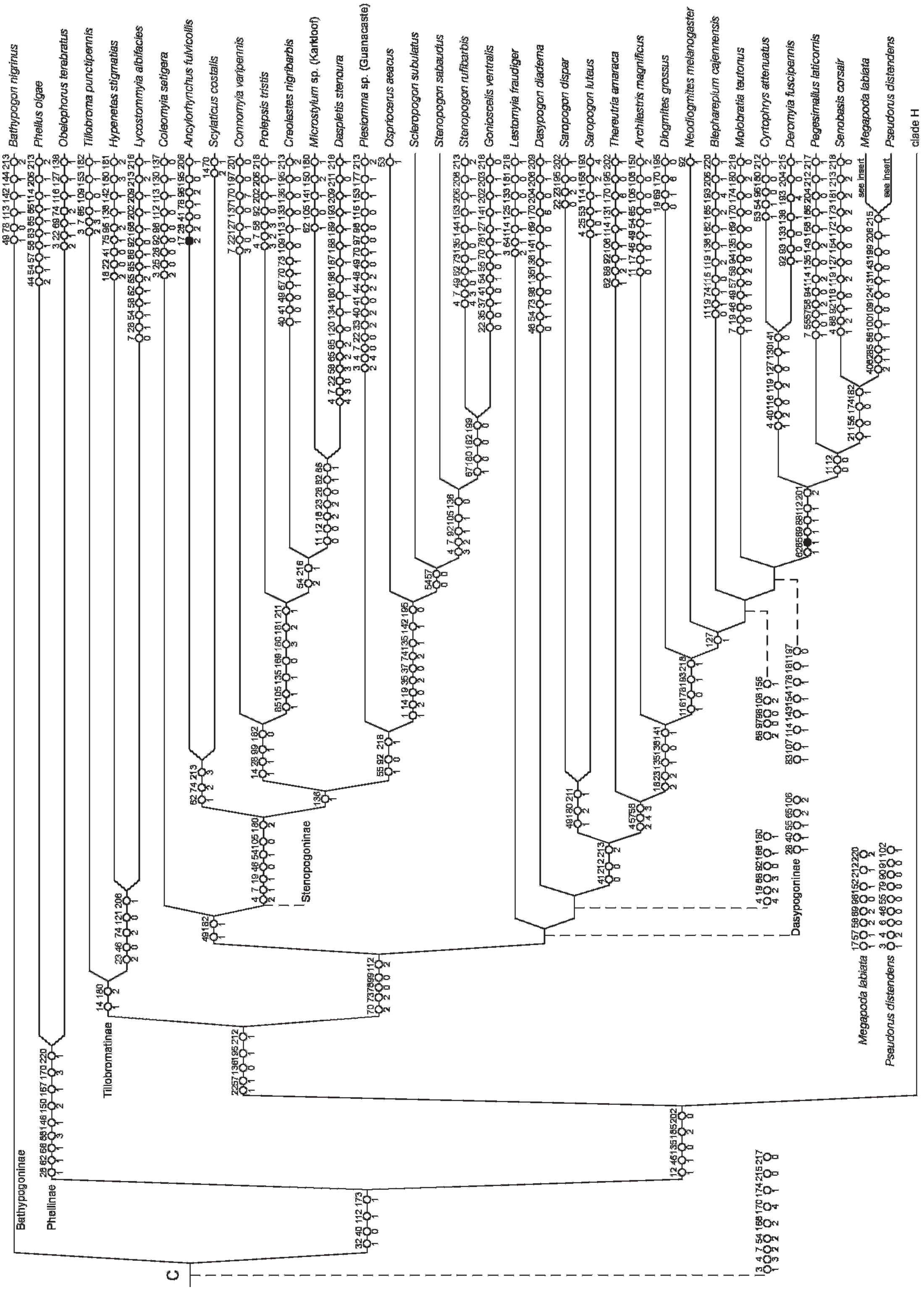


Fig. 124. Clade C without clade H (Bathypogoninae, Phellinae, Tillobromatinae, Dasypogoninae, Stenopogoninae, and *Coleomyia setigera*) of figure 120 with character state optimization and distribution mapped onto cladogram. Character number above circle and character state below circle; filled circle = autapomorphy; open circle = reversal or homoplasy.

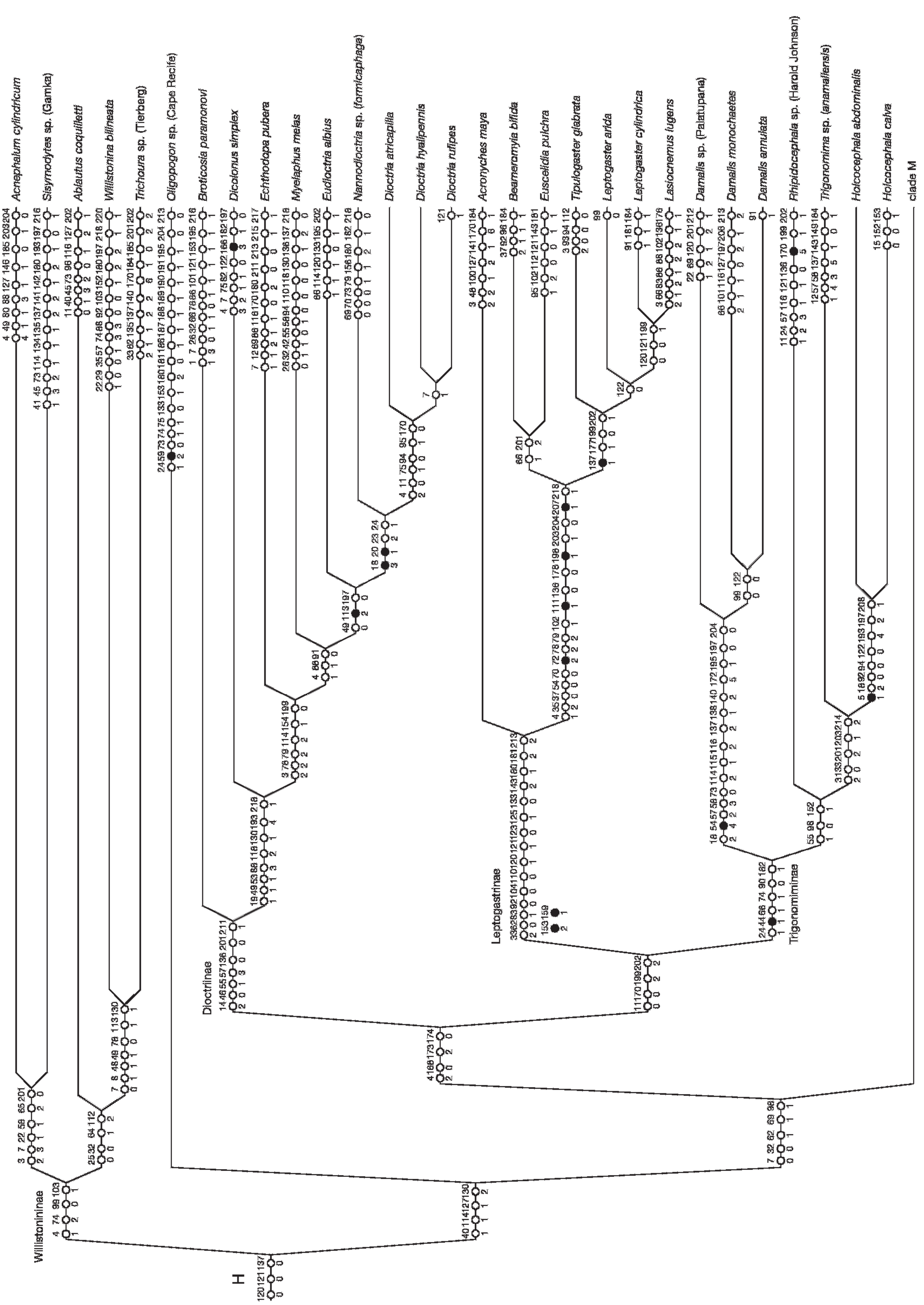


Fig. 125. Clade H without clade M (Willistonininae, Dioctriinae, Leptogastrinae, Trigonomiminae, and *Oligopogon* sp. [Cape Recife]) of figure 120 with character state optimization and distribution mapped onto cladogram. Character number above circle and character state below circle; filled circle = autapomorphy; open circle = reversal or homoplasy.

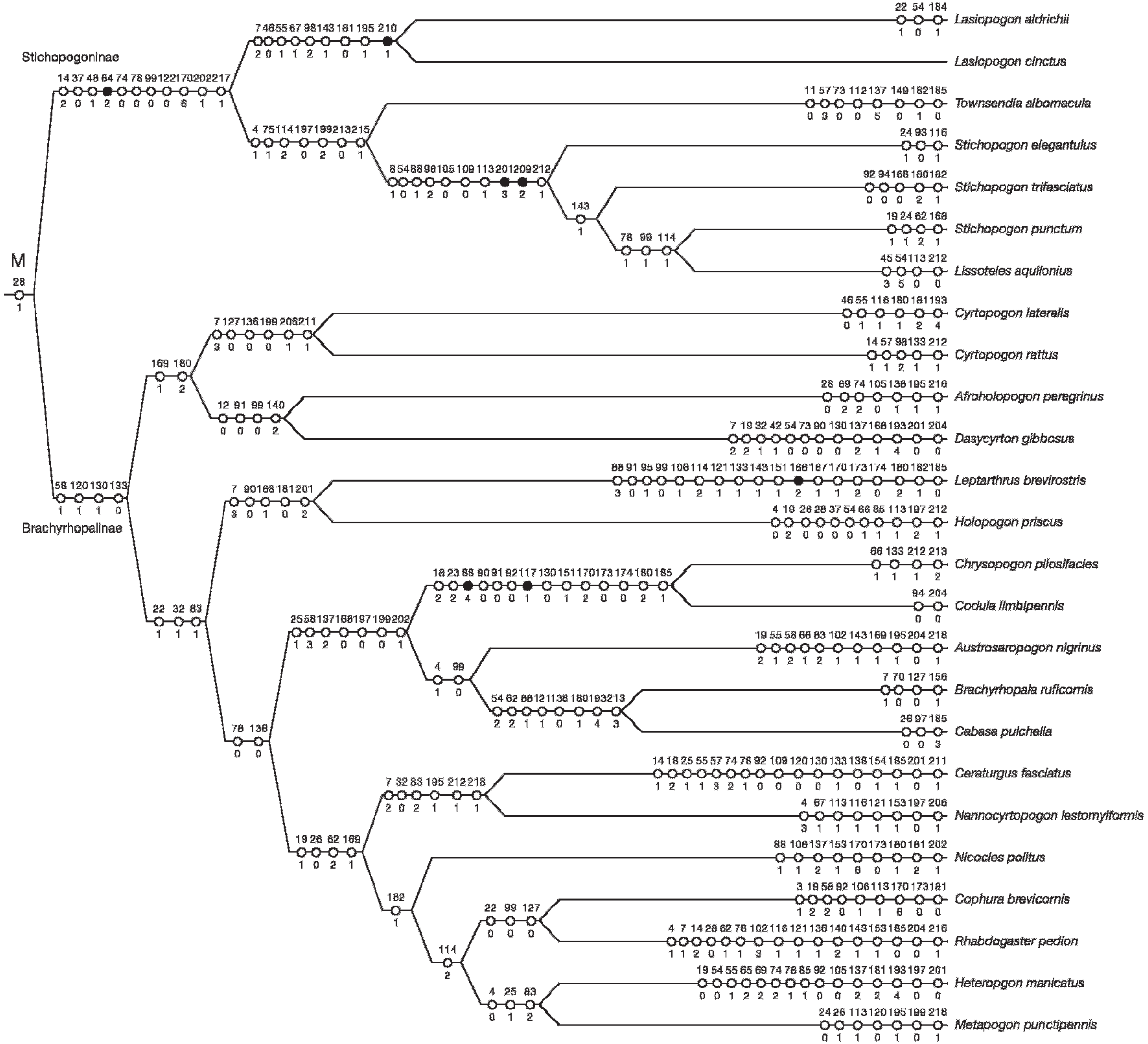


Fig. 126. Clade M (Brachyrhopalinae and Stichopogoninae) of figure 120 with character state optimization and distribution mapped onto cladogram. Character number above circle and character state below circle; filled circle = autapomorphy; open circle = reversal or homoplasy.

fig. 32), pharyngeal pump with entirely sclerotized ring (40; fig. 48), antennal insertion elevated above eye margin with distinct protuberance (53). In addition to the genera listed above, *Laxenecera* and *Nusa* were regarded to belong to Laphriini by previous authors. These two genera do not group with other genera of Laphriini and render it nonmonophyletic. Therefore, they are excluded from the easily diagnosed Laphriini with dorsoventrally flattened setae on the face and appressed setae on the posterior scutum.

1.5. CTENOTINI HULL, 1962.

Type genus *Ctenota* Loew, 1873. Genera included: *Lamyra*, *Stiphrolamyra*. Autapomorphies: Posterior margin of postgenae with large flangelike projection (47). Additional apomorphic character states: Dorsoposterior margin of cibarium simple, no particular ridge connecting cornua developed (35), presutural dorsocentral setae absent (92), macrosetae and setae present on median metathoracic trochanter (114), metathoracic tibiae straight (119), tip of claws blunt (126), male abdominal segments 1–6 well developed, T7–8 and S7 reduced while S8 is well developed (193). Ctenotini is recovered as monophyletic and contains the same taxa as previously postulated.

1.6. ANDRENOSOMATINI HULL, 1962.

Type genus *Andrenosoma* Rondani, 1856. Genera included: *Andrenosoma*, *Dasyllis*, *Hyperechia*, *Pilica*, *Proagonistes*. Autapomorphies: Female T10 is divided into two heavily sclerotized sclerites that are far apart (172; fig. 88). Additional apomorphic character states: Distal maxillary palpomere laterally compressed and leaflike (13), prementum of labium dorsoventrally flattened (18), apex of labella of labium pointed (24), female with median sclerite at posterior end of furca (183), female with long platelike apodeme on furca (185), male with epandrium and gonocoxites entirely free (203). Andrenosomatini is recovered as monophyletic and contains the same taxa as previously postulated. The relationship among the genera, however, is not resolved. Fisher (1986) presented a comprehensive phylogenetic study of Andrenosomatini.

Unplaced genera: *Laxenecera*, *Nusa*, *Perasis*, *Protometer*, *Psilocurus*, *Zabrops*. These genera cannot be assigned to any available family-group taxon and their phylogenetic relationship must be evaluated using a denser taxon sampling within Laphriinae.

Non-monophyletic taxa: Dasytrichini Lynch Arribalzaga, 1882. Representatives of this taxon are now included in Atomosiini with which they have been previously associated by Hermann (1912).

Phylogenetic relationships among Laphriinae: The genera *Perasis*, *Zabrops*, *Protometer*, *Psilocurus*, *Laphystia*, *Hoplistomerus*, and *Trichardis*, which have been previously assigned to the Laphystiinae, form a grade of less inclusive sister taxa that are more closely related to the Laphriinae sensu stricto. *Perasis transvaalensis* is the sister taxon to the remaining Laphriinae, which possess two autapomorphies, i.e., females and males with medial setae on T2 (160, 186), and additional apomorphic character states (54: 2, 69: 1, 180: 2, 195: 1, 204: 0, 212: 1, 213: 2, 219: 1). Laphriinae except *Perasis transvaalensis* and *Zabrops tagax* possess four autapomorphies, i.e., females and males with medial setae on T3–4 (161, 162, 187, 188), and additional apomorphic character states (62: 1, 102: 1, 161: 2, 164: 2). The four speciose taxa Atomosiini, Laphriini, Ctenotini, and Andrenosomatini form a clade characterized by these apomorphic character states: 4: 2, 24: 2, 88: 1, 134: 0, 140: 0, 202: 1. Laphriini, Ctenotini, and Andrenosomatini form a clade (21: 1, 23: 2, 25: 1, 200: 1) and lastly Ctenotini and Andrenosomatini are sister taxa delimited by the following apomorphic character states: 28: 1, 49: 1.

2. OMMATIINAE

Ommatiinae Hardy, 1927. Type genus *Ommatius* Wiedemann, 1821. Species represented: 7. Figures 120–121, 123.

Autapomorphies: Setae on anterior surface of antennal stylus (59). Additional apomorphic character states: At least some median ommatidia larger than surrounding ones (46), postpedicel short and medially broadest (54; fig. 52), postmetacoxal area entirely sclerotized (102). The Ommatiinae has been considered to be a monophyletic taxon that is usually associated with the Asilinae or Apocleinae sensu previous authors (e.g., Karl, 1959; Hull, 1962; Lehr, 1969, 1996; Papavero, 1973a; Bybee et al., 2004). In the present analysis, the included genera *Afroestricus*, *Cophinopoda*, *Emphysomera*, *Michotamia*, and *Ommatius* form a polytomy in the strict consensus hypothesis (fig. 119) and the genus *Ommatius* is paraphyletic with respect to *Afroestricus chiastoneurus*. *Afroestricus* has only recently been described for 20 Afrotropical species previously assigned to *Ommatius* by Scarbrough (2005) and *Afroestricus chiastoneurus* is the sister group to *Ommatius tibialis* (Nearctic), but phylogenetically unrelated to *Ommatius incurvatus* (Neotropical). The genus *Emphysomera* is monophyletic and characterized by a number of apomorphic character states (7: 3, 67: 1, 74: 1, 92: 1, 121: 0, 206: 1). The inclusion of more *Ommatius* species in future studies will help to clarify the monophyly of this worldwide, speciose genus.

3. ASILINAE

Asilinae Latreille, 1802. Type genus *Asilus* Linnaeus, 1758. Species represented: 32. Figures 120–121, 123.

Autapomorphies: None. Additional apomorphic character states: Macrosetae on lateral margin of frons present (49), prosternum and proepisternum separated and prosternum triangular and pointed dorsally (74; fig. 68), female S8 proximally platelike and distally hypogynial valves forming a keel (170; figs. 90, 95), male gonocoxites entirely free (202; fig. 113). The strict consensus topology in figure 119 illustrates the unresolved relationships among Asilinae genera including the Apocleinae sensu previous authors. This highlights the fact that the characters employed here cannot group the morphologically very similar species into less inclusive taxa. The addition of additional features, additional taxa, and other data, for example DNA sequence data, will be necessary to postulate a well-corroborated phylogenetic hypothesis for Asilinae species. The monophyly of Asilinae is, however, corroborated and has never been questioned before by previous authors.

3.1. ASILINI LATREILLE, 1802.

Genera included: *Asilus*. Autapomorphies: None. Additional apomorphic character states: Maxillary stipites fused entirely medially (14; fig. 34), female T2–3 without marginal setae (160, 161), male T2–5 without marginal setae (186, 187, 188, 189). In the present analysis, only the single genus *Asilus* is placed in the Asilini as *Satanas* does not group with *Asilus*.

3.2. APOCLEINI PAPAVERO, 1973A NEW STATUS.

Type genus *Apoclea* Macquart, 1838. Genera included: *Apoclea*, *Megaphorus*, *Philodicus*, *Promachus*. Autapomorphies: None. Additional apomorphic character states: Facial swelling extending over lower facial half (4), postmetacoxal bridge partly developed laterally, but membraneous medially (102), stump vein on R_4 present and reaching base of R_{2+3} (146; figs. 74, 80), female with median sclerite at posterior end of furca (183), male gonocoxal apodeme long and extending well into abdominal segment 8 (204; fig. 113). The Apocleini is the remnant of the Apocleinae sensu Artigas and Papavero (1988) and Geller-Grimm (2004). However, Artigas and Papavero (1997) combined the Asilinae and Apocleinae and the placement of Apocleini within Asilinae is corroborated here. *Megaphorus* is the sister taxon to the remaining Apocleini, which are characterized by the following apomorphic character states: 7: 1, 85: 2, 177: 1, 179: 0, 186: 1, 187: 1, 188: 1, 189: 1. Apoclea and *Philodicus* form a clade supported by these apomorphic character states: 92: 0, 168: 2, 174: 2, 178: 0, 209: 1, 218: 0.

3.3. LYCOMYINI LYNCH ARRIBALZAGA, 1882.

Type genus *Lycomya* Bigot, 1857. Genera included: *Lycomya*. Autapomorphies: None. Additional apomorphic character states: Facial swelling extending over lower half of face (4), prementum of labium dorsoventrally flattened (18), stylus composed of two elements (58), anatergal setae present (82), postmetacoxal bridge partly developed laterally, but membraneous medially (102), setiform empodium reduced in length (127), microtrichia on posterior margin of wing arranged in two divergent planes (141), T2 longer than wide, but less than twice as long (153), male subepandrial sclerite with protuberances medially (208). Lycomyini has been described for the single Chilean genus *Lycomya* by Lynch Arribalzaga (1882).

3.4. MACHIMINI LEHR, 1996.

Type genus *Machimus* Loew, 1849. Genera included: *Machimus*. This taxon is apparently non-monophyletic as the two included species of *Machimus* do not form a clade. In light of the unresolved relationships within the Asilinae, no comments on the monophyly of the genus or the taxon can be made.

3.5. NEOMOCHTHERINI LEHR, 1996.

Type genus *Neomochtherus* Osten-Sacken, 1887. Genera included: *Afromochtherus*, *Neomochtherus*. Autapomorphies: None. Additional apomorphic character states: Setae on posterior basalare absent (81), female T8 with posteriorly directed setae (168). Neomochtherini has been described by Lehr (1996) to also include *Dysmachus*, but this genus is part of the Asilinae genera that cannot be placed in any higher-level taxon.

3.6. PHILONICINI LEHR, 1996.

Type genus *Philonicus* Loew, 1849. Genera included: *Philonicus*. Autapomorphies: None. Additional apomorphic character states: Microtrichia on posterior margin of wing arranged in two divergent planes (141), female T5 without any marginal setae (163), female with spurs on cerci (174; fig. 95). Philonicini has been described by Lehr (1996) based on the single genus *Philonicus*.

Unplaced genera: *Blepharotes*, *Clephydroneura*, *Colepia*, *Congomochtherus*, *Dasophrys*, *Dysmachus*, *Eichoichemus*, *Heligmonevra*, *Lochmorhynchus*, *Machimus*, *Myaptex*, *Neoitamus*, *Neolophonotus*, *Nomomyia*, *Pogonioefferia*, *Proctacanthus*, *Satanas*, *Threnia*, *Tolmerus*, *Zosteria*. Although *Colepia*, *Neoitamus*, and *Threnia* form a monophyletic clade characterized by apomorphic character states—macrosetae on lateral margin of frons (dorsal to antennal insertion) absent (49) and female with spermathecal duct long and extending beyond the tip of furca (177)—no new name is proposed because of the poor resolution of relationships within Asilinae genera and the possibility that this group might not be monophyletic once new characters or taxa are added.

4. BATHYPOGONINAE, NEW STATUS

Bathypogoninae Artigas and Papavero, 1991. Type genus *Bathypogon* Loew, 1851. Species represented: 1. Figures 120–121, 124.

Autapomorphies: None. Additional apomorphic character states: Macrosetae on lateral margin of frons present (49), anterior anepisternal setae absent (78), protuberance on anterior metathoracic coxae present and blunt distally (113), R_{2+3} arching anteriorly in about 90° angle (142), R_4 strongly sinuate (144), male with large cylindrical lateral ejaculatory process (213). The Bathypogonini has been described by Artigas and Papavero (1991) as a taxon within their Stenopogoninae based on the Australian genus *Bathypogon* and on *Carebaricus* Artigas and Papavero, 1991, from Chile and Argentina. The single included species from Australia representing this taxon, *Bathypogon nigrinus*, does not group with any other Stenopogoninae sensu previous authors and therefore is recognized here as a separate taxon. Bathypogoninae is the sister group to the large clade D, which highlights its morphological distinctness. *Carebaricus* is not included in the present analysis and it cannot be confirmed whether it groups with *Bathypogon*. Extant representatives of Bathypogoninae are known only from Argentina, Australia, and Chile (Hennig, 1960; Artigas and Papavero, 1991).

5. PHELLINAE, NEW STATUS

Phellinae Hardy, 1926. Type genus *Phellus* Walker, 1851. Species represented: 2. Figures 120–121, 124.

Autapomorphies: None. Additional apomorphic character states: Maxillae (in lateral view) proximally high and distal tip narrower (28; fig. 38), ocellar setae formed by regular setae (no macrosetae) (63), postocular setae formed by regular setae (no macrosetae) (66), three or more notopleural setae present (88), stump vein on R_4 (not reaching R_{2+3}) (146; fig. 79), M_2 and m-m aligned in a line from distal to proximal (nearly parallel to posterior wing margin) (150; fig. 81), female with 7th and following segments comprising ovipositor (167), female S8 of ovipositor keellike throughout (170; fig. 90), male ejaculatory apodeme triangular in anterior view (two lateral and one dorsal surface) (220; fig. 117). The taxon Phellini was described by Hardy (1926) to include the three Australian genera

Bathypogon, *Phellus*, and *Psilozona* Ricardo, 1912. Hull (1962) transferred the Chilean genus *Obelophorus* into Phellini and Artigas and Papavero (1991) transferred *Bathypogon* to the newly described Bathypogonini. The two included genera *Obelophorus* and *Phellus* form a clade supported by a number of apomorphic character states and are recognized here as a separate taxon that is the sister taxon to clade E. This taxon is biogeographically interesting as the extant representatives are found only in Australia and Chile.

6. TILLOBROMATINAE, NEW STATUS

Tillobromatinae Artigas and Papavero, 1991. Type genus *Tillobroma* (Hull, 1962). Species represented: 3. Figures 120–121, 124.

Autapomorphies: None. Additional apomorphic character states: Maxillary stipites fused medially, but with V-shaped indentation (14), female spermathecal reservoir formed by more or less expanded and coiled ducts (180). The taxon Tillobromatini was described by Artigas and Papavero (1991) for the distinct New World genera *Coleomyia*, *Euthrixius* Artigas, 1971, *Grajahua* Artigas and Papavero, 1991, *Scylaticina* Artigas and Papavero, 1991, *Scylaticodes* Artigas and Papavero, 1991, *Tillobroma*, and *Zabrotica* Hull, 1958. *Tillobroma* was described by Hull (1962) as a subgenus of the South African genus *Hypenetes* highlighting the morphological similarity between these flies from different continents. Artigas et al. (2005) based a divergence time estimate of 180 Million years on the assumption of a sister-group relationship between *Hypenetes* and *Tillobroma*, which is not supported by the present analysis. *Hypenetes* and another South African genus, *Lycostommyia*, form a clade supported by a number of apomorphic character states (23: 2, 46: 0, 74: 2, 121: 0, 206: 1) and these two genera together form the sister group to *Tillobroma*. The western North American genus *Coleomyia* is not recovered within Tillobromatini and is here placed as incertae sedis (see below). As the genera *Hypenetes*, *Lycostommyia*, and *Tillobroma* form a clade distinct from other Dasypogoninae and Stenopogoninae, they are recognized here as a separate taxon. This taxon is biogeographically interesting, as the extant representatives are restricted to southern Africa and South America.

7. DASYPOGONINAE

Dasypogoninae Macquart, 1838. Type genus *Dasypogon* Meigen, 1803. Species represented: 16. Figures 120–121, 124.

Autapomorphies: None. Additional apomorphic character states: Maxillae proximally high and distal tip distinctly narrower (28; fig. 38), pharyngeal pump laterally with sclerotized ring, but medio-anteriorly unsclerotized (40; fig. 49), setae on dorsal postpedicel present (55), more than two macrosetae on median occipital sclerite present (65), large spine originating anteroventrally on prothoracic tibiae (106; figs. 70–71). The Dasypogoninae sensu previous authors has been suspected to be non-monophyletic. However, the *Dasypogon*-like robber flies recognized here within this taxon represent genera that have always been believed to form a monophyletic clade. The large spine on the prothoracic tibiae has been used as a diagnostic character for this group (e.g., Hull, 1962; Papavero, 1973a). Based on the phylogenetic hypothesis derived here this spine has been independently derived at least once in the Australian Brachyrhopalini and Chrysopogonini (Brachyrhopalinae). The spine has been reduced at least once within Dasypogoninae in *Archilestris magnificus*. Only *Thereutria* possesses a small S-shaped spur on the prothoracic tibiae, which is independently derived in *Cophura*, *Leptarthrus*, and *Nicocles* (all Brachyrhopalinae). Eleven subordinate taxa have been proposed to divide the Dasypogoninae by previous authors and with the exception of Archilaphriinae, all are included in the present analysis although some of them are only represented by a single species. Of these available and valid family-group taxa, eight are here recognized within Dasypogoninae (see below) and Brachyrhopalini and Chrysopogonini are transferred to the newly erected Brachyrhopalinae.

7.1. DASYPOGONINI MACQUART, 1838.

Genera included: *Dasypogon*. Autapomorphies: None. Apomorphic character states:

All ommatidia of same size (46), postpedicel cylindrical with same diameter throughout (54), regular setae form postpronotal setae (no macrosetae) (73), medial setae on posterior scutum absent (96), cell m_3 closed (135; fig. 82), cell cu*p* closed (136; fig. 82), microtrichia on posterior wing margin arranged in two divergent planes (141), female anterior T8 simple, no apodeme present (169), female S8 platelike with hypogynial valves separated and surrounded by membrane (170), male gonocoxal apodeme absent (204), male gonostyli positioned medially on gonocoxites (206), male subepandrial sclerite with distal projections (209). Of the included species here, *Lestomyia fraudiger* and *Austrosaropogon nigrinus* are classified as Dasypogonini by Hull (1962) and Papavero (1973b). *Lestomyia* groups with other Dasypogoninae, but not with *Dasypogon* itself and is excluded here from this taxon. The Australian genus *Austrosaropogon* groups with other Australian genera in Brachyrhopalinae (see below).

7.2. SAROPOGONINI HARDY, 1926.

Type genus *Saropogon* Loew, 1847. Genera included: *Saropogon*. Autapomorphies: None. Apomorphic character states: Macrosetae on dorsal frons (dorsal to antennal insertion) present (49), female spermathecal reservoir formed by more or less expanded and coiled ducts (180), male subepandrial plate with lateral protuberances (211). The Saropogonini was originally described by Hardy (1926) for the Australian genera *Rachiopogon* Ricardo, 1912, *Erythropogon* White, 1914, *Questopogon* Dakin and Fordham, 1922, and *Neosaropogon* Ricardo, 1912, and the more widespread genera *Saropogon*, *Stenopogon*, and *Clinopogon* Bezzi, 1910. Oldroyd (1974a, 1974b) used the taxon for a large number of genera, but it is restricted here to the single genus *Saropogon*.

7.3. THEREUTRIINI HULL, 1962.

Type genus *Thereutria* Loew, 1851. Genera included: *Thereutria*. Autapomorphies: None. Apomorphic character states: Ocellar setae formed by regular setae (no macrosetae) (62), two notopleural setae present (88), presutural dorsocentral setae present (92), prothoracic tibiae with small S-shaped spur, which originates on posteroventral surface (106), regular setae on median metathoracic trochanter (no macrosetae) (114), cell r_1 closed, R_1 and R_{2+3} as stalk vein present (131), female S8 platelike and hypogynial valves separated and surrounded by membrane (170), male hypopygium not rotated (195), male gonocoxites and hypandrium fused (202). The Thereutriini was described by Hull (1962) to accommodate the Australian genera *Metalaphria* Ricardo, 1912, and *Thereutria*.

7.4. LASTAURACINI PAPAVERO, 1973b.

Type genus *Lastaurax* Carrera, 1949. Genera included: *Neodiogmites*. Autapomorphies: None. Apomorphic character states: Presutural dorsocentral setae present (92). The Lastauracini was described by Papavero (1973b) for 10 Neotropical genera and *Diogmites*, which is distributed in the Nearctic and Neotropical regions. The original type genus is *Lastaurax* Carrera, 1949, but this genus has been synonymized with *Neodiogmites* by Artigas and Papavero (1988), which is now the type genus of this family group. *Diogmites* does not group with *Neodiogmites* in the present analysis and therefore the Lastauracini is restricted here to the single included genus *Neodiogmites*.

7.5. BLEPHAREPIINI PAPAVERO, 1973b.

Type genus *Blepharepium* Rondani, 1848. Genera included: *Blepharepium*. Autapomorphies: None. Apomorphic character states: Maxillary palpus one-segmented (11), ventral margin of postmentum of labium with median groove in distal part (19), prosternum and proepisternum fused and prosternum narrow above coxa (74; fig. 67), ventral metathoracic femora lacking macrosetae (116), metathoracic tibiae arched medially (119), crossvein r-m in distal half of discal cell (138), female spermathecae occupying more than posterior three abdominal segments (182), female furcal apodeme developed as short platelike apodeme (185), male S8 reduced, all other tergites and sternites well developed (193), male gonostyli positioned medially on gonocoxites (206), male ejaculatory apodeme triangular in anterior view (two lateral and one dorsal surface) (220). The Blepharepiini was described by Papavero (1973b) for the single Neotropical genus *Blepharepium* and the present analysis supports its morphological distinctness as no other genus groups with *Blepharepium*.

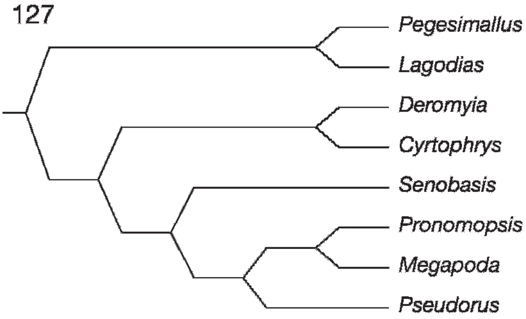
7.6. MOLOBRATIINI LEHR, 1999.

Type genus *Molobratia* Hull, 1958. Genera included: *Molobratia*. Autapomorphies: None. Additional apomorphic character states: Mystax extending over lower facial half (7), ventral margin of postmentum of labium entirely smooth (19), anterior ommatidia all same size (46), macrosetae on lateral margin of frons (dorsal to antennal insertion) present (49), apical "seta-like" sensory element situated apically on stylus (57), stylus composed of one element (58), postsutural dorsocentral setae absent (94), cell m_3 open (135), female T8 anteriorly lacking apodeme (169), female S8 platelike and slightly emarginate mediodistally (170), female without spurs on ovipositor (174), female spermathecal reservoir formed by more or less expanded and coiled ducts (180), male sperm sac appearing weakly sclerotized (218). Hull (1962) placed *Molobratia* in his Dasypogoninae: Dioctriini. The Molobratiini was described by Lehr (1999) originally in Dasypogoninae, but has been grouped in Dioctriinae based on the lack of acanthophorite spurs on the ovipositor and the shape of S8 by the same author (Lehr, 2001). The placement of *Molobratia* within Dioctriinae is not supported in the present study as it is positioned deeply within Dasypogoninae.

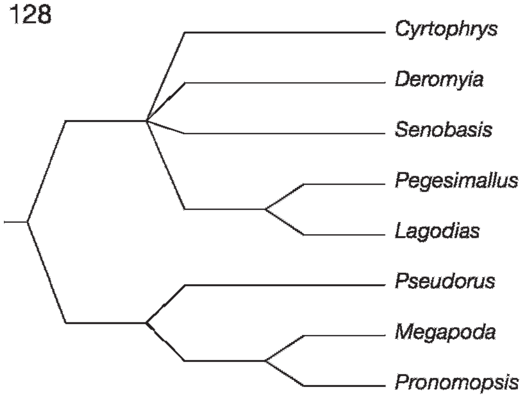
7.7. MEGAPODINI CARRERA, 1949.

Type genus *Megapoda* Macquart, 1834. Genera included: *Cyrtophrys*, *Deromyia*, *Megapoda*, *Pegesimallus*, *Pseudorus*, *Senobasis*. Autapomorphies: Two distinct macrosetae on median occipital sclerite (65; fig. 51). Additional apomorphic character states: Regular setae form ocellar setae (62), regular setae form antepronotum setae (69), one notopleural seta present (88), only regular setae on lateral metathoracic coxae (no macrosetae) (112), male epandrium and hypandrium at least partially fused (201). Megapodini was described by Carrera (1949), and Hull (1962) later labeled it as a separate subfamily taxon. This taxon has been extensively reviewed by Papavero (1975), who also provided a diagram of relationships of the included genera. Although his analysis is not phylogenetic, i.e., no distinction between apomorphic and plesiomorphic character states is made, a character matrix was provided and is re-analysed here (appendix 2). Figure 127 illustrates Papavero's hypothesis of relationships and figure 128 shows the result of the parsimony re-analysis, which results in three equally most parsimonious trees of 33 steps length (CI = 0.78; RI = 0.75) and a strict consensus topology of 35 steps (CI = 0.74; RI = 0.68). *Megapoda*, *Pronomopsis* Hermann, 1912, and *Pseudorus* form a clade in both diagrams, but the relationship between *Cyrtophrys*, *Deromyia*, *Pegesimallus*, and *Senobasis* is unresolved in the re-analysis. *Lagodias* Loew, 1858, has been synonymized with *Pegesimallus* by Londt (1980). Similar results to the re-analysis of Papavero's data are also found in the present analysis in that *Cyrtophrys* and

127



128



Figs. 127–128. Phylogenetic relationships within Megapodini. **127.** Original hypothesis proposed by Papavero (1975). **128.** Phylogenetic re-analysis based on the characters of table 2 in Papavero (1975) summarized in appendix 2. The analysis in TNT results in three equally most parsimonious trees (length = 33; CI = 0.78; RI = 0.75) and shown is strict consensus of these three trees (length = 35; CI = 0.74; RI = 0.68). An outgroup was coded with state 0 for all characters to root the cladogram and is omitted here.

Deromyia form a clade (Cyrtophryina), *Megapoda* and *Pseudorus* form a clade (Megapodina), and all four taxa, including *Pegesimallus* (Lagodiina) and *Senobasis* (Senobasina), are unresolved in a polytomy.

7.7.1. MEGAPODINA CARRERA, 1949.

Genera included: *Megapoda*, *Pseudorus*. Autapomorphies: None. Additional apomorphic character states: Pharyngeal pump with entire sclerotized ring (40), anatergal setae absent (82), only regular setae on posterior meron and metanepisternum (85), setae on superoposterior anepimeron present (86), metkatepisternum large and visible between mesothoracic and metathoracic coxae in ventral view (100), prothoracic and mesothoracic coxae distinctly oriented posteriorly (109), only one dorsal longitudinal ridge on pulvilli (124), cell r_1 closed, R_1 and R_{2+3} as stalk vein present (131), R_4 terminating anterior to wing apex (143), male hypandrium well developed and rectangular or square in shape (199), male gonostyli positioned medially on gonocoxites (206), male dorsal aedeagal sheath long so that sperm sac is entirely enclosed (215).

7.7.2. CYRTOPHRYINA PAPAVERO, 1975.

Type genus *Cyrtophrys* Loew, 1851. Genera included: *Cyrtophrys*, *Deromyia*. Autapomorphies: None. Additional apomorphic character states: Lower facial margin slightly developed (4), pharyngeal pump with entire sclerotized ring (40), ventral metathoracic femora only setose, no macrosetae present (116), metathoracic tibiae arched medially (119), setiform empodium well developed (as long as claws) (127), alula reduced to small lobe (130), microtrichia on posterior wing margin arranged in two divergent planes (140). Papavero (1975) erected the taxon *Cyrtophryina* within his Megapodini for the two Neotropical genera, *Cyrtophrys* and *Deromyia*. The monophyly of this taxon is here corroborated.

7.7.3. LAGODIINA PAPAVERO, 1975.

Type genus *Lagodias* Loew, 1858 = *Pegesimallus* Loew, 1858. Genera included: *Pegesimallus*. Autapomorphies: None. Apomorphic character states: Mystax extending over lower facial half (7), setae on dorsal postpedicel absent (55), apical "seta-like" sensory element situated apically in cavity on stylus (57), stylus composed of one element (58), postsutural dorsocentral setae absent (94), metathoracic trochanter with macrosetae and setae medially (114), cell m_3 open (135), R_4 terminating posterior to wing apex (143), female with setae on T8 directed anteriorly (168), male with marginal setae on T2 (186), male lacking gonocoxal apodeme (204), male with cerci fused to a single sclerite (212), male dorsal aedeagal sheath strongly sclerotized, appearing entirely closed (217). *Pegesimallus* is the type genus of Lagodiina and the only representative as no other Dasypogoninae genus groups with it.

7.7.4. SENOBASINA PAPAVERO, 1975.

Type genus *Senobasis* Macquart, 1838. Genera included: *Senobasis*. Autapomorphies: None. Apomorphic character states: Lower facial margin slightly developed (4), two notopleural setae present (88), presutural dorsocentral setae present (92), only regular setae on metathoracic femora ventrally (no macrosetae) (116), metathoracic tibiae arched medially (119), setiform empodium well developed and as long as claws (127), dorsal surface of T2 smooth, without protuberances (154), female T10 composed of a single sclerite and entirely fused to T9 so that they are indistinguishable (172, 173), female spermathecal reservoir heavily sclerotized (181), male lateral ejaculatory process present and large cylindrical sclerite (213), male sperm sac appearing weakly sclerotized (218).

Unplaced genera: *Archilestris*, *Diogmites*, and *Lestomyia*. *Archilestris*, lacking a prothoracic tibial spine, is grouped within Stenopogoninae: Enigmomorphini by Artigas and Papavero (1991) and is here transferred to the Dasypogoninae, *Diogmites* is considered to be a Lastauracini (see above), and *Lestomyia* has been grouped within Dasypogonini by Papavero (1973b) (see above).

Phylogenetic relationships within Dasypogoninae: *Lestomyia* is the sister group to the remaining Dasypogoninae, which are characterized by the following apomorphic character states: 4: 4, 19: 2, 88: 3, 92: 0, 168: 1, 180: 1. The taxa Dasypogonini, Saropogonini, Thereutriini, Lastauracini and *Diogmites*, Blepharepiini, Molobratiini, and Megapodini form a grade of less inclusive sister taxa. The separate clades are delimited by a number of apomorphic character states, but no autapomorphies emerge from the present analysis.

8. STENOPOGONINAE

Stenopogoninae Hull, 1962. Type genus *Stenopogon* Loew, 1847. Species represented: 13. Figures 120–121, 124.

Autapomorphies: None. Additional apomorphic characters states: Facial swelling and mystax extending over lower facial half (4, 7), postmentum ventrally with median groove in distal part (19), all ommatidia same size (46), postpedicel cylindrical throughout (54), setae on anteroventral prothoracic tibiae absent (105), female spermathecal reservoir formed by more or less expanded and coiled ducts (180). Stenopogoninae sensu previous authors has been suspected to be non-monophyletic and used to be the largest taxon of Asilidae containing 118 genera (Geller-Grimm, 2004) of which 37 are included in the present analysis. It was divided into 10 subordinate taxa to accommodate this diversity in a meaningful way by previous authors. In the new delimitation of Stenopogoninae, only three of the subordinate taxa are recognized here and the remaining taxa are either placed as a higher-level taxon, i.e., Bathypogoninae, Phellinae, Tillobromatinae, and Willistonininae, or transferred to another higher-level taxon, i.e., Acronychini to Leptogastrinae, Ceraturgini and Cyrtopogonini to Brachyrhopalinae.

8.1. ENIGMOMORPHINI HULL, 1962.

Type genus *Enigmomorphus* Hermann, 1912. Genera included: *Connomyia*, *Creolestes*, *Daspletis*, *Microstylum*, *Prolepsis*. Autapomorphies: None. Additional apomorphic character states: Maxillary stipites fused medially, but V-shaped indentation present (14), maxillae proximally high and distal tip distinctly narrower (28), regular setae form discal scutellar setae (99), female spermathecae occupying at most three posterior segments (182). The Enigmomorphini was originally described by Hull (1962) to accommodate the Neotropical genus *Enigmomorphus* Hermann, 1912, and later expanded by Artigas and Papavero (1991) to include 14 genera. The New World genus Archilestris is transferred to the Dasypogoninae and the two Afrotropical genera *Connomyia* and *Daspletis* are transferred here to Enigmomorphini.

8.2. PLESIOMMATINI ARTIGAS AND PAPAVERO, 1991.

Type genus *Plesiomma* Macquart, 1838. Genera included: *Plesiomma*. Autapomorphies: None. Additional apomorphic character states: Vertex between compound eyes sharply depressed (3), facial swelling extending over entire face (4), mystax restricted to lower facial margin (7), dorsal flange medially on prementum absent (22), hypopharynx seta-like spicules spaced far apart (33; fig. 43), pharyngeal pump with entire sclerotized ring on lateral margin and circular in shape (40, 41), anterior tentorial pits well developed and conspicuous anteromedially located (44), frons at antennal insertion markedly approximating medially at level of antennal insertion (48), regular setae on lateral margin of frons dorsal to antennal insertion (no macrosetae) (49), regular setae forming postpronotum setae (no macrosetae) (70), scutellum small and mesopostnotum visible in dorsal view (97), apical scutellar setae absent (98), regular setae forming setation on ventral metathoracic femora (116), T2 longer than wide, but less than twice as long (153), female common spermathecal duct long, extending beyond tip of furca (177), male lateral ejaculatory process present and formed by a large cylindrical sclerite (213). The Plesiommatini was described by Artigas and Papavero (1991) to accommodate the three Neotropical genera *Cystoprosopa* (Hull, 1962), *Dapsilochaetus* (Hull, 1962), and *Plesiomma*.

8.3. STENOPOGONINI HULL, 1962.

Genera included: *Gonioscelis*, *Ospriocerus*, *Scleropogon*, *Stenopogon*. Autapomorphies: None. Additional apomorphic character states: Head circular, as wide as high, in anterior view (1; fig. 29), maxillary stipites divided medially (14), ventral margin of postmentum entirely smooth (19), dorsoposterior margin of cibarium with only one ridge connecting cornua and cornua not originating from ridge (35), cornua developed in anteroposterior orientation (37), prosternum and proepisternum separated and prosternum triangular with pointed dorsal tip (74), cell m_3 closed (135), R_{2+3} apex arching sharply anteriorly in 90° angle (142), male hypopygium not rotated (195). The Stenopogonini is restricted here to only those robber flies with a circular head and with the character combination mentioned above.

Unplaced genera: The two widespread genera *Ancylorhynchus* and *Scylaticus* are part of the Stenopogoninae and form a clade supported by the following apomorphic character states, i.e., 62: 1, 74: 2, 213: 3, but do not group with any other described subordinate taxon.

Phylogenetic relationships within Stenopogoninae: Plesiommatini is the sister taxon to Stenopogonini and this clade is supported by the following apomorphic character states: setae on dorsal postpedicel present (55), presutural dorsocentral setae absent (92), sperm sac appearing more or less heavily sclerotized (218). The three clades, Enigmomorphini, Plesiommatini + Stenopogonini, and *Ancylorhynchus* + *Scylaticus*, form an unresolved polytomy and no comments on their relationship can be made.

9. WILLISTONININAE, NEW STATUS

Willistonininae Artigas and Papavero, 1991. Type genus *Willistonina* Back, 1908. Species represented: 5. Figures 120–121, 125.

Autapomorphies: None. Additional apomorphic character states: Only lower facial margin slightly developed (4), prosternum and proepisternum separated, prosternum triangular and pointed dorsally (74; fig. 68), discal scutellar setae absent (99), setae on legs dorsoventrally flattened (also circular setae present) (103). The taxon Willistoninini was described by Artigas and Papavero (1991) for the single Nearctic genus *Willistonina*. It is here expanded to include the Afrotropical genera *Acnephalum* and *Trichoura*, the Afrotropical and Palaearctic genus *Sisyrnodytes*, and the Nearctic genus *Ablautus*. *Acnephalum* and *Sisyrnodytes* form a clade characterized by a number of apomorphic character states (3: 2, 7: 3, 22: 1, 58: 1, 65: 1, 201: 0). The sister group to this taxon is composed of the remaining genera, which are characterized by the following apomorphic character states: 25: 0, 32: 0, 64: 1, 112: 2. *Trichoura* and *Willistonina* form a clade supported by the following character states: 7: 0, 8: 1, 48: 1, 49: 1, 76: 0, 113: 1, 130: 1. Because of its position as the sister group to a larger clade I, Willistonininae is recognized here as a higher-level taxon.

10. DIOCTRIINAE

Dioctriinae Enderlein, 1936. Type genus *Dioctria* Meigen, 1803. Species represented: 9. Figures 120–121, 125.

Autapomorphies: None. Additional apomorphic character states: Maxillary stipites divided medially (14), ommatidia all same size (46), setae on dorsal postpedicel present (55), apical "seta-like" sensory element situated subapically laterally on stylus (57; fig. 55), cell cu*p* open (136; fig. 83), male hypandrium and epandrium not approximating, separated by gonocoxites (201), subepandrial sclerite with lateral protuberances (211). The Dioctriinae, originally described by Enderlein (1936), was not applied as a higher-level taxon until re-erected by Lehr (2001). It is here shown to be a distinct taxon from other Dasypogoninae and Stenopogoninae sensu previous authors in which Dioctriini has been placed (e.g., Hull, 1962; Adisoemarto and Wood, 1975; Artigas and Papavero, 1991).

10.1. DIOCTRIINI ENDERLEIN, 1936.

Genera included: *Dioctria*, *Eudioctria*, *Nannodioctria*. Autapomorphies: Metathoracic coxae with pointed, peglike protuberance anteriorly (113). Additional apomorphic character states: Macrosetae on lateral margin of frons (dorsal to antennal insertion) absent (49), male epandrium composed of a single sclerite, fused more or less entirely medially (197). *Dioctria* and *Nannodioctria* form a less inclusive clade and it is characterized by two autapomorphies, i.e., cross section of prementum of labium square proximally (18), postmentum of labium platelike and arched (20; fig. 35), as well as additional apomorphic character states (23: 2, 24: 1).

10.2. ECHTHODOPINI ADISOEMARTO AND WOOD, 1975.

Type genus *Echthodopa* Loew, 1866. Genera included: *Echthodopa*. Autapomorphies: None. Additional apomorphic character states: Mystax extending over lower facial half (7), sensory pit in distal maxillary palpomere present (12), antepronotum with macrosetae and setae (69), setae on superoposterior anepimeron present (86), macrosetae present on ventral metathoracic femora (116), female S8 platelike and slightly emarginate mediodistally (170), female spermathecal reservoir formed by more or less expanded and coiled ducts (180), male subepandrial sclerite without lateral protuberances (211), male lacking lateral ejaculatory process (213), male dorsal aedeagal sheath long and sperm sac entirely enclosed (215), male ventral median margin of dorsal aedeagal sheath strongly sclerotized and appearing entirely closed (217).

Unplaced genera: *Broticosia*, *Dicolonus*, *Myelaphus*. The Australian genus *Broticosia* is found here to be the sister taxon to the remaining Dioctriinae. *Dicolonus* is characterized by an autapomorphy, i.e., female S7 reduced in size (166), and by a number of additional apomorphic character states (4: 3, 7: 2, 75: 1, 82: 1, 122: 0, 182: 1, 197: 0). The genus *Myelaphus* is nested deeply within Dioctriinae here as has been suggested before by Hull (1962) and Adisoemarto and Wood (1975). Artigas and Papavero (1991) placed it in Stenopogoninae: Ceraturgini along with *Ceraturgus*, which is here considered to be a Brachyrhopalinae.

Phylogenetic relationships within Dioctriinae: *Broticosia* is the sister group to the remaining Dioctriinae, which are characterized by these apomorphic character states: 19: 1, 49: 1, 53: 1, 88: 3, 118: 2, 130: 1, 193: 4, 218: 1. *Dicolonus*, Echthodopini, *Myelaphus*, and Dioctriini form a grade of less inclusive sister taxa. The separate clades are delimited by a number of apomorphic character states, but no autapomorphies emerged from the present analysis. A phylogenetic analysis of Dioctriini and Echthodopini based on Nearctic species, where these taxa are most diverse, was published by Adisoemarto and Wood (1975). The present analysis contradicts some of the hypotheses postulated by Adisoemarto and Wood in that *Eudioctria* is considered here to be a Dioctriini as it groups with *Dioctria* and *Nannodioctria*, which are considered to be the only representatives of Dioctriini by Adisoemarto and Wood. The Echthodopini are not recovered as monophyletic here because *Dicolonus*, *Echthodopa*, and *Myelaphus* do not form a clade. This taxon is therefore restricted to its type genus *Echthodopa*.

11. LEPTOGASTRINAE

Leptogastrinae Schiner, 1862. Type genus *Leptogaster* Meigen, 1803. Species represented: 7. Figures 120–121, 125.

Autapomorphies: Abdominal T2 more than twice as long as wide (153), S2 divided medially into two equal halves, which are separated by fenestra (159). Additional apomorphic character states: Seta-like spicules on hypopharynx spaced far apart (33; fig. 43), ocellar setae absent (62), only regular setae form katatergal setae (83), presutural dorsocentral setae absent (92), lateral depression on prothoracic coxae absent (104), row of macrosetae on anterodorsal mesothoracic tibiae absent (110), proximal prothoracic and mesothoracic tarsomeres longer than following two tarsomeres combined (120, 121), pulvilli absent (123), claws fairly straight throughout (125), R_4 and R_5 more or less parallel (133; fig. 85), R_4 terminating posterior to wing apex (143; fig. 85), female spermathecal reservoir formed by more or less expanded ducts to sac-shaped reservoir (180), female spermathecal reservoir heavily sclerotized (181), male lateral ejaculatory process present, large cylindrical sclerite (213; fig. 101). The monophyly of Leptogastrinae has never been in question and is corroborated here by many character states. Hull (1962) included the genus *Acronyches* within Leptogastrinae, but this placement was not acknowledged by Martin (1968). As *Acronyches* is the sister taxon to the Leptogastrinae sensu previous authors and two autapomorphies characterize this clade, I include this genus in the newly delimited Leptogastrinae. The relationships within this taxon will not be discussed here in detail as a comprehensive generic-level phylogeny is currently in preparation (Dikow, unpublished).

11.1. ACRONYCHINI ARTIGAS AND PAPAVERO, 1991, NEW PLACEMENT.

Type genus *Acronyches* Williston, 1908. Genera included: *Acronyches*. Autapomorphies: None. Additional apomorphic character states: Vertex sharply depressed (3), frons markedly approximating medially at level of antennal insertion (48), metkatepisternum large and visible between mesothoracic and metathoracic tibiae (100), setiform empodium minute or entirely absent (127), microtrichia on posterior margin of wing arranged in two divergent planes (141), female S8 platelike and hypogynial valves separated (surrounded by membrane) (170), female furca divided into two lateral sclerites (184).

11.2. Leptogastrini Schiner, 1862.

Genera included: *Beameromyia*, *Euscelidia*, *Lasiocnemus*, *Leptogaster*, *Tipulogaster*. Autapomorphies: Postpronotal lobes extended medially and anteriorly and nearly touching medially (72; fig. 65), metathoracic coxae directed anteriorly (111), male with surstylus on epandrium (198; fig. 101), male with lateral process of gonostyli present (207; fig. 101). Additional apomorphic character states: Only lower facial margin developed (4), dorsoposterior margin of cibarium with one transverse ridge connecting cornua (35), cornua on cibarium well developed in anteroposterior orientation (37), postpedicel tapering distally (54), postpronotum setae absent (70), anterior anepisternal and proepimeral setae erect to appressed and anteriorly directed (78, 79), postmetacoxal bridge partly present laterally and membranous area medially (102), cell cu*p* open (136; fig. 85), female with short spermathecal ducts (178; fig. 99), male with gonocoxite or gonocoxite-hypandrial complex partially fused to epandrium (203; fig. 101), male lacking gonocoxal apodemes (204), male with sperm sac appearing more or less heavily sclerotized (218). The clade comprising *Lasiocnemus*, *Leptogaster*, and *Tipulogaster* is characterized by a single autapomorphy, i.e., only crossvein m-m closing cell d and M_1 branching of proximally (137; fig. 85), and additional apomorphic character states (177: 1, 199: 0, 202: 1).

12. Trigonomiminae

Trigonomiminae Enderlein, 1914. Type genus *Trigonomima* Enderlein, 1914. Species represented: 7. Figures 120–121, 125.

Autapomorphies: Anterior tentorial pits well developed and conspicuous anteroventrally located (44; fig. 26). Additional apomorphic character states: Apex of labella pointed (24), postocular setae formed by regular setae (no macrosetae) (66), prosternum and proepisternum fused, prosternum narrow above prothoracic coxae (74), supra-alar setae absent (90), female spermathecae occupying more than posterior three abdominal segments (182). The monophyly of Trigonomiminae has not been questioned previously due to the distinct appearance of these flies that are often referred to as "goggle-eyed" robber flies.

12.1. Trigonomimini Enderlein, 1914.

Genera included: *Holcocephala*, *Rhipidocephala*, *Trigonomima*. Autapomorphies: None. Additional apomorphic character states: Setae on dorsal postpedicel present (55), apical scutellar setae absent (98), T1 divided medially by membraneous area (152). *Rhipidocephala* is characterized by a single autapomorphy, i.e., female with S8 platelike and the distal margin is medially membraneous (170), and additional apomorphic character states (11: 1, 24: 2, 57: 3, 116: 1, 121: 1, 136: 0, 199: 1, 202: 1). *Holcocephala* is characterized by a single autapomorphy, i.e., face divided into a distinct ventral and dorsal half (5), and additional apomorphic character states (18: 2, 92: 0, 94: 0, 122: 0, 193: 4, 197: 2, 206: 1). *Rhipidocephala* is the sister group to the clade *Holcocephala* + *Trigonomima*, which is characterized by these apomorphic character states: 3: 2, 133: 0, 92: 0, 94: 0, 122: 0, 193: 4, 197: 2, 208: 1.

12.2. Xenomyzini Hardy, 1948.

Type genus *Xenomyza* Wiedemann, 1817 = *Damalis* Fabricius, 1805. Genera included: *Damalis*. Autapomorphies: Postpedicel with proximal bulb and distal elongated part (54; fig. 56). Additional apomorphic character states: Antennal stylus reduced to apical "seta-like" sensory element, which is situated subapically in cavity on postpedicel (57, 58; fig. 56), postpronotal setae absent (73), metathoracic trochanter medially with posteriorly directed protuberance (115), short, stout, cone-shaped macrosetae ventrally on metathoracic femora (116), costa terminates at CuA_2 and A_1 (140), female with abdominal T10 lost or fused to cerci (172), male hypopygium rotated (195), male epandrium formed by a single sclerite (197), male lacking gonocoxal apodeme (204), as well as 18: 2, 114: 2, 137: 2, 138: 1. The two Afrotropical species *Damalis annulata* and *D. monochaetes* are the sister taxa to the Oriental *Damalis* sp. (Palatupana) and this Afrotropical clade is characterized by the lack of discal scutellar setae (99) and the short proximal prothoracic tarsomere, which is shorter than the two following tarsomeres combined (122).

Phylogenetic relationships within Trigonomiminae: Trigonomimini and Xenomyzini are adelphotaxa and all genera included in the present analysis are assigned to a subordinate taxon.

13. STICHOPOGONINAE

Stichopogoninae Hardy, 1930. Type genus *Stichopogon* Loew, 1847. Species represented: 7. Figures 120–121, 126.

Autapomorphies: Posterior margin of compound eyes distinctly sinuate in ventral half (64; fig. 60). Additional apomorphic character states: Maxillary stipites divided medially (14; fig. 33), cornua on cibarium well developed in anteroposterior orientation (37), frons markedly and suddenly diverging laterally at level of antennal insertion (48; fig. 27), prosternum and proepisternum fused and prosternum broad above prothoracic coxae (74; fig. 66), anterior anepisternal setae absent (78), discal scutellar setae absent (99), proximal metathoracic tarsomere shorter than two following tarsomeres combined (122), female S8 platelike and hypogynial valves separated (surrounded by membrane) (170; fig. 97), male gonocoxites fused to hypandrium (202), male ventral margin of dorsal aedeagal sheath strongly sclerotized (appearing entirely closed) (217). The monophyly of Stichopogoninae has never been in doubt and has been recently corroborated by a phylogenetic analysis by Cannings (2002).

13.1. STICHOPOGONINI HARDY, 1930.

Genera included: *Lissoteles*, *Stichopogon*. Autapomorphies: Male hypandrium and epandrium fused and connected by a narrow sclerite proximally (201; fig. 112), male subepandrial sclerite with short, stout macrosetae on the distal margin ventrally (209). Additional apomorphic character states: Mystacal setae tightly packed and forming a distinct shield (8), postpedicel tapering distally (54), one seta forming notopleural setae (88), medial setae on posterior scutum erect and directed dorsally to anteriorly (96), setae on anteroventral prothoracic tibiae absent (105), prothoracic and mesothoracic coxae directed distinctly posteriorly (109), blunt protuberance on anterior metathoracic coxae (113), male cerci fused to a single sclerite (212).

Phylogenetic relationships within Stichopogoninae: The genera *Lasiopogon* and *Townsendia* are not placed in any subordinate taxon. *Lasiopogon* is the sister group to the remaining Stichopogoninae and characterized by an autapomorphy, i.e., male subepandrial sclerite with short, stout macrosetae on its entire ventral surface (210), and additional apomorphic character states (7: 2, 46: 0, 55: 1, 98: 2, 143: 1, 181: 1, 195: 1). *Townsendia* is the sister taxon to Stichopogonini and the clade combining both taxa is characterized by a number of apomorphic character states (4: 1, 75: 1, 114: 2, 197: 0, 213: 0, 215: 1). *Townsendia* is excluded from Stichopogonini because it lacks the two autapomorphies of *Lissoteles* and *Stichopogon* and the taxon sampling within this group is very small. Cannings (2002) postulated a phylogeny of Stichopogoninae based on eight genera. The main findings are corroborated by the present analysis. In both studies *Lasiopogon* is found to be the sister group to the remaining Stichopogoninae and *Lissoteles* and *Stichopogon* are most closely related. In fact, *Lissoteles* renders *Stichopogon* paraphyletic in the present analysis, but because of the limited taxon sampling, this finding should not be taken as conclusive evidence for the non-monophyly of *Stichopogon*. Martin (1961), in revising *Lissoteles*, mentioned that both genera are morphologically very similar.

14. BRACHYRHOPALINAE, NEW STATUS

Brachyrhopalinae Hardy, 1926. Type genus *Brachyrhopala* Macquart, 1847. Species represented: 18. Figures 120–121, 126.

Autapomorphies: None. Additional apomorphic character states: Stylus composed of two elements (58), proximal prothoracic tarsomere longer than following two tarsomeres combined (120), alula reduced in size to small lobe (130), R_4 and R_5 more or less parallel (133). The species here summarized within Brachyrhopalinae are the remnant of the Dasypogoninae and Stenopogoninae sensu previous authors. It is a large clade that is not delimited by many unique apomorphic character states. Future phylogenetic studies will hopefully improve the delimitation of this taxon by including additional species that are morphologically similar to the Brachyrhopalinae representatives used here. From the valid and available family-group names represented in this clade, the name Brachyrhopalinae Hardy, 1926, with the type genus *Brachyrhopala* from Australia, is the oldest name and is chosen here to name this taxon.

14.1. CYRTOPOGONINI ARTIGAS AND PAPAVERO, 1991, NEW PLACEMENT.

Type genus *Cyrtopogon* Loew, 1847. Genera included: *Afroholopogon*, *Cyrtopogon*, *Dasycyrton*. Autapomorphies: None. Additional apomorphic character states: Female T8 with anterior rectangular apodeme, which is entirely fused to the tergite (169; fig. 87), female spermathecal reservoir formed by more or less expanded and coiled ducts (180). The Cyrtopogonini was described by Artigas and Papavero (1991) within their Stenopogoninae for 20 genera. Of these, only *Cyrtopogon* and *Dasycyrton* are recovered within this clade and *Afroholopogon* is referred to this taxon. Other genera originally included by Artigas and Papavero and also part of the present analysis are now found within Brachyrhopalinae, i.e., *Heteropogon*, *Holopogon*, *Metapogon*, *Nannocyrtopogon*, and *Rhabdogaster*, or transferred to other higher-level taxa, i.e., *Ablautus* to Willistonininae.

14.2. CHRYSOPOGONINI HARDY, 1934, NEW PLACEMENT.

Type genus *Chrysopogon* von Röder, 1881. Genera included: *Chrysopogon*, *Codula*. Autapomorphies: Single, short, stout macroseta forms notopleural seta (88), cuticular facets on proximal metathoracic femora (117). Additional apomorphic character states: Prementum of labium laterally compressed (18), labellae of labium reduced and fused entirely to prementum (23), supra-alar, postalar, and presutural dorsocentral setae absent (90, 91, 92), alula well developed (130), abdominal tergites indented and setae with large sockets (151), female S8 proximally platelike and hypogynial valves forming a keel distally (170), female with T9–10 separated (not fused) (173), female without spurs on the ovipositor (174), female spermathecal reservoir formed by more or less expanded and coiled ducts (180), female furcal apodeme present and long (185). This exclusively Australian taxon was described by Hardy (1934) and was extensively reviewed by Clements (1985). Originally it included only the genera *Chrysopogon*, *Codula*, and *Opseostlengis*, but Hull (1962) later transferred *Chryseutria* to this taxon. The genus *Codula* was placed in the Stenopogoninae sensu previous authors in contrast to *Chrysopogon*, which was placed in Dasypogoninae sensu previous authors, in the most recent generic catalogue (Geller-Grimm, 2004) based on the absence of a prothoracic tibial spine. The close relationship between these two genera is supported here by autapomorphies and the placement of *Codula* within Chrysopogonini is without doubt.

14.3. BRACHYRHOPALINI HARDY, 1926, NEW PLACEMENT.

Type genus *Brachyrhopala* Macquart, 1847. Genera included: *Austrosaropogon*, *Brachyrhopala*, *Cabasa*. Autapomorphies: None. Additional apomorphic characters states: Lower facial margin slightly developed (4), discal scutellar setae absent (99). The Brachyrhopalini was described by Hardy (1926) for the only genus Brachyrhopala although he considered *Cabasa* to be a junior synonym of *Brachyrhopala*. It is expanded here to include *Austrosaropogon*.

14.4. CERATURGINI ARTIGAS AND PAPAVERO, 1991, NEW PLACEMENT.

Type genus *Ceraturgus* Wiedemann, 1821. Genera included: *Ceraturgus*, *Nannocyrtopogon*. Autapomorphies: None. Additional apomorphic character states: Facial swelling extending over lower facial three quarters (7), hypopharynx parallel-sided throughout and distal tip suddenly pointed (32), regular setae form katatergal setae (83), male hypopygium rotated (195), male cerci fused to single sclerite (212), male sperm sac appearing more or less heavily sclerotized (218). The Ceraturgini was described by Artigas and Papavero (1991) for the two genera *Ceraturgus* and *Myelaphus*. *Myelaphus* is transferred here to the Dioctriinae and *Nannocyrtopogon*, which is placed in Cyrtopogonini by Artigas and Papavero (1991), is placed in Ceraturgini here.

Additional genera of Brachyrhopalinae that do not group with any of the abovementioned family-group taxa are: *Cophura*, *Heteropogon*, *Holopogon*, *Leptarthrus*, *Metapogon*, *Nicocles*, *Rhabdogaster*. *Heteropogon*, *Holopogon*, *Metapogon*, and *Rhabdogaster* were placed in Cyrtopogonini by previous authors, but do not group with *Cyrtopogon* in the present analysis. *Cophura*, *Leptarthrus*, and *Nicocles* were placed in the unavailable Isopogonini within Dasypogoninae by Papavero (1973b) based on the possession of an S-shaped spur on the prothoracic tibiae. These genera do not form a monophyletic clade in the present analysis and therefore a taxon cannot be recognized and I do not provide a new family-group name to replace the unavailable name. Although the genera *Holopogon* and *Leptarthrus* as well as *Cophura*, *Heteropogon*, *Metapogon*, *Nicocles*, and *Rhabdogaster* form clades, respectively, I do not propose any new family-group names for these taxa as I believe a more detailed study focusing on morphologically similar species will shed new light on the phylogenetic relationships within Brachyrhopalinae.

Phylogenetic relationships within Brachyrhopalinae: Cyrtopogonini is the sister group to the remaining Brachyrhopalinae and this clade is characterized by a number of apomorphic character states (22: 1, 32: 1, 83: 1). *Holopogon* and *Leptarthrus* form a clade delimited by these apomorphic character states: 7: 3, 90: 0, 168: 1, 181: 0, 201: 2. A clade comprising Brachyrhopalini, Ceraturgini, Chrysopogonini, and a number of unplaced genera is the sister group to *Holopogon* and *Leptarthrus* and characterized by two apomorphic character states (78: 0, 136: 0). Brachyrhopalini and Chrysopogonini form a clade delimited by a number of apomorphic character states (25: 1, 58: 3, 137: 2, 168: 0, 197: 0, 199: 0, 202: 1) that is restricted to Australia and its sister taxon is characterized by these apomorphic character states: 19: 1, 26: 0, 62: 2, 169: 1. Ceraturgini is the sister group to a clade comprising the five unplaced genera, which are united by a single apomorphic character state, i.e., female spermathecae occupying more than posterior three segments (182).

INCERTAE SEDIS

The two genera *Coleomyia* and *Oligopogon* could not be placed in any of the higher-level taxa and no family-group names are available for them. *Coleomyia* was placed in the Stenopogoninae: Tillobromatini sensu Artigas and Papavero (1991) and Geller-Grimm (2004), but it is not recovered within either taxon and is placed in an unresolved trichotomy with Dasypogoninae and Stenopogoninae. *Oligopogon* is placed as sister taxon to a large clade composed of Brachyrhopalinae, Dioctriinae, Leptogastrinae, Stichopogoninae, and Trigonomiminae. It had been placed in Stenopogoninae and Trigonomiminae before (see Geller-Grimm and Hradský, 2003, for a summary).

The following monogeneric family-group taxa Archilaphriinae (*Archilaphria*), Dasylechiini (*Dasylechia*), and Neophoneini (*Neophoneus*) are not represented in the present analysis and no comment on their phylogenetic relationships can be made. *Archilaphria* was placed within Dasypogoninae sensu previous authors and *Dasylechia* and *Neophoneus* in Laphriinae (Papavero, 1973a; Geller-Grimm, 2004).

PHYLOGENETIC RELATIONSHIPS OF HIGHER-LEVEL TAXA WITHIN ASILIDAE
Figure 120

The most outstanding discovery of the present extensive morphological phylogenetic study is the hypothesis that Laphriinae is the sister taxon to the remaining Asilidae. This relationship has never before been suggested and Laphriinae is generally assumed to be phylogenetically derived Asilidae. Morphologically, however, Laphriinae shares a number of symplesiomorphies with Asiloidea outgroup taxa. In most Asilidae, the prothoracic and mesothoracic coxae are oriented ventrally, which probably facilitates the specialized capture and grasping position of prey items directly underneath the thorax. In Laphriinae except Atomosiini and outgroup taxa, the pro- and mesothoracic coxae are oriented posteriorly, which is the plesiomorphic character state within Asilidae. This state is also found in a few robber-fly species phylogenetically unrelated to Laphriinae. Another interesting character in Laphriinae pertains to the male terminalia. Yeates (1994) and Sinclair et al. (1994) independently proposed the proximal connection of the epandrium and hypandrium as a possible autapomorphy of Asilidae because it is found in most assassin flies. Both studies considered only a small representation of Asilidae, and species of Laphriinae were not represented. In Laphriinae, the hypandrium is generally very small, or even absent, and therefore not connected proximally to the epandrium (figs. 102, 108–109). This condition is homologous to the state found in the included Asiloidea outgroup taxa. Therefore, this character state is autapomorphic for a less inclusive taxon within Asilidae indicated as taxon A in figures 120–121. This clade is characterized by the following apomorphic character states: prosternum and proepisternum separated and the prosternum is square to rectangular and straight dorsally (character 74; fig. 69), prothoracic and mesothoracic coxae more or less directed ventrally (sometimes even anteriorly) (109; fig. 61), female furcal apodeme present, long and platelike in shape (185), hypandrium and epandrium approximating, but not fused proximally (201; fig. 113).

The Asilinae and Ommatiinae form a sister-group relationship (clade B) based on the following apomorphic character states: maxillary stipites fused medially, but V-shaped indentation present (14), tip of maxillae blunt (29; fig. 31), setae on posterior basalare present (81), setae on superoposterior anepimeron present (86), metkatepisternal setae present (101), female spermathecal reservoir not differentiated from spermathecal ducts (180), female spermathecal reservoir weakly sclerotized (181), male hypandrium well developed and rectangular or square (199; figs. 106, 113), male lateral ejaculatory process absent (213; fig. 114). Previous authors have assumed the two taxa were closely related due to their overall morphological similarity (Karl, 1959; Hull, 1962; Papavero, 1973a; Lehr, 1969, 1996).

Taxon C, i.e., Asilidae with the exception of Asilinae, Laphriinae, and Ommatiinae, is characterized by these apomorphic character states: vertex only slightly depressed (3; fig. 27), facial swelling and mystax extending over lower three quarters (4, 7), postpedicel medially broadest and long (54; fig. 52), setae on female T8 with erect setae (168), female S8 platelike with hypogynial valves extending (170), female T10 with acanthophorite spurs (174; figs. 87, 91), male sperm sac entirely free and sheath short (215; fig. 115), male aedeagal sheath weakly sclerotized ventrally and appearing incompletely closed (217; fig. 115). The next inclusive taxon D is characterized by these apomorphic character states: hypopharynx parallel-sided in proximal half and distal half much narrower (32; fig. 41), pharyngeal pump without sclerotized ring laterally (40), metathoracic coxae with regular setae laterally (no macrosetae) (112), female T9 and T10 only partly fused (173). Taxon E is characterized by the following apomorphic character states: sensory pit in distal maxillary palpomere present (12), anterior ommatidia all same size (46), cell m_3 open (135), female furcal apodeme short and platelike (185), male hypandrium and gonocoxites entirely free (202).

Dasypogoninae, Stenopogoninae, Tillobromatinae, and the unplaced genus *Coleomyia* form a clade (taxon F) characterized by the following apomorphic character states: dorsal flange on prementum of labium present (22), apical "seta-like" sensory element situated apically in cavity on stylus (57), cell cu*p* open (136), male hypopygium rotated (195), male cerci fused to a single sclerite (212). Tillobromatinae is the sister group to the remaining two taxa plus *Coleomyia* (taxon G), which is characterized by the presence of macrosetae and setae on the postpronotum (70), postpronotal lobes with macrosetae and setae (73), anterior anepisternal setae absent (78), discal scutellar setae absent (99), lateral metathoracic coxae with macrosetae and setae (112). Dasypogoninae, Stenopogoninae and *Coleomyia* are part of an unresolved polytomy and the phylogenetic relationships and placement of *Coleomyia* need to be addressed with a denser taxon and character sampling informative for this particular group.

Clade H is characterized by prothoracic and mesothoracic tarsomeres shorter than following two tarsomeres combined (120, 121), discal cell closed by M_2 and m-m in a single line (137). Taxon I includes the unplaced genus *Oligopogon*, and clade J and is characterized by the following apomorphic character states: pharyngeal pump laterally with sclerotized ring, but medio-anteriorly unsclerotized (40; fig. 49), metathoracic trochanter medially with regular setae (no macrosetae) (114), setiform empodium reduced in length to varying degree (127), alula reduced entirely so that the wing margin is nearly straight (130; fig. 85). *Oligopogon* is the sister taxon to a larger clade J, which is delimited by: mystax restricted to lower facial margin (7), hypopharynx parallel-sided throughout and only distal tip suddenly pointed (32; figs. 39–40), ocellar setae formed by regular setae (no macrosetae) (62), antepronotum with regular setae (no macrosetae) (69), apical scutellar setae formed by regular setae (no macrosetae) (98). This clade includes four taxa previously thought to be monophyletic as well as the Brachyrhopalinae, which is a clade in which several genera previously assigned to Dasypogoninae and Stenopogoninae sensu previous authors are united.

Taxon K, which comprises Dioctriinae, Leptogastrinae, and Trigonomiminae, has never been postulated before, but is here supported by the following apomorphic character states: facial swelling extending over lower facial half (4), female T8 with posteriorly directed setae (168), female T9 and T10 entirely fused, not discernible (173), female T10 without acanthophorite spurs (174). Leptogastrinae and Trigonomiminae together form the sister group (taxon L) of Dioctriinae and are delimited by these apomorphic character states: maxillary palpus one-segmented (11), female S8 platelike and slightly emarginate mediodistally (170), male hypandrium reduced or not differentiated (199), male gonocoxite and hypandrium fused to form a gonocoxite-hypandrial complex (202).

The sister group to taxon K is a clade comprising Brachyrhopalinae and Stichopogoninae (taxon M). This taxon is only supported by a single apomorphic character state, i.e., maxillae (in lateral view) proximally high and distal tip distinctly narrow (28; fig. 38), and future studies with an increased taxon sampling particularly within the Brachyrhopalinae will hopefully provide more substantial morphological support.

DISCUSSION

PREVIOUS VERSUS THE PRESENT PHYLOGENETIC HYPOTHESIS FOR ASILIDAE

As outlined in the introduction, Hull's (1962) and Papavero's (1973a) classifications and postulated diagrams of relationships are not phylogenetic in nature and cannot be compared to the present cladistic hypothesis. Karl's (1959; fig. 129) study is phylogenetic, but the limited taxon sampling especially in his "übrige Dasypogoninae," which entails a significant number of species, makes a meaningful comparison difficult. Karl does not include Atomosiini in Laphriinae nor *Lasiopogon* in Stichopogoninae in contrast to the findings of the present study. The Leptogastrinae and Trigonomiminae (his "*Damalis* Gruppe") are unresolved within Asilidae and do not form a monophyletic clade as postulated here. Karl pointed out, though, that Asilinae and Ommatiinae are sister taxa and Laphriini and Hoplistomerini are closely related, findings that have been corroborated here. The re-analysis of the character matrix provided by Karl (1959: fig. 47) results in a single most parsimonious tree (length = 26; CI = 0.69; RI = 0.78; fig. 129, appendix 3). The topology is identical to the one illustrated by Karl in his figure 49, however, those relationships labeled as questionable by Karl are resolved. In summary, a clade Asilinae and Ommatiinae is the sister taxon to Leptogastrinae, *Damalis* is the sister group to Laphriinae (including Atomosia, Hoplistomerini, and Laphriini), and *Lasiopogon* and *Stichopogon* do not form a monophyletic clade.

The only phylogenetic analysis of Asilidae representing most of the higher-level taxa sensu previous authors is the molecular study published by Bybee et al. (2004; fig. 130). The results are limited in their applicability

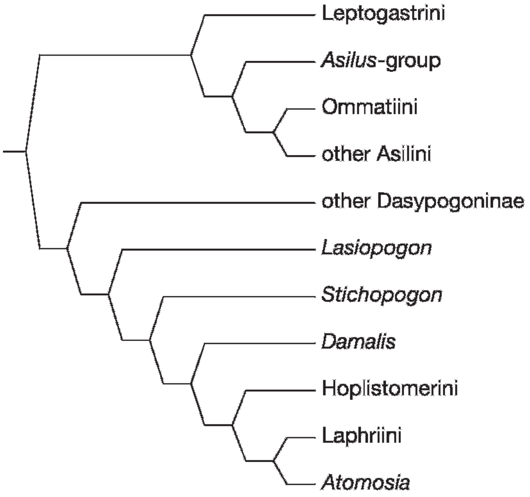


Fig. 129. Phylogenetic re-analysis of relationships of Asilidae based on the characters of figure 47 in Karl (1959) and summarized in appendix 3. The analysis in TNT results in a single most parsimonious tree (length = 26; CI = 0.69; RI = 0.78). An outgroup was coded with state 0 for all characters to root the cladogram and is omitted here.

because the analysis is based only on 26 Asilidae species and Ommatiinae, Stichopogoninae, Trigonomiminae, as well as Laphystiinae sensu previous authors are represented by only a single species, so that their monophyly could not be tested. However, the results can be compared to the present morphological study. Bybee et al. (2004) published two cladograms, one based on parsimony as the optimality criterion and the other based on maximum likelihood, without stating which is the preferred hypothesis. Although both hypotheses depict somewhat similar relationships there are differences in the position of certain species. I will base my discussion solely on the parsimony results (Bybee et al., 2004: fig. 3), which is illustrated in fig. 130, as the present morphological analysis is also based on this optimality criterion.

The most striking difference between the phylogenetic hypothesis postulated here and the hypothesis of Bybee et al. (2004) is the position of the Leptogastrinae (figs. 120, 130). When Martin (1968) elevated the Leptogastrinae to family status, he regarded them as the sister group to Asilidae. This hypothesis is followed by Papavero (1973a), who excluded these slender flies from his exhaustive review of the Asilidae of the world. Oldroyd (1969), on the other hand, refuted Martin's study and emphasized that Leptogastrinae should be retained in Asilidae, although his arguments are not based on phylogenetic considerations. In the molecular study by Bybee et al. (2004), the Leptogastrinae groups as the sister taxon to the remaining Asilidae, which would support Martin's view and potentially allow for the separation of Leptogastrinae as a separate family taxon. However, in the present extensive morphological phylogeny, the Leptogastrinae is positioned deeply within Asilidae as sister taxon to the Trigonomiminae. I have much more confidence in the present grouping as a suite of apomorphic character states

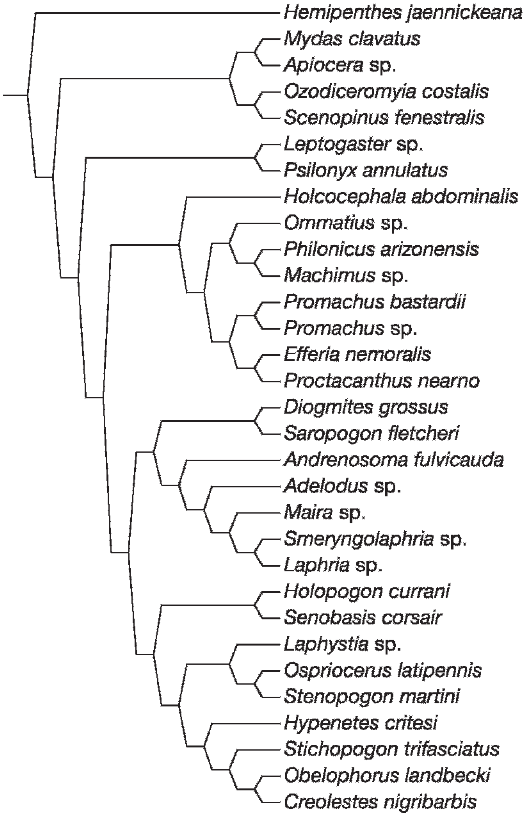


Fig. 130. Previously published phylogenetic hypothesis of Asilidae by Bybee et al. (2004: fig. 3) based on parsimony analysis under direct optimization in POY of 16S, 18S, and 28S rDNA and COII DNA sequences.

supports this hypothesis (fig. 120). Additionally, my own combined analysis of the morphological matrix presented here and DNA sequence data of five nuclear genes also supports a grouping of Leptogastrinae deeply within Asilidae (Dikow, submitted).

The higher-level relationships within Asilidae postulated by Bybee et al. (2004) are in general very different from the present hypothesis as is the monophyly or non-monophyly of certain higher-level taxa. Laphriinae is supported as monophyletic in the molecular study, but the genus *Laphystia* is not placed close to this group, and is considered the sister group to Stenopogonini. In the present study the Laphriinae sensu previous authors is also supported as monophyletic, but *Laphystia* is closely related to it and is part of the revised taxon Laphriinae. Apocleinae and Asilinae sensu previous authors are found to be paraphyletic with respect to each other in the present analysis, but are supported as monophyletic by Bybee et al. Furthermore, Ommatiinae is more closely related to Asilinae sensu previous authors in the molecular analysis, in contrast to it being the sister group to the revised Asilinae including the Apocleinae sensu previous authors as supported here. The Dasypogoninae is considered non-monophyletic in the molecular study, but the three genera included by Bybee et al., *Diogmites*, *Saropogon*, and *Senobasis*, are part of the Dasypogoninae sensu stricto in the present morphological study. The Stenopogoninae sensu previous authors is non-monophyletic in Bybee et al. and representatives appear in four different clades. The grouping *Creolestes* and *Obelophorus* as a clade is at odds with the findings of the present study, in which these two genera are placed in separate and phylogenetically unrelated higher-level taxa, i.e., *Creolestes* in Stenopogoninae: Enigmomorphini and *Obelophorus* in Phellinae. One must conclude that a DNA sequence study based on limited exemplars of a hyperdiverse insect taxon is a misguided exercise.

BIOLOGY OF ASILIDAE

The newly proposed hypothesis that the Laphriinae constitutes the sister group to the remaining Asilidae makes a discussion of some biological phenomena possible. Larvae of Asilidae were described very early (see summary in Melin, 1923), but to date we know larvae of only a very few species and have limited knowledge of larval morphology and habitats. The most commonly encountered larvae of robber flies are those of *Laphria* and relatives, which are found within decaying wood in forest habitats where the majority of Laphriinae sensu previous authors occur. Based on this knowledge, one could assume that all larvae of Laphriinae develop in wood in contrast to all other known robber-fly larvae, which have been observed to develop in soil and sandy habitats (e.g., Melin, 1923; Fisher, in press). The new delimitation of Laphriinae includes all of those species previously assigned to Laphystiinae of which a single species is known in the larval stage. The larva of *Laphystia carnea* Hermann, 1906, was described by Krivosheina (1973) from Turkmenistan and, in contrast to other Laphriinae, the larva develops in sandy loam. Among the outgroup taxa, some Mydidae larvae are known to occur in wood whereas others, together with all Apioceridae larvae described so far, develop in sandy soil (e.g., Wilcox, 1981; Peterson, 1981). With this limited knowledge about larvae, one cannot, at this stage, postulate whether soil or wood is the ancestral larval habitat for Asilidae.

A similar scenario can be envisioned for the evolution of mimicry within Asilidae. Many Laphriinae species closely resemble various Aculeata bees and wasps (Hymenoptera). The earliest studies on mimicry in Asilidae were published by Brauer (1885) and Poulton (1904), who summarized some of the early observations by naturalists, and later Melin (1923) considered the problem in more detail. As Batesian mimics, robber flies can avoid predators such as birds. Furthermore, assassin flies that resemble their prey species can approach their prey items without being detected as was observed by Poulton (1904) or remain unnoticed at their perching site (Grimaldi and Engel, 2005). Many Laphriinae have been shown to feed on Aculeata although not exclusively (e.g., Londt, 1995, 2006b) as the majority of assassin flies are not specialized hunters. Mimicry of Hymenoptera is not restricted to Laphriinae, though, as some genera included in the present analysis, e.g., *Megaphorus* (Asilinae), *Blepharepium* and *Diogmites* (Dasypogoninae), and *Ospriocerus* (Stenopogoninae), have been observed to mimic Aculeata in Arizona and New Mexico (Linsley, 1960). Poulton (1904) observed *Dasypogon diadema* (Dasypogoninae) mimicking *Anoplius viaticus* Linnaeus, 1758 (as *Pompilus*; Pompilidae), in Europe. Enderlein (1914) described three genera, i.e., *Ammophilomima*, *Ophionomima* (both Leptogastrinae), and *Trigonomima* (Trigonomiminae), and named them based on the hypothesis that they mimic species of *Ammophila* Kirby, 1798 (Sphecidae), *Ophion* Fabricius, 1798 (Ichneumonidae), and *Trigona* Jurine, 1807 (Apidae), respectively. Londt (1991) described a bee-mimicking genus from southern Namibia in yet another clade, i.e., Stenopogoninae sensu previous authors. Some Mydidae, e.g., *Mydas clavatus* and *Opomydas townsendi* included in the present study, resemble Pompilidae and Vespidae wasps, respectively. Hesse (1969) described Vespiodes from southern Africa and highlighted the observation that species of this genus together with *Mydaselpis* Bezzi, 1924 (Syllegomydinae), resemble Vespidae wasps in this biodiverse region of Africa. In the arid southwestern United States and adjacent Mexico a robber fly, *Wyliea mydas* (Brauer, 1885) (Asilinae), and similar species of *Mydas* Fabricius, 1794, both mimic sympatrically occurring *Pepsis* Fabricius, 1804, wasps (Pompilidae) with an entirely black body and bright orange-red wings (Brauer, 1885). In contrast, *Apiocera* species are not known to mimic any other distasteful or dangerous insects. Based on the phylogenetic relationships of the above-mentioned taxa, one can postulate with certainty that mimicry has evolved independently several times within Asilidae. Only a more thorough study of Batesian mimicry of Asilidae and Mydidae species and a more comprehensive phylogenetic study including many more assassin-fly species can shed light on the question.

Biogeographical Implications

Although many of the higher-level taxa proposed previously and corroborated here are worldwide in distribution, some of the clades are biogeographically restricted (fig. 131). Laphriinae, the sister taxon to the remaining Asilidae, is worldwide in distribution as are Asilinae, Dasypogoninae, Leptogastrinae, Ommatiinae, Trigonomiminae, Stenopogoninae, and Stichopogoninae (figs. 120, 131). The extant representatives of Bathypogoninae, the sister group to a large clade D, are restricted to Australia (and possibly South America) and representatives of Phellinae, sister group to clade E, occur only in Australia and Chile (figs. 120, 131). Extant Tillobromatinae are found in southern Africa and South America whereas Willistonininae is distributed in the Afrotropical and Nearctic regions and *Sisyrnodytes* also occurs in the Palaearctic Region (figs. 120, 131). Dioctriinae are most speciose in the Northern Hemisphere, but *Broticosia*, the sister taxon to the remaining Dioctriinae, is found only in Australia (figs. 121, 131). Brachyrhopalinae is found throughout the world, but the Brachyrhopalini and Chrysopogonini are restricted to Australia (figs. 121, 131). Although I attempted to include representatives from all zoogeographical regions the Oriental Region is certainly underrepresented. This is partly due to the lack of well-organized collections from which specimens can be borrowed, but also due to the lack of expertise and interest in this particular fauna. Perhaps most interesting is the repeated restriction of adelphotaxa to hyperdiverse radiations to areas in the Southern Hemisphere, especially Australia and southern South America, i.e., Bathypogoninae, Phellinae, and Tillobromatinae (figs. 120, 131).

Some Morphological Characters Revisited

Not all of the autapomorphies previously postulated for Asilidae by Hennig (1973) and Woodley (1989) could be corroborated in the present analysis. Hennig (1973) attributed a proximally constricted abdomen to Hull (1962), but I am unable to find any reference to this feature in Hull's publication. This character does not hold up as autapomorphic because in most Asilidae T2–3 are more or less square or rectangular, and only in a few species of Brachyrhopalinae, Dasypogoninae, Dioctriinae, Laphriinae, and Ommatiinae is the abdomen constricted, or waistlike (see character 156). Hennig (1973) also postulated densely bristled raptorial legs as autapomorphic for Asilidae, and although many species possess macrosetae on the legs, they could not be coded as such because the setal positions vary greatly among the species, making homologizing them difficult. Only a row of macrosetae on the anterodorsal mesothoracic tibia is coded here (see character 110) because it is found in most Asilidae. However, these setae are also present in most outgroup taxa and therefore not autapomorphic for assassin flies.

Oldroyd (1974a) and Woodley (1989) postulated the presence of the mystax as an autapomorphy, and in the present analysis it is absent in only *Pseudorus distendens* (Dasypogoninae) among Asilidae. However, macrosetae are also present on the face of Mydidae, as mentioned by Hardy (1927a) and Woodley (1989) although neither author homologized these setae with the ones in robber flies. I code them to be homologous as they are found at the same position on the head and cannot be separated otherwise (see character 6). The character optimization for the mystax is ambiguous at the root of the Asilidae and there are three equally parsimonious explanations for the character transformation. As the mystacal setae are absent in Apioceridae, *Neorhaphiomidas* (Mydidae), and *Pseudorus*, they could have originated (1) in the most recent common ancestor of Asilidae + (Apioceridae + Mydidae) and then become lost independently in Apioceridae, *Neorhaphiomidas*, and *Pseudorus* (4 steps, fast optimization), (2) independently in Asilidae and Mydidae and are reduced once in each of these taxa (4 steps, slow optimization), or (3) independently in *Rhaphiomidas*, in Mydidae except *Neorhaphiomidas* and *Rhaphiomidas*, and Asilidae and are reduced in *Pseudorus* (4 steps, unambiguous optimization). One morphological difference is evident in that Mydidae, with the exception of *Mydas clavatus* and *Rhaphiomidas maehleri*, possess an area medially on the face from which the mystacal setae are absent. I am unable to comment on this feature and a more detailed analysis of mystacal setae within Mydidae might shed light on the homology to the mystacal setae in Asilidae.

Hull (1962) and Papavero (1973a) discussed several morphological characters that were believed to contain important phylogenetic information for classifying Asilidae. Some of these will be discussed briefly in light of the phylogenetic hypothesis presented here, with the character transformation from the plesiomorphic to the apomorphic condition outlined.

Both authors argued that the open wing cells r_1, r_5, m_3, and cu*p* represent the plesiomorphic condition within Asilidae. That this is not the case is exemplified, for example, by clade L (Leptogastrinae + Trigonomiminae) (fig. 120), which is a phylogenetically derived clade and in which all wing cells are generally open (only cell cu*p* is closed in *Acronyches* and *Lasiocnemus* within Leptogastrinae and all Trigonomiminae except *Rhipidocephala*) (figs. 84–85). Furthermore, cells r_1, m_3, and cu*p* are closed in Asilinae, Laphriinae (r_1 is open in *Psilocurus*), and Ommatiinae (figs. 73–80) as well as Apioceridae and Mydidae as the sister group, but the same cells are generally open in taxon C, i.e., the remaining Asilidae (figs. 81–83, 120). Cell m_3 and cu*p* are also closed in Bathypogoninae and Phellinae, which are representatives of clade C, and open in the majority of species of taxon E (fig. 120). This indicates that the closed condition of these wing cells is actually the plesiomorphic state. The only exception is cell r_5, which is closed in very few Asilidae (figs. 73, 75) and Asiloidea outgroup taxa, and the plesiomorphic condition is an open cell r_5.

Previous classifications emphasized the one- or two-segmented maxillary palpi as an important character (e.g., Hull, 1962; Papavero, 1973a). Hull (1962) used this character in the first couplet to his identification key to higher-level taxa and Oldroyd (1974a: 11) stated, "It seems to me, therefore, that the number of palpal segments is too elusive and enigmatic a character to be given such prominence." Hennig (1973) and Woodley (1989) postulated a two-segmented maxillary palpus as an autapomorphy for the Brachycera. It has been assumed that a two-segmented palpus is the plesiomorphic condition within Asilidae (Hull, 1962; Papavero, 1973a; Oldroyd, 1974a) and this hypothesis is

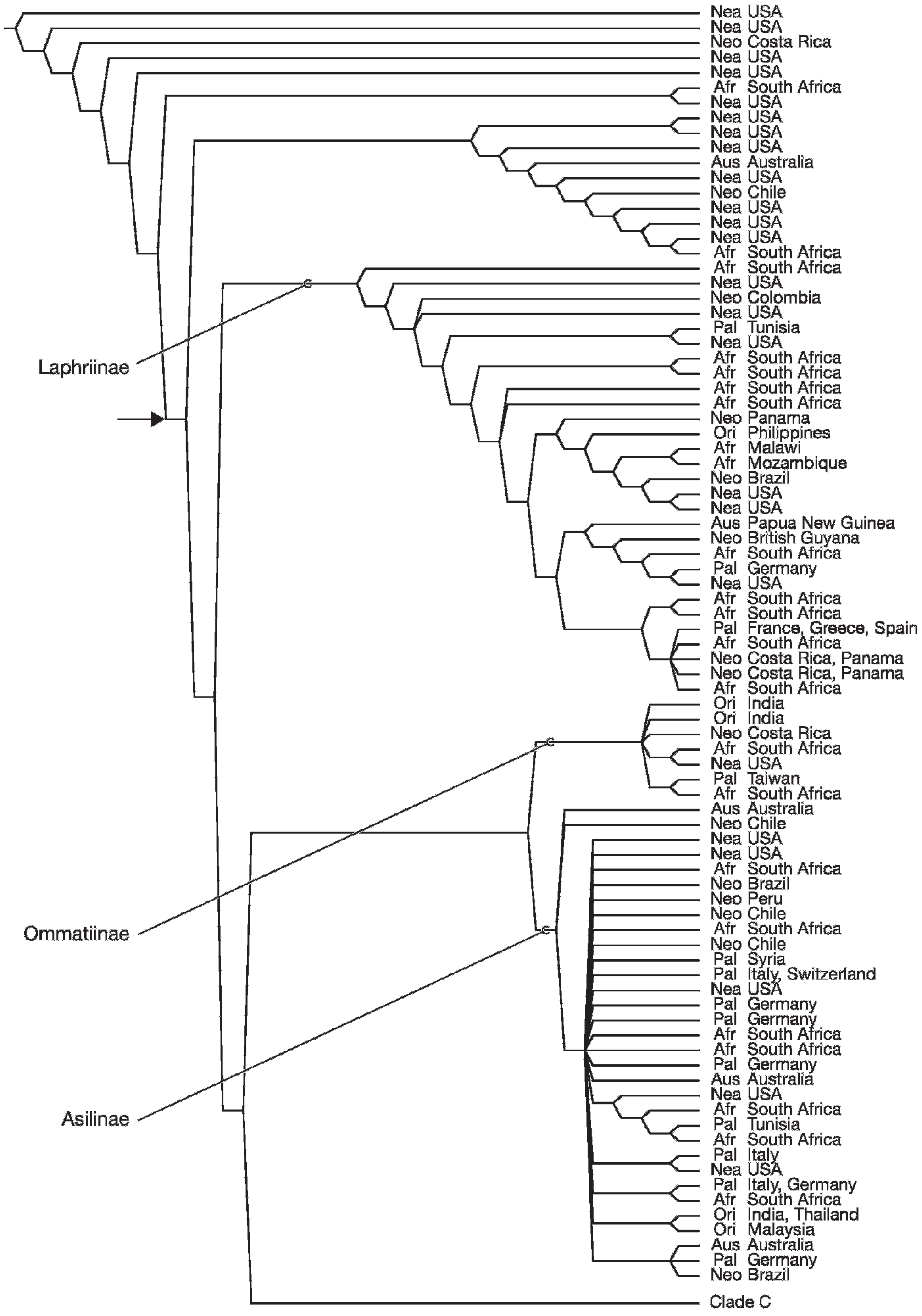


Fig. 131. Strict consensus topology as in figure 118, but taxon names substituted with zoogeographical region and country of origin of specimens examined. Arrow indicates root of Asilidae.

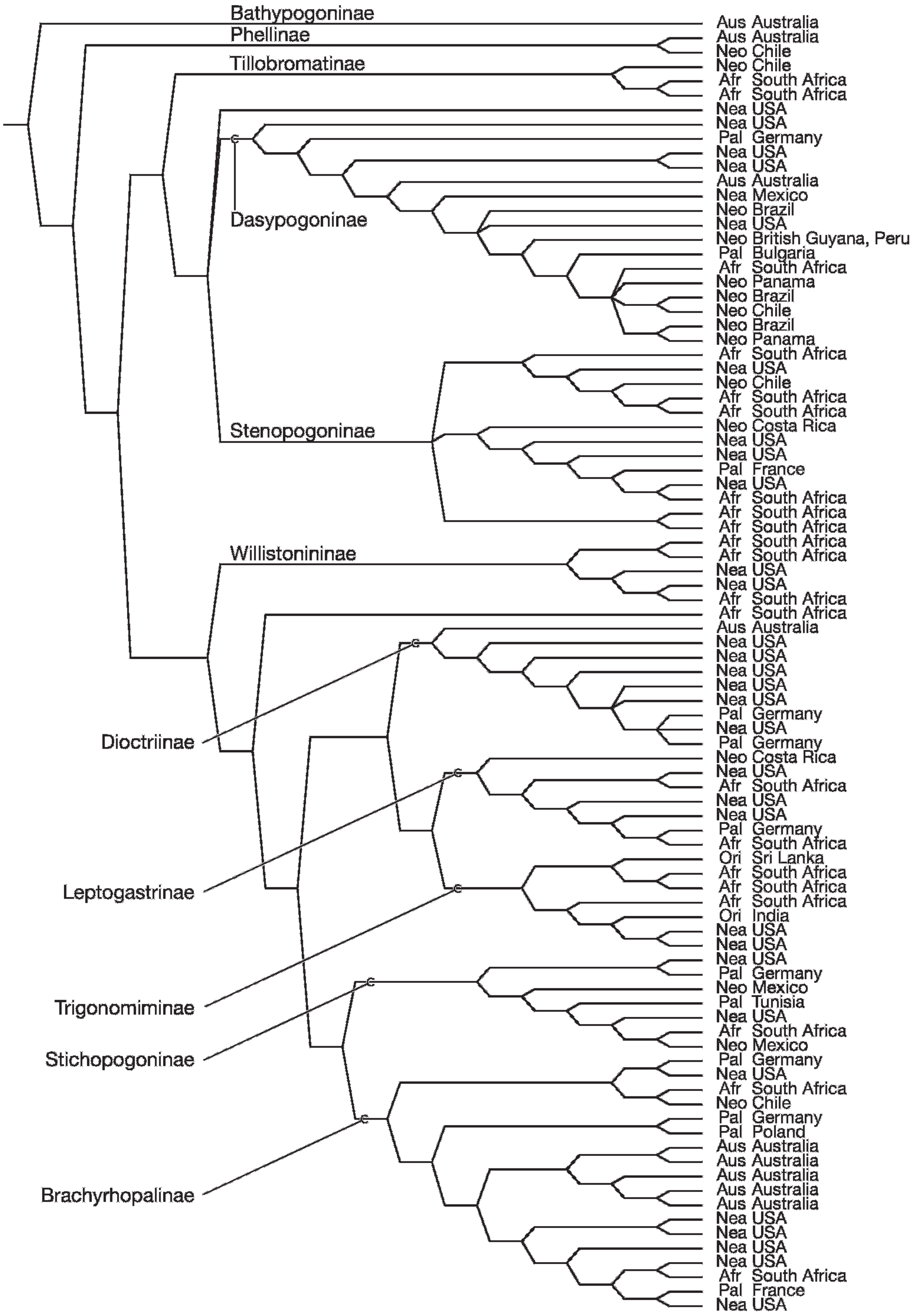


Fig. 131. Continued

corroborated here as this state is optimized at the root of Asilidae. It has been independently reduced to a single palpomere at least 13 times in all Asilinae, Bathypogoninae, Leptogastrinae, and Ommatiinae and at least some taxa of Dasypogoninae, Dioctriinae, Laphriinae, Stenopogoninae, Stichopogoninae, Trigonomiminae, and Willistonininae (see character 11).

Another character Hull (1962) and Papavero (1973a) emphasized is the development of the prosternum and its lateral fusion to the proepisternum. Clements (1951: 14) studied many species in detail and concluded that, "Examination of the prosternum in all groups showed that too much variation occurs for it to be used as a diagnostic or supplementary character." There is no doubt that a diversity of shapes of the prosternum exists among assassin flies, but they are of value and can be easily delimited in five distinct character states (see character 74; figs. 66–69). Hardy (1948), Hull (1962), and Papavero (1973a) concluded that a complete broad prosternum, which is entirely fused to the proepisternum, is the plesiomorphic condition within Asilidae. This hypothesis is corroborated here as this character state is optimized at the root of Asilidae and a separated prosternum is an apomorphic state for taxon A. A complete prosternum is found in all Mydidae and those Laphriinae which form the basalmost clades, i.e., Hoplistomerini, Laphystiini, *Perasis*, *Protometer*, *Psilocurus*, and *Zabrops*, as well as in all Stichopogoninae and most Leptogastrinae in a phylogenetically derived position (fig. 66).

Adisoemarto and Wood (1975) considered the acanthophorite spurs (character 174; figs. 87, 91, 97) on the female ovipositor to be a ground-pattern feature of Asiloidea and Griffiths (1994) recognized them as an autapomorphy of this taxon. Yeates (1994) postulated that these spurs have actually been derived independently within Bombyliidae and the remaining Asiloidea. Papavero (1973a: 231) stated with regard to Asilidae that

> The primitive female terminalia has spines on the acanthophorites; reduction of spines, fusion of the two halves of the acanthophorites and their subsequent elongation and modification leads to the formation of the several types of ovipositor presented by the different groups. This character, like the prosternum, is extremely important to determine the primitive branchings of the family.

The presence of acanthophorite spurs is an apomorphic character state for taxon C because the spurs are absent in Asilinae, Laphriinae, and Ommatiinae whereas they are present in a less inclusive clade within Asilidae (fig. 120). There are two equally parsimonious explanations for the character transformation. Because Apioceridae + Mydidae, as the sister group to Asilidae, possess acanthophorite spurs, these spurs (1) are reduced in the most recent common ancestor of Asilidae and then originated as a novel structure in the most recent common ancestor of taxon C (2 steps, fast optimization) or (2) are independently reduced in Laphriinae and taxon B (Asilinae + Ommatiinae), respectively (2 steps, slow optimization). Acanthophorite spurs are also absent in taxon K (Dioctriinae + (Leptogastrinae + Trigonomiminae)) and the absence is an apomorphic character state for this speciose clade. This highlights the fact that it is important not to consider the absence of spurs as the result of a single reduction, but to allow for independent losses among phylogenetically unrelated taxa of Asilidae. In contrast to Papavero's opinion (1973a), this character is therefore not of great importance to decipher the early cladogenesis of Asilidae. Based on the taxon sampling within the outgroup taxa, it appears that the spurs have also been independently derived in *Bombylius major* (Bombyliidae), *Prorates* sp. (El Hacha) (Scenopinidae), and *Phycus frommeri* (Therevidae).

Papavero (1973a: 231) postulated in reference to the presence of projections on the prothoracic tibiae that, "This character is very probably derived and monophyletic [sic], as all the steps in its transformation can still be traced. Genera presenting this character were segregated under one subfamily." The pattern of evolution of this feature occurred differently based on the present phylogenetic hypothesis. The large spine on the prothoracic tibiae is found in Dasypogoninae as well as the Australian Brachyrhopalini and Chrysopogonini (Brachyrhopalinae) (figs. 70, 121). A small S-shaped spur, believed to be the intermediary stage by Papavero (1973a; fig. 72), is present in *Thereutria* in the Dasypogoninae and *Cophura*, *Leptarthrus*, and *Nicocles* of the Brachyrhopalinae. This highlights the fact that the S-shaped spur of *Thereutria* is homologous to the large spine of other Dasypogoninae although the shape has been transformed, but not homologous to the S-shaped spur found in *Cophura*, *Leptarthrus*, and *Nicocles*. In fact, the present hypothesis based on 220 characters rejects the homology of the S-shaped spur even among these three genera as they do not form a clade. Furthermore, the large spine of Dasypogoninae is not homologous to the one found in the Australian taxa despite its morphological similarity. Interestingly, *Archilestris* groups within Dasypogoninae based on a suite of morphological characters, but was excluded from this taxon by Artigas and Papavero (1991) because of the absence of tibial projections, which is postulated here to be the result of the reduction of this feature. It is shown here that a taxon based on only the presence of tibial projections is not recognizable as monophyletic, and the delimitation of Dasypogoninae is therefore adjusted.

Martin (1968) examined the lack of pulvilli in Diptera in detail to support the hypothesis that his Leptogastridae is more plesiomorphic than the remaining Asilidae and should therefore be grouped as a separate family taxon. He stated, ''On the basis of the above discussion I suggest that the dipterous tarsal segment without pulvilli is primitive, and not homoplastic as Janssens hypothesized when he used the term convergent'' (Martin, 1968: 81). This hypothesis is not corroborated here because the pulvilli are present in all outgroup taxa as well as most Asilidae, and are reduced only two independent times within Asilidae, i.e., once in the most recent common ancestor of Leptogastrinae and probably once in the most recent common ancestor of a subordinate taxon of Willistonininae, as not all Willistonininae lack pulvilli. Oldroyd (1969) also provided a detailed rebuttal of the lack of pulvilli in Diptera in response to Martin's study.

TRANSFORMATION SERIES WITHIN MULTISTATE CHARACTERS

Thirty-one of the 106 multistate characters could be considered to be part of an evolutionary transformation series in contrast to the remaining multistate characters, which are coded in this way for convenience only as they deal with a particular character system. One should keep in mind that any multistate character can be recoded into a suite of binary characters without losing any information. Although these 31 ''true'' multistate characters could have been made additive to restrict the transformation from one state to another, all characters are treated as nonadditive so that no constraints on evolutionary transformation sequences are imposed. The ''true'' multistate characters are: 3 (vertex shape), 14 (stipites fusion), 19 (postmentum development), 23 (labella), 33 (hypopharynx dorsal protuberances), 40 (pharyngeal pump), 58 (stylus), 62 (ocellar setae), 64 (compound eye margin), 65 (macrosetae on median occipital sclerite), 66 (postocular setae), 69 (antepronotal setae), 70 (lateral postpronotal setae), 72 (postpronotal lobes), 73 (dorsal postpronotal setae), 83 (katatergal setae), 98 (apical scutellar setae), 102 (postmetacoxal bridge), 110 (setae on mesothoracic tibia), 112 (setae on metathoracic coxa), 114 (setae on metathoracic trochanter), 118 (fringe of parallel setae on metathoracic femur and tibia), 127 (empodium), 130 (alula), 153 (T2 length), 173 (T9–10 fusion), 175 (spermathecae number), 181 (spermathecal reservoir), 202 (hypandrium and gonocoxite fusion), 206 (gonostyli position), and 214 (aedeagus prongs). Table 8 summarizes those 20 multistate characters from the above list in which a transformation, for example, from state 0 to state 2 or vice versa occurs while the intermediate state 1 is not observed (based on the character optimization on the most parsimonious topology in fig. 118). All of the remaining 11 characters exhibit an additive transformation including all character states.

When the 20 multistate characters of table 8 are recoded to be additive the tree length of the most parsimonious topology increases from 2760 to 2834 steps. Many of the characters are associated with setal

TABLE 8

Summary of transformation of character states in 20 multistate characters based on most parsimonious topology in figure 118

All optimizations unambiguous except where indicated with slow and fast

Character	transfor-mation	species/clades
3 vertex	0 » 2	root Asilidae
14 stipites fusion	0 » 2	root of taxon (Therevidae (Asilidae (Apioceridae + Mydidae)); once within Asilinae; *Rhabdogaster pedion*; root Dioctriinae; twice within Stenopogoninae; root Stichopogoninae
	2 » 0	*Phellus olgae* (slow)
19 postmentum	0 » 2	root Therevidae; three times within Brachyrhopalinae; once within Dasypogoninae
	2 » 0	twice within Dasypogoninae
40 pharyngeal pump	0 » 2	*Plesiomma* sp. (Guanacaste)
58 stylus	1 » 3	root Brachyrhopalini
	0 » 2	root of taxon (Scenopinidae (Apsilocephalidae (Therevidae (Asilidae (Apioceridae + Mydidae)))))
64 compound eye	0 » 2	root Stichopogoninae
65 macrosetae median occipital sclerite	0 » 2	*Heteropogon manicatus*; *Acnephalum cylindricum* + *Sisyrnodytes* sp. (Gamka); *Daspletis stenoura*; *Lycostommyia albifacies*; *Hyperechia nigripennis*; *Megapoda labiata* (fast); root Dasypogoninae
	2 » 0	*Archilestris magnificus*
69 antepronotal setae	0 » 2	*Acronyches maya* (fast)
	2 » 0	*Opomydas townsendi* (slow)
73 dorsal postpronotal setae	0 » 2	*Heteropogon manicatus* + *Metapogon punctipennis* (fast)
	2 » 0	*Molobratia teutonus* (slow)
83 katatergal setae	0 » 2	root Asilidae (slow); *Gonioscelis ventralis* + *Stenopogon* species (slow); *Phycus frommeri* (slow); root of taxon (Therevidae (Asilidae (Apioceridae + Mydidae)) (fast)
98 apical scutellar setae	2 » 0	once within Dasypogoninae; *Michotamia aurata*; *Perasis transvaalensis*; *Plesiomma* sp. (Guanacaste); *Protometer* sp. (El Tuparro); *Trichardis effrena* (slow)
102 postmetacoxal bridge	0 » 2	*Townsendia albomacula* (slow)
	0 » 3	root Ommatiinae; *Rhabdogaster pedion*; *Damalis* sp. (Palatupana) (slow)
	1 » 3	once within Laphriinae
110 setae on mesothoracic tibia	2 » 0	root Leptogastrinae; four times within Asilinae (slow); twice within Laphriinae; twice within Mydidae; *Prorates* sp. (Escalante)
	0 » 2	once within Asilinae
130 alula	0 » 2	root of taxon comprising *Oligopogon* sp. (Cape Recife), Brachyrhopalinae, Dioctriinae, Leptogastrinae, Stichopogoninae, and Trigonomiminae; *Goneccalypsis argenteoviridis* + *Loewinella nigripes*
	2 » 0	*Damalis* species (slow)
153 T2 length	0 » 2	root Leptogastrinae
175 spermathecae number	0 » 2	*Mitrodetus dentitarsis*
181 spermathecal reservoir	0 » 2	*Brachyrhopala ruficornis* + *Cabasa pulchella* (fast); *Apoclea algira* (slow); once within Asilinae (slow)
	2 » 0	once within Asilinae
202 hypandrium and gonocoxite fusion	0 » 2	root of taxon comprising Leptogastrinae and Trigonomiminae; *Trichoura* sp. (Tierberg)
	2 » 0	*Opomydas townsendi*
206 gonostyli position	0 » 2	three times within Asilinae
	2 » 0	root Asilinae (fast)
214 aedeagus prongs	0 » 2	twice within Asilinae (slow); twice within Laphriinae (slow); once within Trigonomiminae
	2 » 0	four times within Asilinae (fast); once within Laphriinae (fast)

development where either no setae (state 0), regular setae (state 1), or macrosetae (state 2) are developed. When coded nonadditive, i.e., counting only one step from state 0 to state 2, it is shown that macrosetae can evolve without the prior existence of regular setae. Similarly, a complete postmetacoxal bridge (character 102) has evolved three independent times within Asilidae from an entirely membraneous postmetacoxal area (transformation from state 0 to state 3). These three phylogenetically independent occurrences of this particular transformation series indicate that the same pattern can be derived by different evolutionary processes if one acknowledges that no fixed genetic basis is responsible for the development of a postmetacoxal bridge.

The development of the posterior compound eye margin (character 64; figs. 58–60) illustrates the independence of character states. The distinctly sinuate eye of Stichopogoninae (state 2; fig. 60) has evolved from a straight or lightly curved eye margin (state 0; fig. 58) and the presumably intermediate state (sinuate eye in ventral quarter; fig. 59) is found only in some species of the phylogenetically unrelated Asilinae, Dasypogoninae, and Willistonininae. Coding this character as additive would not only increase the length of the most parsimonious cladogram by one step, it would also suggest that the most recent common ancestor of Stichopogoninae first evolved a slightly sinuate eye margin (state 1) and then later, in a second evolutionary event, developed a distinctly sinuate eye margin (state 2). As this phylogenetic analysis is based only on extant taxa and actual phenotypical observations, there is no justification to propose a particular sequence of evolutionary transformations a priori. To impose a particular additivity (or order) on character states would assume that every character state evolves with the same evolutionary rate (homogeneity assumption of molecular data) and evolutionary direction no matter where they are optimized on the cladogram. In some instances, e.g., fusion of labella to prementum (character 23; figs. 31, 36), the transformation series from state 0 to state 1 and finally to state 2 is optimized as the most parsimonious solution, but in other instances (see table 8) such a transformation has not been observed in light of the congruence test with all other included characters.

Phylogenetic Placement of the Two Oldest Known Fossil Robber Flies

The two oldest extinct robber flies, i.e., *Araripogon axelrodi* Grimaldi, 1990, from the Crato Formation of Brazil and an undescribed species from New Jersey amber (Grimaldi and Cumming, 1999), date to the late Cretaceous and provide a minimum age of Asilidae (see Introduction). Both species have not yet been placed in any higher-level taxon within Asilidae although Grimaldi and Cumming (1999) suggested that the New Jersey amber species shows similarities to extant species of Leptogastrinae. Based on the morphological study of the present phylogenetic hypothesis a placement of these two species in higher-level taxa is possible. Apioceridae and Mydidae, as the sister taxon to Asilidae, and Laphriinae and Asilinae + Ommatiinae, as the two basalmost clades of Asilidae, exhibit closed wing cells r_1 and cu*p* (among other closed wing cells). In contrast, all wing cells are open in *Araripogon axelrodi* and therefore this species can be placed at the root of clade C (see fig. 121). A more precise placement within this clade is currently not possible as additional information from other morphological characters is needed. D. Grimaldi (personal commun.) has located additional fossil fragments of this species and more character systems can be examined in the future to help place *Araripogon axelrodi*.

The undescribed species from New Jersey amber can be placed at the root of Leptogastrinae as has been suggested by Grimaldi and Cumming (1999) (see fig. 121). Leptogastrinae, as here delimited, includes the genus *Acronyches*, which shares characters with the Leptogastrinae sensu stricto, but still retains a few plesiomorphic features. Of the apomorphic character states delimiting Leptogastrinae, the following are present in the extinct species: seta-like spicules on hypopharynx spaced far apart (33; fig. 43), ocellar setae absent (62), presutural dorsocentral setae absent (92). Additional characters supporting the placement are the reduced alula, the few mystacal setae, and the shape of the postpedicel. An autapomorphy of Leptogastrinae sensu previous authors, i.e., anteriorly and medially extended postpronotal lobes (72; fig. 65), is neither present in the fossil nor in *Acronyches*, which exhibit the plesiomorphic state, corroborating the placement of this extinct species at the root of Leptogastrinae. Another character supporting this particular position is the shape of the frons. The extinct species exhibits a parallel-sided frons as also found in Leptogastrinae sensu previous authors (see, e.g.; fig. 28) whereas in *Acronyches* the frons is markedly approximating at its dorsal margin. This can be taken as evidence that the extinct species is not more closely related to *Acronyches* (based on the shape of the postpronotal lobes) than to other Leptogastrinae sensu previous authors.

Based on these two fossil species the minimum age for a taxon composed of clade C and its sister group Asilinae + Ommatiinae can be postulated to be at least 110 Million years (fig. 121). The minimum age for a clade composed of Leptogastrinae and its sister taxon Trigonomiminae can be postulated to be at least 90 Million years (fig. 121).

Sister Group to the Asilidae

As has been summarized in the introduction, there is no previous agreement regarding which taxon represents the sister group to Asilidae within Asiloidea. The present analysis, which includes 16 Asiloidea outgroup taxa, supports a sister-group relationship between Asilidae + (Apioceridae + Mydidae) (figs. 118–121). Representatives of these three taxa share the autapomorphic presence of a lateral depression on the prothoracic coxae (character 104). This depression is absent only in Leptogastrinae among Asilidae, and *Pseudonomoneura hirta* among Mydidae. Additional apomorphic character states supporting the monophyly of this taxon are: clypeal-facial margin forming a distinct ridge (10; figs. 27–31), sensory pit in distal maxillary palpomere absent (12), propresternum square (76; fig. 66), upper calypter small (129), female spermathecal reservoir not differentiated from spermathecal ducts (same diameter) (180; fig. 100). The monophyly of a taxon composed of these three taxa is also supported by the presence of muscles M5, M33, and M38 in the male terminalia (Ovtshinnikova, 1989; Ovtshinnikova and Yeates, 1998) although these characters are uninformative within this clade. I believe that this sister-group relationship is well supported and it has been independently postulated by Yeates and Irwin (1996) in a morphological phylogenetic analysis focused on Apioceridae.

Hennig (1973), Wood (1981), Woodley (1989), and Yeates and Irwin (1996) discussed the depressed vertex in regard to these three taxa and state that it could possibly be informative for deciphering the sister-group relationships. In the present analysis, I divide the depressed vertex into two character states (see character 3) and a sharply depressed vertex of an angle of about 90° is optimized at the root of Asilidae and found in all Asilinae, Laphriinae, and Ommatiinae as well as additional robber flies in clade C (figs. 28, 120). A slightly depressed vertex is found in about half of the species of taxon C as well as among Mydidae with the exception of *Neorhaphiomidas* and *Rhaphiomidas* (figs. 27, 30). In these two Mydidae genera, Apioceridae, and all remaining outgroup taxa, the vertex is at the same level as the median compound eye margin. Therefore, the most parsimonious explanation is that the slightly depressed vertex found in some Asilidae of clade C and some Mydidae of a less inclusive clade originated independently as has been suggested previously by Woodley (1989).

Apioceridae and Mydidae form a clade supported by two autapomorphies, i.e., postgenae with medial projection (16) and anterior ocellus separate and situated anteriorly (60; fig. 30), and additional apomorphic character states (54: 5, 55: 1, 116: 1, 124: 0, 127: 2, 145: 0, 147: 0, 174: 1). The single dorsal longitudinal ridge on the pulvilli (see character 124) could be interpreted as another autapomorphy of Apioceridae + Mydidae as suggested by Yeates and Irwin (1996), as it is only found outside of this taxon in Megapodina (Dasypogoninae) and this is certainly an independent reduction from two ridges to one. Woodley (1989) and Yeates and Irwin (1996) found that wing veins R_5 and M_1 (see characters 145 and 147) terminate anterior to the wing apex in Apioceridae and Mydidae (in some Mydidae they do not reach the wing margin at all) and this development is postulated to be an autapomorphy. This is corroborated in the present analysis as this arrangement of veins is only found in the phylogenetically unrelated Nemestrinidae and a few Asilinae species. Woodley (1989), Yeates and Irwin (1996), and Yeates (2002) postulated the supernumerary rectal papillae as an autapomorphy of this clade. Although it appears as if it could be an important character, it has not been examined in many species. Future studies, including more Apioceridae, Mydidae, but also Asilidae, are necessary. Other autapomorphies postulated by Yeates and Irwin (1996) for the clade Apioceridae + Mydidae are: postpedicel ovate, empodium absent, R_4 not reaching costa, male epandrium divided into two halves, female T9 with dorsal ridge, female lateral margin of T9 joining ventrally (not investigated here). Characters that are included in the present analysis and corroborated as apomorphic character states for Apioceridae + Mydidae are: (1) empodium minute or entirely absent (127, also found among several Asilidae clades), (2) female T9 with dorsal ridge (171), (3) divided epandrium (197, also found among many Asilidae with the notable exception of all Laphriinae and some additional taxa). R_4 is found here to reach the wing margin in the genera *Apiocera* and *Rhaphiomidas*, but not in the remaining Mydidae, therefore suggesting that this character is autapomorphic for a less inclusive clade (see character 143). The phylogenetic relationships between *Apiocera*, *Neorhaphiomidas*, *Rhaphiomidas*, and remaining Mydidae and family taxon delimitation proposed by Yeates and Irwin (1996) are corroborated here. Apioceridae is supported as monophyletic by the following apomorphic character states: distal maxillary palpomere laterally compressed and leaflike (13), stipites of maxillae entirely fused medially (14), prosternum and proepisternum not fused and prosternum triangular with pointed tip (74), male dorsal aedeagal sheath short and sperm sac entirely free (215). Mydidae is characterized by a single autapomorphy, i.e., male gonostyli absent (205), and a number of apomorphic character states: maxillary palpus one-segmented (11), maxillae shorter than labrum (27), maxillae tapering gradually toward tip (28), apical "seta-like" sensory element apically in cavity on postpedicel (57), postpronotal lobes only partly fused to scutum and lobes elevated above scutum posteriorly (71; fig. 63), cervical sclerite extending medially to cover sensory area on propresternum (77), cell d closed by M_2 and M_3 and these veins not aligned (137), male hypandrium reduced or not differentiated (199), male hypandrium and gonocoxites form gonocoxite-hypandrial complex (202), male lateral ejaculatory process absent (213).

CONCLUSIONS

This study presents the most comprehensive phylogenetic hypothesis for Asilidae. The monophyly of Asilidae is supported and a clade composed of Apioceridae + Mydidae is established as the sister group to robber flies. The Leptogastrinae is deeply placed within Asilidae based on a suite of morphological characters. This placement refutes the hypothesis that Leptogastrinae should be considered the sister-group to assassin flies (sensu Martin, 1968; Papavero, 1973a; Bybee et al., 2004). The Laphriinae is postulated to be the sister taxon to the remaining robber flies and a number of classificatory changes are made to accept only monophyletic higher-level taxa.

It is hoped the present extensive phylogenetic analysis of Asilidae will be of value for future studies dealing with the evolutionary relationships within specific higher-level taxa. The phylogenetic hypothesis highlights some interesting taxa that are both adelphotaxa to speciose clades and are biogeographically restricted. Particular attention should be directed to investigating the phylogenetic relationships within Asilinae. The Brachyrhopalinae, which represents a conglomeration of genera previously assigned to Dasypogoninae and Stenopogoninae, is also of interest and I suspect that many more genera will have to be assigned to this taxon. All genera classified by Geller-Grimm (2004) in Apocleinae + Asilinae (174, of which 29 are represented here), Dioctriinae (11, 6 represented here), Laphriinae + Laphystiinae (109, 27 represented here), Leptogastrinae (18, 5 represented here), Ommatiinae (8, 4 represented here plus *Afroestricus*), Stichopogoninae (11, 4 represented here), and Trigonomiminae (11, 4 represented here) can easily be placed within the revised classification as all of these taxa have been diagnosed sufficiently to evaluate whether the remaining unstudied genera are representatives of these monophyletic taxa. Fifty-nine genera of Dasypogoninae and Stenopogoninae sensu previous authors are represented in the present study so that only 127 genera of these two taxa remain to be addressed in future phylogenetic analyses and placed within the higher-level taxa proposed here. This, however, assumes that all genera are monophyletic, which should be another focus in future studies employing phylogenetic methodology rather than morphological similarity and biogeography. Monophyly of speciose genera with more than 200 described species, such as *Laphria*, *Leptogaster*, *Neolophonotus*, *Ommatius*, and *Promachus*, or more than 100 species, e.g., *Microstylum*, *Stenopogon*, and *Stichopogon*, should be tested.

ACKNOWLEDGMENTS

This study would not have been possible without the discussions with and support of Jason Londt (Pietermaritzburg, South Africa), Fritz Geller-Grimm (Frankfurt am Main, Germany), and Eric Fisher (Sacramento, California). Their knowledge of Asilidae and interest in my dissertation have contributed immensely to the outcome of this monograph. I gratefully thank them for their input. I would also like to sincerely thank the many museum curators who have agreed to lend the often old and fragile specimens for morphological study and their hospitality when I visited the collections. My Ph.D. advisors Jim Liebherr (Cornell University, Ithaca, New York) and David Grimaldi (AMNH) are thanked for supporting my dissertation from day one and being of valuable help in refining the present publication. I thank Eduardo Almeida (Curitiba, Brazil) and Roberto Keller (AMNH) for always encouraging my work and for discussions of all matters of entomology, taxonomy, and systematics. Kurt Pickett (Burlington, Vermont) is thanked for providing help with analyzing matrices in TNT, and Pablo Goloboff and Norberto Giannini (Tucumán, Argentina) for providing help in calculating support values in TNT. I thank Rebecca Budinoff (AMNH) for meticulously reading the manuscript and providing many helpful suggestions. Martin Hauser (Sacramento, California), Shaun Winterton (Brisbane, Australia), and Neal Evenhuis (Honolulu, Hawaii) are thanked for help in selecting outgroup taxa and providing specimens of Apsilocephalidae, Scenopinidae, and Therevidae. Cornell University and the American Museum of Natural History supported my dissertation with Ph.D. fellowships as well as grants for travelling, attending conferences, and collecting specimens. I thank Jason Londt, Michael Thomas, and Chris Maier (both New Haven, Connecticut), Christiane Weirauch (Riverside, California), and Rudolf Meier (Singapore) for accompanying me in the field in South Africa, Connecticut and Rhode Island, and Malaysia and Singapore, respectively. Greg Courtney (Ames, Iowa) is thanked for organizing the North American Dipterists Society Field Meeting in Oregon. Crucial specimens for the present study have been collected on all of these collecting trips. Michael Thomas and Giff Beaton (Georgia) kindly provided the color photographs of Asilidae species. The assistance from agencies granting collecting permits in Malaysia (Pahang, Selangor), Singapore, South Africa (Limpopo, KwaZulu-Natal, Northern Cape), and the United States of America (Arizona, Oregon) is gratefully acknowledged. The two peer reviewers highlighted inconsistencies and suggested a few clarifications for which I am grateful. A Doctoral Dissertation Improvement Grant from the National Science Foundation (DEB 0608258) supported part of the present project.

REFERENCES

Adisoemarto, S., and D.M. Wood. 1975. The Nearctic species of *Dioctria* and six related genera (Diptera, Asilidae). Quaestiones Entomologicae 11: 505–576.

Artigas, J.N. 1971. Las estructuras quitinizadas de la spermatheca y funda del pene de los Asilidos y su valor sistematico a traves del estudio por taxonomica numerica (Díptera – Asilidae). Gayana Zoologia 18: 1–106.

Artigas, J.N., N. Papavero, and T. Pimentel. 1988. The American genera of Asilidae (Diptera): keys for identification with atlas of female spermathecae and other morphological details. IV. Key to the genera of Laphriinae Macquart (except tribe Atomosiini Hermann), with the descriptions of three new tribes and five new species. Boletin Museo Paraense Emilio Goeldi, ser. Zoologia 4(2): 211–256.

Artigas, J.N., P.D. Lewis, and L.E. Parra. 2005. Review and phylogeny of the genus *Tillobroma* Hull with the description of ten new species and its relation with the genus *Hypenetes* Loew (Diptera, Asilidae, Stenopogoninae). Revista Chilena de Historia Natural 78(3): 519–588.

Artigas, J.N., and N. Papavero. 1988. The American genera of Asilidae (Diptera): keys for identification with atlas of female spermathecae and other morphological details. II. Subfamily Dasypogoninae Macquart, with descriptions of new genera and species and new synonymies. Gayana Zoologia 52(3–4): 199–260.

Artigas, J.N., and N. Papavero. 1991. The American genera of Asilidae (Diptera): keys for identification with atlas of female spermathecae and other morphological details. VII. Subfamily Stenopogoninae Hull: a preliminary classification into tribes. Gayana Zoologia 55: 139–144.

Artigas, J.N., and N. Papavero. 1997. The American genera of Asilidae (Diptera): keys for identification with an atlas of female spermathecae and other morphological details. IX. 1. Subfamily Asilinae Leach (including Apocleinae Lehr): key to generic group. Arquivos de Zoologia 34(1–4): 57–63.

Bequaert, M. 1961. Contribution à la connaissance morphologique et à la classification des Mydaidae (Diptera). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 37(19): 1–18.

Brauer, F. 1885. Systematisch-zoologische Studien. Sitzungsberichte der Akademie der Wissenschaften in Wien (1) 91: 237–413.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.

Bybee, S.M., S.D. Taylor, C.R. Nelson, and M.F. Whiting. 2004. A phylogeny of robber flies (Diptera: Asilidae) at the subfamilial level: molecular evidence. Molecular Phylogenetics and Evolution 30: 789–797.

Cannings, R.A. 2002. The systematics of Lasiopogon (Diptera: Asilidae). Victoria: Royal British Columbia Museum.

Carrera, M. 1949. Contribuição ao conhecimento dos Asilidae neotropicais (Diptera). I. Sôbre as espécies brasileiras com esporão no tíbia. Arquivos de Zoologia 7(2): 1–148.

Clements, A.N. 1951. The use of the prosternum in classifying Asilidae. Proceedings of the Royal Entomological Society of London. Series B, Taxonomy 20(1–2): 10–14.

Clements, A.N. 1985. A taxonomic revision of the tribe Chrysopogonini (Diptera: Asilidae). Australian Journal of Zoology Supplementary Series 109: 1–93.

Cole, F.R. 1927. A study of the terminal abdominal structures of male Diptera (two-winged flies). Proceedings of the California Academy of Sciences 4th Ser. 16(14): 397–499.

Crampton, G.C. 1942. Guide to insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. First Fasc.: the external morphology of the Diptera. State Geological and Natural History Survey of Connecticut Bulletin 64: 10–165.

Cumming, J.M., B.J. Sinclair, and M.D. Wood. 1995. Homology and phylogenetic implications of male genitalia in Diptera – Eremoneura. Entomologica Scandinavica 26: 120–151.

Darlington, P.J. 1971. The carabid beetles of New Guinea. Part VI. General considerations; analysis and history of fauna; taxonomic supplement. Bulletin of the Museum of Comparative Zoology 142(2): 129–337.

Dikow, T. 2004. Family-group names in the Asilidae (Diptera). Studia Dipterologica 10(2): 459–471.

Dikow, T. submitted. Phylogenetic hypothesis of Asilidae based on a combined total evidence analysis of morphological and DNA-sequence data (Insecta: Diptera: Brachycera: Asiloidea)..

Dikow, T., and J.G.H. Londt. 2000. A review of the genera *Anasillomos* Londt, 1983, *Oratostylum* Ricardo, 1925, and *Remotomyia* Londt, 1983, with description of a new genus and two new species (Diptera: Asilidae: Stenopogoninae). Annals of the Natal Museum 41: 107–121.

Emden, F. van., and W. Hennig. 1970. 21. Diptera. *In* S.L. Tuxen (editor), Taxonomist's glossary of genitalia in insects. 2nd revised and enlarged ed., 130–141. Copenhagen: Munksgaard.

Enderlein, G. 1914. Dipterlogische Studien XII. Zur Kenntnis der Asilidensubfamilien Dasypogoninae und Archilaphriinae. Wiener Entomologische Zeitung 33(5–6): 151–174.

Enderlein, G. 1936. Asilidae 30. Familie. *In* P. Brohmer, P. Ehrmann, and G. Ulmer (editors), Die Tierwelt Mitteleuropas. Band 6. Insekten 3. Teil Abteilung 16: 91–95. Leipzig: Quelle and Meyer.

Evenhuis, N.L. 1994. Catalogue of the fossil flies of the world (Insecta: Diptera). Leiden: Backhuys.

Farris, J.S. 1979. The information content of the phylogenetic system. Systematic Zoology 28(4): 483–519.

Farris, J.S., V.A. Albert, M. Källersjö, D.L. Lipscomb, and A.G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99–124.

Fisher, E.M. 1986. A reclassification of the robber fly tribe Andrenosomini, with a revision of the genus *Dasyllis* Loew (Diptera: Asilidae). Ph.D. dissertation, University of California Riverside: Riverside, CA.

Fisher, E.M. In press. Asilidae. *In* B.V. Brown, A. Borkent, J. Cumming, N. Woodley, D.M. Wood, and M. Zumbado (editors), Manual of Central American Diptera, Vol. 1: chap. 45. Ottawa: NRC Press.

Gaffney, E.S. 1979. An introduction to the logic of phylogeny reconstruction. *In* J. Cracraft and N. Eldredge (editors), Phylogenetic analysis and paleontology, 79–111. New York: Columbia University Press.

Geller-Grimm, F. 2004. World catalogue of the genera of the family Asilidae (Diptera). Studia Dipterologica 10(2): 473–526.

Geller-Grimm, F., and M. Hradský. 2003. The genus *Oligopogon* Loew, 1847 (Diptera: Asilidae) in the Palaearctic region, including the description of new species and comments on the placement of this genus. Studia Dipterologica 9(2): 165–179.

Giannini, N.P., and S. Bertelli. 2004. Phylogeny of extant penguins based on integumentary and breeding characters. Auk 121(2): 422–434.

Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415–428.

Goloboff, P.A., and J.S. Farris. 2001. Methods for quick consensus estimation. Cladistics 17: S26–S34.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2001. TNT – tree search using new technologies (version 1.0, July 2004). Tucumán, Argentina: Distributed by the authors.

Griffiths, G.C.D. 1974. On the foundations of biological systematics. Acta Biotheoretica 23(3–4): 85–131.

Griffiths, G.C.D. 1994. Relationships among the major subgroups of Brachycera (Diptera): a critical review. Canadian Entomologist 126: 861–880.

Grimaldi, D. 1990. Diptera. *In* D. Grimaldi (editor), Insects from the Santana Formation, lower Cretaceous, of Brazil. Bulletin of the American Museum of Natural History 195: 164–183.

Grimaldi, D., and J. Cumming. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. Bulletin of the American Museum of Natural History 239: 1–124.

Grimaldi, D., and M.S. Engel. 2005. Evolution of the insects. Cambridge: Cambridge University Press.

Hardy, G.H. 1926. A new classification of Australian robberflies belonging to the subfamily Dasypogoninae (Diptera, Asilidae). Proceedings of the Linnean Society of New South Wales 51: 305–312.

Hardy, G.H. 1927a. On the phylogeny of some Diptera Brachycera. Proceedings of the Linnean Society of New South Wales 52(3): 380–386.

Hardy, G.H. 1927b. Further notes on a new classification of Australian robberflies (Diptera-Asilidae). Proceedings of the Linnean Society of New South Wales 52(3): 387–398.

Hardy, G.H. 1930. Fifth contribution towards a new classification of Australian Asilidae (Diptera). Proceedings of the Linnean Society of New South Wales 55(1): 249–260.

Hardy, G.H. 1934. The Asilidae of Australia. Part 1. Annals and Magazine of Natural History 10(13): 498–525.

Hardy, G.H. 1944. Miscellaneous notes on Australian Diptera. X. Distribution, classification and the *Tabanus posticus*-group. Proceedings of the Linnean Society of New South Wales 69: 76–86.

Hardy, G.H. 1948. On classifying Asilidae. Entomologist's Monthly Magazine 84: 116–119.

Hennig, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Berlin: Deutscher Zentralverlag.

Hennig, W. 1954. Flügelgeäder und System der Dipteren unter Berücksichtigung der aus dem Mesozoikum beschriebenen Fossilien. Beiträge zur Entomologie 4(3–4): 245–388.

Hennig, W. 1960. Die Dipteren-Fauna von Neuseeland als systematisches und tiergeographisches Problem. Beiträge zur Entomologie 10(3–4): 212–329.

Hennig, W. 1966. Phylogenetic systematics. Urbana-Champain: University of Illinois Press.

Hennig, W. 1972. Eine neue Art der Rhagionidengattung *Litoleptis* aus Chile, mit Bemerkungen über die Fühlerbildung und Verwandtschaftsbeziehungen einiger Brachycerenfamilien (Diptera: Brachycera). Stuttgarter Beiträge zur Naturkunde 242: 1–18.

Hennig, W. 1973. Diptera (Zweiflügler). *In* J.G. Helmcke, D. Starck, and H. Wermuth (editors), Handbuch der Zoologie: eine Naturgeschichte der Stämme des Tierreichs. 4: Band 2, Hälfte 2, Teil 31: 1–200. Berlin: De Gruyter.

Hennig, W. 1975. "Cladistic analysis or cladistic classification?": a reply to Ernst Mayr. Systematic Zoology 24(2): 244–256.

Hennig, W. 1976. Das Hypopygium von *Lonchoptera lutea* Panzer und die phylogenetischen Verwandtschaftsbeziehungen der Cyclorrhapha (Diptera). Stuttgarter Beiträge zur Naturkunde Serie A 283: 1–63.

Hermann, F. 1909. Beitrag zur Kenntnis der Apioceriden (Dipt.) nebst Bemerkungen über die systematische Stellung der Mydaiden und Asiliden. Beiträge zur Entomologie 1909 Beiheft, 104–122.

Hermann, F. 1912. Beiträge zur Kenntnis der südamerikanischen Dipterenfauna auf Grund der Sammelergebnisse einer Reise in Chile, Peru und Bolivia, ausgeführt in den Jahren 1902–1904 von W. Schnuse. Familie Asilidae. Nova Acta. Abhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher 96(1): 1–275.

Hermann, F. 1920. Beitrag zur allgemeinen Systematik der Asiliden. Zoologische Jahrbücher 43: 161–194.

Hesse, A.J. 1969. The Mydaidae (Diptera) of southern Africa. Annals of the South African Museum 54: 1–388.

Hull, F.M. 1962. Robber flies of the world. Bulletin of the United States National Museum 224(1–2): 1–907.

Irwin, M.E. 1976. Morphology of the terminalia and known ovipositing behaviour of female Therevidae (Diptera: Asiloidea), with an account of correlated adaptations and comments on phylogenetic relationships. Annals of the Natal Museum 22(3): 913–935.

Irwin, M.E., and B.M. Wiegmann. 2001. A review of the southern African genus *Tongamya* (Diptera: Asiloidea: Mydidae: Megascelinae), with a molecular assessment of the phylogenetic placement of *Tongamya* and the Megascelinae. African Invertebrates 42: 225–253.

Karl, E. 1959. Vergleichend-morphologische Untersuchungen der männlichen Kopulationsorgane bei Asiliden. Beiträge zur Entomologie 9(5–6): 619–680.

Krivosheina, N.P. 1973. Larvae and pupae of robber flies from the genus *Laphystia* Lw. (Diptera, Asilidae). Zoologichesky Zhurnal 52(3): 457–459.

Lameere, A. 1906. Notes pour la classification des Diptères. Mémoirs de la Société Entomologique de Belgique 12: 105–140.

Lehr, P.A. 1969. Ecologo-morphological analysis of robber flies (Diptera, Asilidae) 2. Entomologicheskoe Obozrenie 48: 532–560. [in Russian, English translation in Entomological Review 48: 341–357]

Lehr, P.A. 1996. Robber flies of subfamily Asilinae (Diptera, Asilidae) of Palaearctic: ecological and morphological analysis, taxonomy and evolution. Vladivostok: Russian Academy of Sciences Far Eastern Branch.

Lehr, P.A. 1999. Asilidae 52. Family. *In* P.A. Lehr (editor), Key to the insects of Russian Far East. Vol. 6. Diptera and Siphonaptera. Part 1, 591–640. Vladivostok: Dalnuka.

Lehr, P.A. 2001. Robber flies of the subfamily Dioctriinae stat. n. (Diptera, Asilidae) from Asia: 1. Taxonomy, ecology, and phylogeny. Entomologicheskoe Obozrenie 80(1): 194–208. [in Russian, English translation in Entomological Review 81: 59–70]

Linsley, E.G. 1960. Ethology of some bee-and wasp-killing robber flies of southeastern Arizona and western New Mexico (Diptera: Asilidae). University of California Publications in Entomology 16(7): 357–392.

Londt, J.G.H. 1980. Afrotropical Asilidae (Diptera) 4. The genus *Pegesimallus* Loew, 1858 (= *Lagodias* Loew, 1858, *Neolaparus* Williston, 1889), including species from other zoogeographical regions and the descriptions of two new genera, *Brevirostrum* and *Caroncoma*. Annals of the Natal Museum 24(1): 233–347.

Londt, J.G.H. 1983. The genus *Daspletis* Loew, 1858 and the description of two new genera, *Anasillomos* and *Remotomyia* (Diptera: Asilidae: Stenopogoninae). Journal of the Entomological Society of Southern Africa 46(2): 283–309.

Londt, J.G.H. 1988. Afrotropical Asilidae (Diptera) 16. An illustrated key to the genera of the subfamily Laphriinae, a revision of *Gerrolasius* Hermann, 1920 and the description of a new genus *Pilophoneus*. Annals of the Natal Museum 29(2): 509–521.

Londt, J.G.H. 1991. *Bana*, a new genus of bee-micking assassin fly from southern Namibia (Diptera: Asilidae: Stenopogoninae). Cimbebasia 13: 91–97.

Londt, J.G.H. 1992. Revision of three small Afrotropical asilid genera, *Empodiodes* Oldroyd, *Hynirhynchus* Lindner and *Lycostommyia* Oldroyd (Diptera: Asilidae: Stenopogoninae). Journal of African Zoology 105: 55–80.

Londt, J.G.H. 1995. Afrotropical Asilidae (Diptera) 27: predation of Asilidae by Asilidae. Annals of the Natal Museum 36: 161–167.

Londt, J.G.H. 1998. Analysis of twenty-six years of robberfly data from Willowmore in the Eastern Cape Province of South Africa (Diptera: Asilidae). African Entomology 6(1): 47–54.

Londt, J.G.H. 2004. The status of *Neolophonotus* Engel, 1929 and *Megadrillus* Bigot, 1857 within the Afrotropical asilid fauna (Diptera: Asilidae:

Apocleinae). Studia Dipterologica 10(2): 393–394.

Londt, J.G.H. 2005a. A review of afrotropical *Afroholopogon* Londt, 1994 with the description of a new genus and new species (Diptera: Asilidae: Stenopogoninae). African Invertebrates 46: 203–252.

Londt, J.G.H. 2005b. An annotated key to the genera of Afrotropical Apocleinae, with description of six new genera (Diptera: Asilidae). Tijdschrift voor Entomologie 148: 39–62.

Londt, J.G.H. 2006a. A review of the Afrotropical genus *Rhabdogaster* Loew, 1858 with descriptions of new species (Diptera: Asilidae: Stenopogoninae). African Invertebrates 47: 243–313.

Londt, J.G.H. 2006b. Predation by Afrotropical Asilidae (Diptera): an analysis of 2000 prey records. African Entomology 14(2): 317–328.

Lynch Arribalzaga, E. 1882. Catalogo de los Dipteros hasta ahora descritos que se encuentran en las Republicas del Rio de la Plata. Boletin de la Academia Nacional de Ciencas (Cordoba) 4: 109–152.

Macquart, P.J.M. 1838. Diptères exotiques nouveaux ou peu connus. Mémoires de la Société Royale des Sciences, de l'Agriculture et des Artes 1(2): 5–207.

Maddison, D.R., and W.P. Maddison. 2005. MacClade 4: analysis of phylogeny and character evolution. Version 4.08. Sunderland, MA: Sinauer Associates.

Martin, C.H. 1961. A revision of the genus *Lissoteles* (Diptera, Asilidae). American Museum Novitates 2027: 1–13.

Martin, C.H. 1968. The new family Leptogastridae (the grass flies) compared with the Asilidae (robber flies) (Diptera). Journal of the Kansas Entomological Society 41(1): 70–100.

Mayr, E. 1974. Cladistic analysis or cladistic classification? Zeitschrift für Zoologische Systematik und Evolutionsforschung 12: 94–128.

Mayr, E. 1981. Biological classification: towards a synthesis of opposing methodologies. Science 214(4520): 510–516.

Mazzarolo, L.A. 1999. Morfologia externa e análise filogenética de Laphriinae (Diptera: Asilidae). Ph.D. dissertation, Universidade de São Paulo, Ribeirão Preto: São Paulo, Brazil.

McAlpine, J.F. 1981. Morphology and terminology—adults. *In* J.F. McAlpine, B.V. Peterson, G.E. Shell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood (editors), Manual of Nearctic Diptera. Vol. 1. Research Branch Monograph 27: 9–63. Hull (Quebec): Agriculture Canada.

Melin, D. 1923. Contributions to the knowledge of the biology, metamorphosis and distribution of the Swedish asilids in relation to the whole family of asilids. Zoologiska Bidrag från Uppsala 8: 1–317.

Mickoleit, G. 1973. Über den Ovipositor der Neuropteroidea und Coleoptera und seine phylogenetische Bedeutung (Insecta, Holometabola). Zeitschrift für Morphologie der Tiere 74: 37–64.

Mostovski, M.B. 1999. A brief review of brachycerous flies (Diptera, Brachycera) in the Mesozoic, with descriptions of some curious taxa. *In* Proceedings of the First Palaeoentomological Conference, Moscow, 1998, 103–110. Bratislava: Amba Projects, AM/PFICM98/1.99. P.

Nichols, S.W. 1989. The Torre-Bueno glossary of entomology. New York: New York Entomological Society.

Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407–414.

Nixon, K.C. 2001. WinClada (version 0.9.99.88beta). Ithaca, NY: Cornell University. Distributed by the author.

Oldroyd, H. 1964. The natural history of flies. New York: W.W. Norton.

Oldroyd, H. 1969. The family Leptogastridae (Diptera). Proceedings of the Royal Entomological Society of London. Series B, Taxonomy 38(1–2): 27–31.

Oldroyd, H. 1974a. Some comments on the tribal classification of Asilidae (Diptera). Israel Journal of Entomology 9: 5–21.

Oldroyd, H. 1974b. An introduction to the robber flies (Diptera: Asilidae) of South Africa. Annals of the Natal Museum 22(1): 1–172.

Osten-Sacken, C.R. 1884. An essay of comparative chaetotaxy, or the arrangement of characteristic bristles of Diptera. Transactions of the Entomological Society of London 1884(4): 497–517.

Ovtshinnikova, O.G. 1989. Musculature of the male genitalia in Brachycera-Orthorrhapha (Diptera). Proceedings of the Zoological Institute USSR Academy of Sciences 190: 1–167.

Ovtshinnikova, O.G., and D.K. Yeates. 1998. Male genital musculature of Therevidae and Scenopinidae (Diptera: Asiloidea): structure, homology and phylogenetic implications. Australian Journal of Entomology 37: 27–33.

Owsley, W.B. 1946. The comparative morphology of internal structures of the Asilidae (Diptera). Annals of the Entomological Society of America 39: 33–68.

Papavero, N. 1973a. Studies of Asilidae (Diptera) systematics and evolution. I. A preliminary classification in subfamilies. Arquivos de Zoologia 23(3): 217–274.

Papavero, N. 1973b. Studies of Asilidae (Diptera) systematics and evolution. II. The tribes of

Dasypogoninae. Arquivos de Zoologia 23(4): 275–294.

Papavero, N. 1975. Studies of Asilidae (Diptera) systematics and evolution. IV. Tribe Megapodini Carrera (Dasypogoninae), with a review of the Neotropical species. Arquivos de Zoologia 26(3): 191–318.

Papavero, N., and J. Wilcox. 1974. Studies of Mydidae (Diptera) systematics and evolution. I. A preliminary classification in subfamilies, with the description of two new genera from the Oriental and Australian regions. Arquivos de Zoologia 25(1): 1–34.

Peterson, B.V. 1981. Family Apioceridae. *In* J.F. McAlpine, B.V. Peterson, G.E. Shell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood (editors), Manual of Nearctic Diptera. Vol. 1. Research Branch Monograph 27: 541–548. Hull (Quebec): Agriculture Canada.

Poulton, E.B. 1904. The mimicry of Aculeata by the Asilidae and *Volucella*, and its probable significance. Transactions of the Entomological Society of London 1904(3): 661–665.

Reichardt, H. 1929. Untersuchungen über den Genitalapparat der Asiliden. Zeitschrift für Wissenschaftliche Zoologie 135(3–4): 257–301.

Sabrosky, C.W. 1999. Family-group names in Diptera: an annotated catalog. Myia 10: 1–360.

Scarbrough, A.G. 2005. *Afroestricus*, a new Afrotropical ommatine (Diptera: Asilidae) genus with twenty species and two species groups. Zootaxa 1041: 1–76.

Schiner, J.R. 1862. Fauna Austriaca. Die Fliegen (Diptera): nach der analytischen Methode bearbeitet. 1. Vienna: C. Gerold's Sohn.

Sinclair, B.J., and J.M. Cumming. 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). Zootaxa 1180: 1–172.

Sinclair, B.J., J.M. Cumming, and D.M. Wood. 1994. Homology and phylogenetic implications of male genitalia in Diptera – Lower Brachycera. Entomologica Scandinavica 24: 407–432.

Snodgrass, R.E. 1902. The inverted hypopygium of *Dasyllis* and *Laphria*. Psyche 9: 399–400.

Snodgrass, R.E. 1944. The feeding apparatus of biting and sucking insects affecting man and animals. Smithsonian Miscellaneous Collections 104(7): 1–113.

Stuckenberg, B.R. 1999. Antennal evolution in the Brachycera (Diptera), with a reassessment of terminology relating to the flagellum. Studia Dipterologica 6(1): 33–48.

Stuckenberg, B.R. 2001. Pruning the tree: a critical review of classification of the Homeodactyla (Diptera, Brachycera), with new perspectives and an alternative classification. Studia Dipterologica 8(1): 3–41.

Theodor, O. 1976. On the structure of the spermathecae and aedeagus in the Asilidae and their importance in the systematics of the family. Jerusalem: Israel Academy of Sciences and Humanities.

Walker, F. 1851. Insecta Britannica. Diptera. Vol. I. London: Reeve and Benham.

Webb, D.W. 1974. A revision of the genus *Hilarimorpha* (Diptera: Hilarimorphidae). Journal of the Kansas Entomological Society 47: 172–222.

Wheeler, Q.D. 1995. The "old systematics": classification and phylogeny. *In* J. Pakaluk and S.A. Slipinski (editors), Biology, phylogeny, and c lassification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson, 31–62. Warsawa: Muzeum i Instytut Zoologii PAN.

Wilcox, J. 1981. Family Mydidae. *In* J.F. McAlpine, B.V. Peterson, G.E. Shell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood (editors), Manual of Nearctic Diptera. Vol. 1. Research Branch Monograph 27: 533–540. Hull (Quebec): Agriculture Canada.

Wood, G.C. 1981. Family Asilidae. *In* J.F. McAlpine, B.V. Peterson, G.E. Shell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood (editors), Manual of Nearctic Diptera. Vol. 1. Research Branch Monograph 27: 549–573. Hull (Quebec): Agriculture Canada.

Woodley, N.E. 1989. Phylogeny and classification of the 'orthorrhaphous' Brachycera. *In* J.F. McAlpine and D.M. Wood (editors), Manual of Nearctic Diptera. Vol. 3. Research Branch Monograph 32: 1371–1395. Hull (Quebec): Agriculture Canada.

Yeates, D.K. 1994. The cladistics and classification of the Bombyliidae (Diptera: Asiloidea). Bulletin of the American Museum of Natural History 219: 1–191.

Yeates, D.K. 2002. Relationships of extant lower Brachycera (Diptera): a quantitative synthesis of morphological characters. Zoologica Scripta 31: 105–121.

Yeates, D.K., and M.E. Irwin. 1996. Apioceridae (Insecta: Diptera): cladistic reappraisal and biogeography. Zoological Journal of the Linnean Society 116: 247–301.

Yeates, D.K., and B.M. Wiegmann. 1999. Congruence and controversy: toward a higher-level phylogeny of Diptera. Annual Review of Entomology 44: 397–428.

Yeates, D.K., and B.M. Wiegmann. 2005. Phylogeny and evolution of Diptera: recent insights and new perspectives. *In* D.K. Yeates and B.M. Wiegmann (editors), The evolutionary biology of flies, 14–44. New York: Columbia University Press.

APPENDIX 1

Morphological matrix of 220 characters for 158 Asilidae species plus 17 outgroup taxa summarized in FASTA format (footnote is on page 169)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Neorhynchocephalus volaticus																																				
0	1	0	0	0	0	-	-	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0	1	1	2	1	0	1	0	0	0	0	1	2
Bombylius major																																				
0	1	0	0	0	0	-	-	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1	0	1	0	1	2	0	0	0	1	1
Poecilognathus sp. (El Hacha)																																				
0	1	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1	0	1	0	0	2	0	0	0	1	1
Prorates sp. (Escalante)																																				
0	1	0	0	0	0	-	-	2	1	1	1	0	0	0	0	0	4	0	0	0	0	0	3	0	1	0	0	1	0	0	2	0	0	0	1	1
Apsilocephala longistyla																																				
0	0	0	0	0	0	-	-	2	1	1	1	0	0	0	0	0	4	0	0	0	0	0	3	1	1	1	2	1	0	0	2	0	0	0	1	1
Hemigephyra atra																																				
0	0	0	0	0	0	-	-	2	1	1	1	0	2	0	0	0	4	2	0	0	0	0	3	0	1	0	0	1	0	0	2	0	0	0	1	1
Phycus frommeri																																				
0	0	0	0	0	0	-	-	2	1	1	1	0	2	0	0	0	4	2	0	0	0	0	3	1	1	1	2	1	0	0	2	0	0	0	1	1
Nemomydas brachyrhynchus																																				
0	0	1	4	2	1	3	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	3	1	1	0	2	1	0	0	2	0	0	0	1	1
Opomydas townsendi																																				
0	0	1	4	2	1	3	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	3	1	1	0	2	1	0	0	2	0	0	0	1	1
Pseudonomoneura hirta																																				
0	0	1	4	2	1	3	0	1	0	0	0	0	2	0	0	0	4	0	0	0	0	0	3	0	1	0	2	1	0	0	2	0	0	0	1	1
Afroleptomydas sp. (Clanwilliam)																																				
0	0	1	4	2	1	3	0	2	0	0	0	0	0	0	0	0	4	0	0	0	0	0	3	0	1	0	2	1	0	0	2	0	0	0	1	1
Mydas clavatus																																				
0	0	1	4	2	1	3	0	1	0	0	0	0	2	0	0	0	4	0	0	0	0	0	3	1	1	0	2	1	0	0	2	0	0	0	2	2
Mitrodetus dentitarsis																																				
0	0	1	4	2	1	3	0	0	0	0	0	0	2	0	0	0	4	0	0	0	0	0	3	0	1	0	2	1	0	0	2	0	0	0	1	1
Rhaphiomidas maehleri																																				
0	0	0	4	0	1	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	3	0	1	0	2	1	0	0	2	0	0	0	1	1
Neorhaphiomidas sp. (Mandurah)																																				
0	0	0	0	0	0	-	-	0	0	0	0	0	2	0	1	0	4	0	0	0	0	0	3	0	1	0	2	1	0	0	2	0	0	0	1	1
Apiocera aldrichi																																				
0	0	0	0	0	0	-	-	2	0	1	0	1	0	1	1	0	4	0	0	0	0	0	3	1	1	1	0	1	0	0	0	0	0	0	1	1
Apiocera painteri																																				
0	0	0	0	0	0	-	-	2	0	1	0	1	0	1	1	0	4	0	0	0	0	0	3	1	1	1	0	1	0	0	0	0	0	0	1	1
Apoclea algira																																				
0	0	2	2	0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Philodicus tenuipes																																				
0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Pogonioefferia pogonias																																				
0	0	2	4	0	1	3	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Proctacanthus philadelphicus																																				
0	0	2	3	0	1	2	0	2	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	1	1	2	0	0
Promachus amastrus																																				
0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Blepharotes splendidissimus																																				
0	0	2	4	0	1	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	2	0	1	1	0	1	1	2	0	0
Dasophrys crenulatus																																				
0	0	2	4	0	1	3	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Eichoichemus pyrrhomystax																																				
0	0	2	3	0	1	2	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Lochmorhynchus albicans																																				
0	0	2	3	0	1	2	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0

APPENDIX 1
(Extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Neorhynchocephalus volaticus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	-	1	0	1	2
Bombylius major	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	1	0	0	1	-	1	0	1	2
Poecilognathus sp. (El Hacha)	0	0	-	-	0	0	3	0	0	0	0	0	0	0	1	0	1	1	0	4	3	-	0	0	1	1	0	0	1	0	0	1	-	1	0	1	2
Prorates sp. (Escalante)	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	2	-	1	1	2	0
Apsilocephala longistyla	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	2	-	0	0	1	0
Hemigephyra atra	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0	0	0	0	0	0	0	2	0	1	2	1	0	0	2	1
Phycus frommeri	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	2	0	1	2	1	0	0	1	1
Nemomydas brachyrhynchus	0	0	-	-	0	1	2	0	0	0	0	0	0	1	0	0	3	0	1	4	3	-	1	1	0	1	0	0	1	0	1	1	1	1	0	1	0
Opomydas townsendi	0	0	-	-	0	1	2	0	0	0	0	0	0	1	0	0	3	1	1	4	3	-	1	1	0	1	0	0	1	0	1	0	1	1	0	1	0
Pseudonomoneura hirta	0	0	-	-	0	1	2	0	0	0	0	0	0	1	0	0	3	0	1	4	3	-	1	1	0	1	0	0	1	0	1	1	1	1	0	1	0
Afroleptomydas sp. (Clanwilliam)	0	0	-	-	0	1	2	0	0	0	0	0	0	1	0	0	3	0	1	4	3	-	1	1	0	1	0	0	2	0	1	1	1	1	0	1	0
Mydas clavatus	0	0	-	-	0	1	2	0	0	0	0	0	0	1	0	0	3	0	1	4	3	-	1	1	0	1	0	0	1	0	1	1	1	1	0	1	0
Mitrodetus dentitarsis	0	0	-	-	0	1	2	0	0	0	0	0	0	1	0	0	3	0	1	4	3	-	1	1	1	1	0	0	1	0	1	1	1	1	0	1	0
Rhaphiomidas maehleri	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	4	3	-	1	0	1	0	0	0	2	0	1	2	2	1	0	2	0
Neorhaphiomidas sp. (Mandurah)	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	5	1	0	4	3	-	1	0	1	0	0	0	2	0	1	2	1	1	0	1	0
Apiocera aldrichi	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	5	1	0	0	2	0	1	0	1	0	0	0	2	0	1	2	2	0	0	2	2
Apiocera painteri	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	5	1	0	0	2	0	1	0	1	0	0	0	2	0	1	2	2	0	0	2	2
Apoclea algira	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2
Philodicus tenuipes	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	5	1	0	0	2	0	0	0	1	0	1	0	2	0	1	2	1	0	1	1	2
Pogonioefferia pogonias	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	5	1	0	0	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2
Proctacanthus philadelphicus	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	5	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	2	0	1	2	2
Promachus amastrus	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	5	1	0	0	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2
Blepharotes splendidissimus	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	2	0	0	0	1	0	0	0	2	0	1	2	1	0	1	1	2
Dasophrys crenulatus	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	5	1	0	0	1	0	0	0	1	0	1	0	2	1	1	2	1	0	1	1	2
Eichoichemus pyrrhomystax	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	5	0	0	0	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2
Lochmorhynchus albicans	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	5	1	0	0	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2

APPENDIX 1
(Extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Neorhynchocephalus volaticus	0	0	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	2	1	1	1	1	1	0	0	0	0	0	-	0	0	0	0
Bombylius major	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	-	0	0	2	0
Poecilognathus sp. (El Hacha)	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	-	0	0	2	0
Prorates sp. (Escalante)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0
Apsilocephala longistyla	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	0	0	0	-	0	0	2	0
Hemigephyra atra	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	-	0	0	2	0
Phycus frommeri	0	0	0	1	0	0	0	0	2	0	0	0	0	2	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	0	0	0	-	0	0	2	0
Nemomydas brachyrhynchus	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	1	0	0	-	0	0	0	0
Opomydas townsendi	1	2	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	2	0	1	1	1	1	0	0	1	0	0	-	0	0	2	0
Pseudonomoneura hirta	1	2	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	2	0	0	0	1	1	0	0	0	0	0	-	0	0	2	0
Afroleptomydas sp. (Clanwilliam)	1	2	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	0	2	0	0	0	1	1	0	0	1	0	0	-	0	0	2	0
Mydas clavatus	1	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	0	0	1	0	0	-	0	0	2	0
Mitrodetus dentitarsis	1	2	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	1	0	0	1	0	0	-	0	0	2	0
Rhaphiomidas maehleri	0	1	1	0	1	0	1	0	0	1	0	0	0	3	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	0	0	-	0	0	2	0
Neorhaphiomidas sp. (Mandurah)	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	2	1	1	1	1	1	0	0	1	0	0	-	0	0	0	0
Apiocera aldrichi	0	1	0	0	1	0	0	0	0	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	0	0	-	0	0	2	0
Apiocera painteri	0	1	0	0	0	0	0	0	0	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	0	0	-	0	0	2	0
Apoclea algira	0	1	0	1	1	0	1	0	2	0	2	0	0	3	1	1	1	0	1	1	0	2	1	2	1	0	1	0	0	1	1	0	-	0	1	1	0
Philodicus tenuipes	0	1	0	0	1	0	1	0	2	0	2	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	1	0
Pogonioefferia pogonias	0	1	0	1	1	0	0	0	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	0	0
Proctacanthus philadelphicus	0	1	0	1	1	0	0	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Promachus amastrus	0	1	0	1	1	0	1	0	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	2	0
Blepharotes splendidissimus	0	1	0	0	1	0	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	0	0
Dasophrys crenulatus	0	1	0	1	1	0	0	0	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Eichoichemus pyrrhomystax	0	1	0	1	1	0	0	0	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Lochmorhynchus albicans	0	1	0	1	1	0	0	0	2	0	1	1	0	3	1	1	1	0	1	1	0	1	1	1	1	0	1	0	0	1	1	0	-	0	1	1	0

APPENDIX 1
(Extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Neorhynchocephalus volaticus	1	0	1	0	0	0	0	0	1	1	1	1	1	0	0	-	0	0	0	0	0	4	0	1	0	3	-	0	0	0	0	0	0	0	0	0	1
Bombylius major	1	0	1	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	-	0	-	1	1	0	0	0	0	1	1	0	1	0
Poecilognathus sp. (El Hacha)	1	0	1	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	1	0	-	1	-	1	1	0	0	0	0	0	1	1	1	0
Prorates sp. (Escalante)	0	1	1	0	0	0	0	0	1	1	1	1	1	0	0	2	0	1	0	0	0	1	0	0	1	2	1	0	1	0	0	0	0	1	0	1	0
Apsilocephala longistyla	2	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0
Hemigephyra atra	2	1	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0
Phycus frommeri	1	1	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0
Nemomydas brachyrhynchus	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	4	0	1	1	3	2	0	4	0	0	3	0	2	1	0	1
Opomydas townsendi	1	0	2	0	1	0	0	0	1	0	1	1	0	0	0	2	0	0	0	1	1	4	0	1	1	3	2	0	0	0	0	3	0	2	1	0	1
Pseudonomoneura hirta	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	4	1	1	1	3	2	0	4	0	0	3	0	2	1	2	1
Afroleptomydas sp. (Clanwilliam)	1	0	1	0	2	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	4	0	1	1	3	2	0	4	0	0	3	0	2	1	0	1
Mydas clavatus	1	0	1	1	2	0	0	1	0	0	0	1	0	0	0	2	0	0	0	1	1	4	0	1	1	3	2	0	0	0	0	3	0	2	0	0	1
Mitrodetus dentitarsis	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	2	0	0	0	1	1	4	1	1	1	3	2	0	4	2	0	3	0	2	0	0	1
Rhaphiomidas maehleri	2	0	0	0	1	0	0	0	1	1	1	1	0	0	0	2	0	0	0	1	0	4	0	1	1	3	2	0	0	0	0	0	0	0	0	0	0
Neorhaphiomidas sp. (Mandurah)	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	2	0	0	0	1	1	4	1	1	1	3	0	0	4	2	0	3	0	2	0	0	1
Apiocera aldrichi	2	1	1	0	1	0	0	0	1	1	1	1	0	0	0	2	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0
Apiocera painteri	2	1	1	0	1	0	0	0	1	1	1	1	0	0	0	2	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0
Apoclea algira	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0	0	1	1	1	0
Philodicus tenuipes	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	2	1	0
Pogonioefferia pogonias	2	0	2	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	3	0	1	1	2	0	0	0	0	0	0	0	0	1	1	0
Proctacanthus philadelphicus	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	3	0	1	1	2	0	0	0	0	0	0	0	0	0	1	0
Promachus amastrus	2	0	2	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0	1	0	1	1	2	0	0	0	0	0	0	0	1	2	1	0
Blepharotes splendidissimus	2	0	2	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	3	0	1	1	2	0	0	0	2	0	0	0	1	0	1	0
Dasophrys crenulatus	1	0	2	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Eichoichemus pyrrhomystax	2	0	2	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	3	0	1	1	2	0	0	0	0	0	0	0	1	2	1	0
Lochmorhynchus albicans	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	3	0	1	1	2	1	0	0	0	0	0	0	0	0	1	0

APPENDIX 1
(Extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Neorhynchocephalus volaticus	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	1	0	0	1	0	3	2	0	0	0	0
Bombylius major	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	8	1	2	1	1	0	0	0	1	1	3	2	0	0	0	0
Poecilognathus sp. (El Hacha)	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	0	0	1	1	1	1	0	0	0	0
Prorates sp. (Escalante)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	2	2	1	?	?	?	?	?	?	?	?	0	0	0
Apsilocephala longistyla	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	3	2	0	0	0	2
Hemigephyra atra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	7	-	0	2	0	1	0	0	1	1	3	1	0	0	1	0
Phycus frommeri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	2	2	1	0	0	0	1	1	3	1	0	0	0	0
Nemomydas brachyrhynchus	1	0	0	0	0	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Opomydas townsendi	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	2	1	0	1	0	1	1	0	1	0	0	1	3
Pseudonomoneura hirta	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	2	1	1	0	0	0	0	0	1	0	0	0	3
Afroleptomydas sp. (Clanwilliam)	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	2	1	1	0	0	0	1	0	1	0	0	0	3
Mydas clavatus	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	0	1	0	0	0	0	0	0
Mitrodetus dentitarsis	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2	2	1	2	-	-	0	0	1	2	0	0	0	1
Rhaphiomidas maehleri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2	2	1	0	0	0	1	0	1	0	0	0	1	0
Neorhaphiomidas sp. (Mandurah)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	2	2	2	1	?	?	?	?	?	?	?	?	0	0	1
Apiocera aldrichi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	2	2	2	1	0	?	0	1	1	?	?	0	0	0	0
Apiocera painteri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	7	2	2	2	1	0	?	0	1	1	?	?	0	0	0	0
Apoclea algira	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	-	0	2	2	0	0	1	0	0	3	2	0	1	0	1
Philodicus tenuipes	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	-	0	2	2	0	0	1	0	0	1	1	0	1	0	1
Pogonioefferia pogonias	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	1	1	0	0	0	1
Proctacanthus philadelphicus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	-	0	2	2	1	0	0	1	1	3	2	0	1	0	1
Promachus amastrus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	1	2	0	0	0	1	1	0	0	0	0	1	0	1
Blepharotes splendidissimus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	0	2	0	0	0	0	1	1	1	0	0	0	0	1
Dasophrys crenulatus	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	0	1	0	0	1	0	1
Eichoichemus pyrrhomystax	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	3	2	0	?	0	1
Lochmorhynchus albicans	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	3	2	0	1	0	1

APPENDIX 1
(Extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Neorhynchocephalus volaticus	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	2	0	0	1	2	0	0	1	0	0	0	2	0	1	0	0	0	0	1
Bombylius major	0	0	0	0	0	0	0	0	0	1	0	0	0	1	-	0	1	0	0	1	2	0	1	0	0	0	0	2	0	0	0	0	1	0	0
Poecilognathus sp. (El Hacha)	0	0	0	0	0	0	0	1	0	0	0	0	0	1	-	0	1	0	0	1	2	0	0	0	0	0	0	2	0	0	0	0	1	0	0
Prorates sp. (Escalante)	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	2	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0
Apsilocephala longistyla	0	0	0	0	0	0	0	0	0	0	0	0	2	1	-	0	1	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hemigephyra atra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0
Phycus frommeri	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	1	1	1	0
Nemomydas brachyrhynchus	0	0	0	0	0	0	1	5	0	0	0	1	0	2	0	0	2	0	0	0	-	-	0	0	0	0	0	0	0	1	0	1	1	-	0
Opomydas townsendi	0	0	0	0	0	0	1	5	0	0	0	0	0	1	-	0	0	0	1	0	-	-	0	0	0	0	0	0	0	1	0	1	0	-	0
Pseudonomoneura hirta	0	0	0	0	0	0	1	5	0	0	0	1	0	2	0	0	2	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0	-	0
Afroleptomydas sp. (Clanwilliam)	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	2	0	0	0	-	-	0	0	0	0	0	0	1	1	0	1	1	-	0
Mydas clavatus	0	0	0	0	0	0	1	5	0	0	0	1	0	2	0	0	2	0	1	0	-	-	0	0	0	0	0	0	0	1	0	1	1	-	0
Mitrodetus dentitarsis	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	0	2	0	1	0	-	-	0	0	0	1	0	2	0	1	0	1	1	1	0
Rhaphiomidas maehleri	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	2	0	1	0	-	-	0	0	0	0	0	0	0	1	0	1	1	-	0
Neorhaphiomidas sp. (Mandurah)	0	0	0	0	0	0	0	5	0	0	0	1	0	2	0	0	2	0	1	0	-	-	1	0	0	0	0	0	0	1	0	1	1	-	0
Apiocera aldrichi	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Apiocera painteri	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Apoclea algira	1	1	1	1	1	0	0	0	0	0	0	1	0	0	-	1	0	0	2	1	0	0	0	1	0	0	0	0	2	1	0	1	0	-	0
Philodicus tenuipes	1	1	1	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	2	1	0	0	0	1	0	0	0	0	2	1	0	1	0	-	0
Pogonioefferia pogonias	0	0	0	0	0	0	0	0	0	0	1	1	0	0	-	2	0	0	0	1	0	0	0	1	0	0	0	0	2	1	0	1	0	-	0
Proctacanthus philadelphicus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	-	0
Promachus amastrus	1	1	1	1	1	0	0	0	0	0	0	1	0	0	-	1	0	0	2	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Blepharotes splendidissimus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Dasophrys crenulatus	1	1	1	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Eichoichemus pyrrhomystax	1	1	0	0	0	0	0	0	0	0	1	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Lochmorhynchus albicans	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0

APPENDIX 1
(Continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Megaphorus pulchrus	0	0	2	2	0	1	3	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Myaptex brachyptera	0	0	2	2	0	1	1	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Neolophonotus bimaculatus	0	0	2	4	0	1	3	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Nomomyia murina	0	0	2	3	0	1	2	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Asilus crabroniformis	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	1	1	2	0	0
Asilus sericeus	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Satanas gigas	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	1	2	0	0
Lycomya germainii	0	0	2	1	0	1	0	0	2	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Machimus chrysitis	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Machimus occidentalis	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Neomochtherus pallipes	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Afromochtherus mendax	0	0	2	2	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Dysmachus trigonus	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Philonicus albiceps	0	0	2	2	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Clephydroneura sundaica	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Clephydroneura sp. (Kepong)	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Colepia rufiventris	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	2	0	0
Congomochtherus inachus	0	0	2	2	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Heligmonevra laevis	0	0	2	2	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Neoitamus cyanurus	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Threnia carbonaria	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Tolmerus atricapillus	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Zosteria rosevillensis	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Blepharepium cajennensis	0	0	1	2	0	1	0	0	2	0	0	1	0	0	1	0	0	2	1	0	0	0	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Brachyrhopala ruficornis	0	0	2	1	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Cabasa pulchella	0	0	2	1	0	1	0	0	2	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1

APPENDIX 1

(Continued, extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Megaphorus pulchrus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	1	0	1	0	1	0	1	1	1	0	1	1	2
Myaptex brachyptera	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2
Neolophonotus bimaculatus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	1	1	2	1	0	1	1	2
Nomomyia murina	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	2	0	1	1	1	0	1	1	2
Asilus crabroniformis	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	1
Asilus sericeus	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	2	0	0	0	1	0	1	0	2	0	1	2	1	0	1	1	1
Satanas gigas	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	0	2	0	1	2	2	0	1	1	1
Lycomya germainii	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	0	0	0	2	0	0	0	2	0	1	2	1	0	1	1	2
Machimus chrysitis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	1
Machimus occidentalis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	2	0	1	2	1	0	1	1	1
Neomochtherus pallipes	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	2	0	1	2	1	0	1	1	1
Afromochtherus mendax	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	1
Dysmachus trigonus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	1
Philonicus albiceps	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	1
Clephydroneura sundaica	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	2	0	1	2	1	0	1	1	1
Clephydroneura sp. (Kepong)	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	2	0	1	2	1	0	1	1	1
Colepia rufiventris	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	2	0	1	2	1	0	1	1	3
Congomochtherus inachus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	1
Heligmonevra laevis	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	2	0	0	0	2	0	0	0	2	0	1	2	1	0	1	1	1
Neoitamus cyanurus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	1	1	2	1	0	1	1	3
Threnia carbonaria	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	0	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	2
Tolmerus atricapillus	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	2	0	1	2	1	0	1	1	1
Zosteria rosevillensis	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	3
Blepharepium cajennensis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	4	3	-	0	0	2	0	0	2	2	0	1	2	1	0	1	2	1
Brachyrhopala ruficornis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	1	0	0	1	1	3
Cabasa pulchella	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	3

APPENDIX 1
(Continued, extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Megaphorus pulchrus	0	1	0	1	1	0	1	0	1	0	1	1	0	2	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0	-	0	1	0	0
Myaptex brachyptera	0	1	0	1	1	0	0	0	2	0	1	2	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	2	0
Neolophonotus bimaculatus	0	1	0	1	1	0	0	0	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Nomomyia murina	0	1	0	1	1	0	0	0	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	1	0
Asilus crabroniformis	0	1	0	1	1	0	1	1	2	0	2	2	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Asilus sericeus	0	1	0	0	1	0	1	1	2	0	2	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	0/1	0
Satanas gigas	0	1	0	1	1	0	1	1	2	0	2	2	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Lycomya germainii	0	1	0	1	1	0	1	1	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	0/1	0
Machimus chrysitis	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Machimus occidentalis	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Neomochtherus pallipes	0	1	0	1	1	0	0	1	2	0	2	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Afromochtherus mendax	0	1	0	1	1	0	0	1	2	0	2	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Dysmachus trigonus	0	1	0	1	1	0	1	1	2	0	2	1	0	3	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Philonicus albiceps	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Clephydroneura sundaica	0	1	0	1	1	0	1	1	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0	-	0	1	2	0
Clephydroneura sp. (Kepong)	0	1	0	1	1	0	1	1	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0	-	0	1	2	0
Colepia rufiventris	0	1	0	1	1	0	1	1	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	0	0
Congomochtherus inachus	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Heligmonevra laevis	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	0	0
Neoitamus cyanurus	0	1	0	1	1	0	1	1	2	0	2	2	0	3	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Threnia carbonaria	0	1	0	1	1	0	1	1	2	0	2	2	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	2	0
Tolmerus atricapillus	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	0	0	1	1	0	-	0	1	2	0
Zosteria rosevillensis	0	1	0	1	1	0	1	1	2	0	2	1	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	1	0	1	1	0	-	0	1	0	0
Blepharepium cajennensis	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	1	2	0	2	1	2	0
Brachyrhopala ruficornis	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	1	1	2	0	1	1	2	0
Cabasa pulchella	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	2	0	0	0	0	0	1	1	2	0	1	1	2	0

APPENDIX 1

(Continued, extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Megaphorus pulchrus	1	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	0	1	1	2	0	0	1	0	0	0	0	1	2	1	0
Myaptex brachyptera	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Neolophonotus bimaculatus	1	0	2	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Nomomyia murina	1	0	2	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	1	1	1	0
Asilus crabroniformis	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Asilus sericeus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	2	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Satanas gigas	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	3	0	1	1	2	0	0	1	2	0	0	0	0	0	2	0
Lycomya germainii	2	0	2	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	2	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Machimus chrysitis	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Machimus occidentalis	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Neomochtherus pallipes	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Afromochtherus mendax	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Dysmachus trigonus	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Philonicus albiceps	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Clephydroneura sundaica	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Clephydroneura sp. (Kepong)	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Colepia rufiventris	2	0	2	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Congomochtherus inachus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Heligmonevra laevis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Neoitamus cyanurus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Threnia carbonaria	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Tolmerus atricapillus	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Zosteria rosevillensis	1	0	2	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	2	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Blepharepium cajennensis	2	0	2	0	0	0	0	2	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	2	1	0	0	1	0	0	0	1	0	1	0
Brachyrhopala ruficornis	1	0	1	0	2	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0
Cabasa pulchella	1	0	1	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0

APPENDIX 1
(Continued, extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Megaphorus pulchrus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	1	2	0	0	0	0	1	1	1	0	0	1	0	1
Myaptex brachyptera	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	2	0	3	-	0	2	0	1	0	0	1	1	3	2	0	1	0	1
Neolophonotus bimaculatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	-	0	2	0	0	0	1	0	0	0	0	0	0	0	1
Nomomyia murina	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	2	-	1	2	0	0	0	0	1	1	1	0	0	0	0	1
Asilus crabroniformis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	-	0	2	0	0	0	0	1	1	0	0	0	1	0	1
Asilus sericeus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	-	0	2	0	0	0	0	1	1	1	1	0	1	0	1
Satanas gigas	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	2	-	0	2	2	0	0	0	1	1	0	0	0	0	0	1
Lycomya germainii	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	0	2	0	0	0	0	1	1	1	0	0	0	0	1
Machimus chrysitis	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	1	1	0	1	0	1
Machimus occidentalis	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	1	1	0	1	0	1
Neomochtherus pallipes	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	2	-	0	2	0	0	0	0	1	1	1	0	0	1	0	1
Afromochtherus mendax	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	2	-	0	2	0	0	0	0	1	1	1	1	0	1	0	1
Dysmachus trigonus	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	1	0	0	1	0	1
Philonicus albiceps	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	2	-	0	2	2	0	0	0	1	1	1	1	0	1	0	1
Clephydroneura sundaica	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	2	2	0	1	0	1
Clephydroneura sp. (Kepong)	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	2	2	0	1	0	1
Colepia rufiventris	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	2	-	0	2	0	0	0	1	0	1	3	1	0	0	0	1
Congomochtherus inachus	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	2	0	2	-	0	2	0	0	0	0	1	1	1	1	0	1	0	1
Heligmonevra laevis	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	2	-	0	2	0	0	0	0	1	1	2	0	0	0	0	1
Neoitamus cyanurus	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	2	0	2	-	0	2	0	0	0	1	1	1	0	0	0	0	0	1
Threnia carbonaria	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	6	-	0	2	0	0	0	1	0	1	0	0	0	0	0	1
Tolmerus atricapillus	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	2	0	3	-	0	2	0	0	0	0	1	1	0	0	0	1	0	1
Zosteria rosevillensis	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	2	-	1	2	2	0	0	0	1	0	3	1	0	0	0	1
Blepharepium cajennensis	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	2	0	1	0	0	0	0	1	1	2	1	0	0	2
Brachyrhopala ruficornis	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	1	1	0	0	1	1	1	1	2	0	0	0	2
Cabasa pulchella	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	1	1	0	0	1	1	1	1	2	0	0	0	3

APPENDIX 1
(Continued, extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Megaphorus pulchrus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	2	1	1	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Myaptex brachyptera	1	1	1	1	1	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0	-	0
Neolophonotus bimaculatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Nomomyia murina	1	1	1	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Asilus crabroniformis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Asilus sericeus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Satanas gigas	1	1	1	1	1	1	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Lycomya germainii	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	1	1	-	0
Machimus chrysitis	1	1	1	1	0	0	0	0	1	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Machimus occidentalis	1	1	1	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	0	1	1	-	0
Neomochtherus pallipes	1	1	1	1	1	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	0	1	1	-	0
Afromochtherus mendax	1	1	1	1	0	0	0	0	2	0	0	1	0	0	-	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	0	1	1	-	0
Dysmachus trigonus	1	1	1	1	1	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Philonicus albiceps	1	1	1	1	1	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Clephydroneura sundaica	1	1	1	0	0	0	0	0	0	0	1	1	0	0	-	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	0	1	1	-	0
Clephydroneura sp. (Kepong)	1	1	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	1	0	0	0	0	2	1	0	1	1	-	0
Colepia rufiventris	1	1	1	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	1	1	-	0
Congomochtherus inachus	1	1	1	1	1	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Heligmonevra laevis	1	1	1	1	1	0	0	0	2	0	0	1	0	0	-	1	0	0	1	1	2	0	0	1	0	0	0	0	2	1	0	1	1	-	0
Neoitamus cyanurus	1	1	1	1	0	0	0	0	0	0	1	1	0	0	-	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	-	0
Threnia carbonaria	1	1	1	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	2	0	0	1	0	1	0	0	0	1	0	0	0	-	0
Tolmerus atricapillus	1	1	1	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	1	-	0
Zosteria rosevillensis	1	1	1	1	1	1	0	0	2	0	0	1	0	0	-	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	1	-	0
Blepharepium cajennensis	0	0	0	0	0	0	0	4	0	1	0	1	0	1	-	1	0	0	1	1	1	0	0	0	0	0	0	2	0	0	0	0	1	0	1
Brachyrhopala ruficornis	0	0	0	0	0	0	0	4	0	0	0	0	0	0	-	1	1	0	1	1	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Cabasa pulchella	0	0	0	0	0	0	0	4	0	0	0	0	0	0	-	1	1	0	1	1	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0

APPENDIX 1
(Continued, extended)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Chrysopogon pilosifacies	0	0	1	4	0	1	0	0	2	0	1	1	0	0	1	0	0	2	0	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Codula limbipennis	0	0	1	4	0	1	0	0	2	0	1	1	0	0	1	0	0	2	0	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Cyrtophrys attenuatus	0	0	2	1	0	1	0	0	2	0	1	1	0	0	1	0	0	2	2	0	0	0	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Deromyia fuscipennis	0	0	2	1	0	1	0	0	2	0	1	1	0	0	1	0	0	2	2	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Dasypogon diadema	0	0	1	4	0	1	1	0	2	0	1	1	0	0	1	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Austrosaropogon nigrinus	0	0	1	1	0	1	0	0	2	0	1	1	0	0	1	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Lestomyia fraudiger	0	0	2	3	0	1	2	0	2	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Megapoda labiata	0	0	2	4	0	1	0	0	2	0	0	0	0	0	1	0	1	2	2	0	1	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Pseudorus distendens	0	0	1	2	0	0	-	-	2	0	0	0	0	0	1	0	0	2	2	0	1	0	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Molobratia teutonus	0	0	2	4	0	1	1	0	2	0	1	1	0	0	1	0	0	2	0	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Neodiogmites melanogaster	0	0	2	4	0	1	0	0	2	0	1	1	0	0	1	0	0	2	2	0	0	0	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Diogmites grossus	0	0	1	2	0	1	0	0	2	0	1	1	0	0	1	0	0	2	0	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Pegesimallus laticornis	0	0	2	4	0	1	1	0	2	0	0	0	0	0	1	0	0	2	2	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Saropogon dispar	0	0	1	4	0	1	0	0	2	0	1	1	0	0	1	0	0	0	2	0	0	0	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Saropogon luteus	0	0	1	1	0	1	0	0	2	0	1	1	0	0	1	0	0	0	2	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1
Senobasis corsair	0	0	2	1	0	1	0	0	2	0	0	0	0	0	1	0	0	2	2	0	1	0	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1
Thereutria amaraca	0	0	1	2	0	1	1	0	2	0	1	1	0	0	1	0	0	0	2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Cophura brevicornis	0	0	1	4	0	1	0	0	2	0	1	1	0	0	1	0	0	0	2	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1
Leptarthrus brevirostris	0	0	1	4	0	1	3	0	2	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1
Nicocles politus	0	0	2	4	0	1	0	0	2	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1
Dioctria atricapillus	0	0	2	2	0	1	0	0	2	0	0	0	0	2	1	0	0	3	1	1	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Dioctria hyalipennis	0	0	2	2	0	1	1	0	2	0	0	0	0	2	1	0	0	3	1	1	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Dioctria rufipes	0	0	2	2	0	1	1	0	2	0	0	0	0	2	1	0	0	3	1	1	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Broticosia paramonovi	1	0	1	2	0	1	3	0	2	0	1	0	0	2	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	1
Nannodioctria sp. (formicaphaga)	0	0	2	1	0	1	0	0	2	0	1	0	0	2	1	0	0	3	1	1	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Echthodopa pubera	0	0	2	2	0	1	1	0	2	0	1	1	0	2	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1	1	1	0	1

APPENDIX 1

(Continued, extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Chrysopogon pilosifacies	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	2	3	-	0	0	1	0	0	0	1	0	1	1	1	0	1	1	3
Codula limbipennis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	2	3	-	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Cyrtophrys attenuatus	1	1	2	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	5	3	-	0	0	1	0	0	1	2	0	1	1	1	0	1	1	3
Deromyia fuscipennis	1	1	2	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	2	3	-	0	0	1	0	0	1	2	0	1	1	1	0	1	0	3
Dasypogon diadema	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	2	0	0	0	2	0	0	2	2	0	1	2	2	0	1	1	3
Austrosaropogon nigrinus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	3
Lestomyia fraudiger	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	1	2	0	0	0	2	0	1	2	2	0	1	2	2	0	1	2	3
Megapoda labiata	1	1	2	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	1	2	0	0	0	1	0	0	2	2	0	1	2	1	0	1	1	3
Pseudorus distendens	1	1	2	0	0	0	0	-	0	0	0	0	0	1	1	0	2	0	0	4	3	-	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Molobratia teutonus	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	2	1	0	0	2	0	0	0	2	0	0	2	2	0	1	2	1	0	1	0	3
Neodiogmites melanogaster	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	4	3	-	0	0	2	0	0	2	2	0	1	2	2	0	1	2	3
Diogmites grossus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	4	3	-	0	0	2	0	0	2	2	0	1	1	1	0	1	2	3
Pegesimallus laticornis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	1	0	0	1	2	0	1	1	1	0	1	1	3
Saropogon dispar	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	2	1	0	1	2	0	0	0	2	0	0	2	2	0	1	2	2	0	1	2	3
Saropogon luteus	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	1	2	1	0	1	2	0	0	0	2	0	0	2	2	0	1	2	2	0	1	2	3
Senobasis corsair	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	4	3	-	0	0	1	0	0	1	2	0	1	1	1	0	1	1	3
Thereutria amaraca	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	2	1	0	4	3	-	0	0	1	0	0	2	2	0	1	2	2	0	1	2	3
Cophura brevicornis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	2	0	0	0	2	0	0	0	2	0	1	1	1	0	1	0	3
Leptarthrus brevirostris	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Nicocles politus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	1	1	1	0	1	1	3
Dioctria atricapillus	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	3	2	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Dioctria hyalipennis	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	3	2	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Dioctria rufipes	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	3	2	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Broticosia paramonovi	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	3	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	3
Nannodioctria sp. (formicaphaga)	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	2	1	0	3	2	0	0	0	1	0	0	0	2	0	1	0	0	0	1	0	3
Echthodopa pubera	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	3	2	0	0	0	2	0	0	0	2	1	1	2	1	0	1	1	3

APPENDIX 1

(Continued, extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Chrysopogon pilosifacies	0	1	0	0	1	0	0	0	1	0	0	0	0	4	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	1	1	2	0	1	1	2	0
Codula limbipennis	0	1	0	0	1	0	0	0	1	0	0	0	0	4	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Cyrtophrys attenuatus	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	2	1	2	1	2	0
Deromyia fuscipennis	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	2	1	2	1	2	0
Dasypogon diadema	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	0	1	2	0	0	0	0	0	1	1	2	1	2	1	2	0
Austrosaropogon nigrinus	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	1	0	1	1	2	0	1	1	2	0
Lestomyia fraudiger	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	2	0	1	1	2	0
Megapoda labiata	0	1	0	0	1	0	0	1	1	0	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	0	0	1	1	2	1	2	0	2	0
Pseudorus distendens	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0	1	1	2	1	2	0	2	0
Molobratia teutonus	0	1	0	0	1	0	0	0	1	0	0	0	0	2	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	2	1	2	1	2	0
Neodiogmites melanogaster	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	2	0	1	1	2	0
Diogmites grossus	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	1	2	0	1	1	2	0
Pegesimallus laticornis	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	1	0	1	1	0	0	0	0	1	1	2	1	2	1	2	0
Saropogon dispar	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	1	2	1	2	1	2	0
Saropogon luteus	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	1	2	1	2	1	2	0
Senobasis corsair	0	1	0	0	1	0	0	0	1	0	0	0	0	2	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0	1	1	2	1	2	1	2	0
Thereutria amaraca	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	1	0	1	1	2	0
Cophura brevicornis	0	1	0	0	1	0	0	0	1	0	0	0	0	2	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	1	1	0	0	1	2	0
Leptarthrus brevirostris	0	1	0	1	1	0	0	0	1	0	0	0	0	3	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	0	0	1	2	0
Nicocles politus	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	1	0	0	1	2	0
Dioctria atricapillus	1	1	0	2	2	0	0	0	2	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Dioctria hyalipennis	1	1	0	2	2	0	0	0	2	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Dioctria rufipes	1	1	0	2	2	0	0	0	2	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Broticosia paramonovi	0	1	0	0	1	0	0	0	2	0	0	1	0	2	1	1	1	1	1	1	0	1	1	1	1	0	1	0	0	1	1	0	-	0	1	2	0
Nannodioctria sp. (formicaphaga)	0	1	0	0	1	0	0	0	2	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	0	0	0	0	0	1	1	0	-	0	1	2	0
Echthodopa pubera	0	1	0	2	2	0	0	0	2	0	1	1	0	3	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0

APPENDIX 1

(Continued, extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Chrysopogon pilosifacies	1	0	1	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Codula limbipennis	1	0	1	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Cyrtophrys attenuatus	1	0	1	0	0	0	0	2	1	1	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	2	0	0	0	0	0	1	0	1	0	1	0
Deromyia fuscipennis	1	0	1	0	0	0	0	2	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	2	1	0	0	0	0	1	0	1	0	1	0
Dasypogon diadema	2	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Austrosaropogon nigrinus	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	1	0	1	0
Lestomyia fraudiger	2	0	1	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Megapoda labiata	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Pseudorus distendens	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Molobratia teutonus	2	0	1	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1	0	1	0	1	0	1	0
Neodiogmites melanogaster	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	1	0	1	0
Diogmites grossus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	1	0	1	0
Pegesimallus laticornis	1	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	1	0	2	0	1	0	1	0
Saropogon dispar	2	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Saropogon luteus	2	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Senobasis corsair	1	0	1	0	0	0	0	2	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	1	0	0	1	0	1	0	1	0	1	0
Thereutria amaraca	2	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Cophura brevicornis	1	1	2	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Leptarthrus brevirostris	1	0	2	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0
Nicocles politus	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Dioctria atricapillus	1	2	2	0	0	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Dioctria hyalipennis	1	2	2	0	0	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Dioctria rufipes	1	2	2	0	0	0	2	0	0	1	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Broticosia paramonovi	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Nannodioctria sp. (formicaphaga)	1	2	2	0	0	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Echthodopa pubera	1	0	2	0	1	0	2	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0

APPENDIX 1
(Continued, extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Chrysopogon pilosifacies	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	1	1	1	2	1	0	0	0	1
Codula limbipennis	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	1	1	1	2	1	0	0	0	1
Cyrtophrys attenuatus	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	1	0	0	0	0
Deromyia fuscipennis	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	1	1	0	0	0	0
Dasypogon diadema	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	2	1	1	0	0	0	1	1	1	1	0	0	0	2
Austrosaropogon nigrinus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	2	1	1	0	0	0	1	1	0	0	0	0	0	2
Lestomyia fraudiger	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	0	0	0	0	2
Megapoda labiata	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0	0	0	1	1	1	?	?	?	?	?
Pseudorus distendens	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	3	-	2	1	0	0	0	0	1	1	1	1	1	0	0	0
Molobratia teutonus	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	2	2	0	0	0	0	1	1	2	1	0	0	0	0
Neodiogmites melanogaster	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	2	0	1	0	0	0	0	1	1	2	0	0	0	0
Diogmites grossus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	2	1	1	0	0	0	0	1	1	2	0	0	0	0
Pegesimallus laticornis	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	2	1	1	0	0	0	1	1	1	1	0	0	0	0
Saropogon dispar	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	2	1	1	0	0	0	1	1	2	2	0	0	0	2
Saropogon luteus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	2
Senobasis corsair	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	-	0	2	0	0	0	0	1	1	1	2	1	0	0	0
Thereutria amaraca	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	6	0	2	1	1	0	0	0	1	1	1	2	0	0	0	0
Cophura brevicornis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	6	0	2	0	1	0	0	0	1	1	0	0	1	0	0	2
Leptarthrus brevirostris	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	-	2	2	0	0	0	0	1	1	2	0	1	0	0	0
Nicocles politus	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	6	0	2	0	1	0	0	0	1	1	1	2	1	0	0	2
Dioctria atricapillus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	0	1	0	0	1	0
Dioctria hyalipennis	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	0	1	0	0	1	0
Dioctria rufipes	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	0	1	0	0	1	0
Broticosia paramonovi	1	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Nannodioctria sp. (formicaphaga)	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	-	0	2	0	0	0	0	1	1	2	1	1	0	1	0
Echthodopa pubera	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	2	1	0	0	1	0

APPENDIX 1
(Continued, extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Chrysopogon pilosifacies	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	1	1	2	0	0	0	0	0	1	2	0	0	0	0	0	0	0
Codula limbipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cyrtophrys attenuatus	0	0	0	0	0	0	0	1	0	1	0	0	0	1	-	2	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Deromyia fuscipennis	0	0	0	0	0	0	0	4	0	1	0	0	0	1	-	2	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	1	-	0
Dasypogon diadema	0	0	0	0	0	0	0	0	0	1	0	0	0	1	-	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0
Austrosaropogon nigrinus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	1	1	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Lestomyia fraudiger	0	0	0	0	0	0	0	0	0	1	0	0	0	1	-	1	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Megapoda labiata	0	0	0	0	0	0	0	1	0	1	0	0	0	0	-	2	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	1	-	2
Pseudorus distendens	0	0	0	0	0	0	0	1	0	1	0	0	0	0	-	2	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	-	0
Molobratia teutonus	0	0	0	0	0	0	0	1	0	1	0	0	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Neodiogmites melanogaster	0	0	0	0	0	0	0	1	0	1	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Diogmites grossus	0	0	0	0	0	0	0	1	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	1	0	0
Pegesimallus laticornis	1	0	0	0	0	0	0	1	0	1	0	0	0	1	-	2	0	0	0	1	2	0	0	0	0	0	1	0	0	0	0	1	1	-	0
Saropogon dispar	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	1	0	1	1	2	0	0	0	0	1	0	2	0	0	0	0	0	0	0
Saropogon luteus	0	0	0	0	0	0	0	4	0	1	0	1	0	0	-	1	0	0	1	1	2	0	0	0	0	1	0	2	0	0	0	0	0	0	0
Senobasis corsair	0	0	0	0	0	0	0	1	0	1	0	0	0	1	-	2	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Thereutria amaraca	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	1	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Cophura brevicornis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Leptarthrus brevirostris	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	2	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Nicocles politus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	1	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Dioctria atricapillus	0	0	0	0	0	0	0	4	-	0	0	0	0	1	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Dioctria hyalipennis	0	0	0	0	0	0	0	4	-	0	0	0	0	1	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Dioctria rufipes	0	0	0	0	0	0	0	4	-	0	0	0	0	0	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Broticosia paramonovi	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Nannodioctria sp. (formicaphaga)	0	0	0	0	0	0	0	4	-	0	0	0	0	0	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Echthodopa pubera	0	0	0	0	0	0	0	4	-	0	0	1	0	0	-	0	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	-	0

APPENDIX 1

(Continued, extended)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Dicolonus simplex	0	0	1	3	0	1	2	0	2	0	1	0	0	2	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	1	0	1
Eudioctria albius	0	0	2	1	0	1	0	0	2	0	1	0	0	2	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1	1	1	0	1
Andrenosoma cyrtoxys	0	0	2	4	0	1	3	0	2	0	0	0	1	1	1	0	0	1	1	0	1	0	2	1	1	-	1	1	1	1	1	0	1	1	1	0	1
Hyperechia nigripennis	0	0	2	2	0	1	1	0	2	0	0	0	1	0	1	0	0	1	0	0	1	0	2	1	1	-	1	1	1	1	1	0	1	1	1	0	1
Pilica formidolosa	0	0	2	3	0	1	2	0	2	0	0	0	1	0	1	0	3	1	0	0	1	0	2	1	1	-	1	1	1	1	1	0	1	1	1	0	1
Dasyllis funebris	0	0	2	2	0	1	1	0	2	0	0	0	1	0	1	0	3	1	1	0	1	0	2	1	1	-	1	2	1	1	1	0	1	1	1	0	1
Proagonistes praeceps	0	0	2	3	0	1	2	0	2	0	0	0	1	1	1	0	3	1	1	0	1	0	2	1	1	-	1	1	1	1	1	0	1	1	1	0	1
Atomosia puella	0	0	2	2	0	1	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Aphestia annulipes	0	0	2	2	0	1	3	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	2	0	1	-	1	0	1	1	1	0	1	1	1	0	1
Cerotainia albipilosa	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1
Goneccalypsis argenteoviridis	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	-	1	0	1	1	1	0	1	1	1	0	1
Loewinella nigripes	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	-	1	0	1	1	1	0	1	1	1	0	0
Lamyra gulo	0	0	2	2	0	1	0	0	2	0	0	0	0	1	1	0	0	0	0	0	1	0	2	2	1	-	1	1	1	1	1	0	1	1	0	0	1
Stiphrolamyra angularis	0	0	2	4	0	1	2	0	2	0	0	0	0	0	1	0	0	0	0	0	1	0	2	2	1	-	1	1	1	1	1	0	1	1	0	0	1
Orthogonis scapularis	0	0	2	2	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	1	0	1	1	1	0	1	1	1	0	1
Smeryngolaphria numitor	0	0	2	3	0	1	3	0	2	0	0	0	0	1	1	0	0	0	1	0	0	0	1	2	0	0	1	0	1	1	1	0	1	1	1	0	1
Laphria flava	0	0	2	2	0	1	1	0	2	0	1	0	0	1	1	0	0	2	0	0	1	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1
Laphria aktis	0	0	2	2	0	1	1	0	2	0	1	0	0	1	1	0	0	2	0	0	1	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1
Choerades bella	0	0	2	2	0	1	1	0	2	0	1	0	0	1	1	0	0	2	0	0	1	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1
Lampria clavipes	0	0	2	2	0	1	1	0	2	0	1	0	0	1	1	0	0	2	0	0	1	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1
Laxenecera albicincta	0	0	2	4	0	1	3	0	2	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1
Maira aenea	0	0	2	2	0	1	1	0	2	0	1	0	0	1	1	0	0	2	0	0	1	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1
Nusa infumata	0	0	2	4	0	1	3	0	2	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1
Hoplistomerus nobilis	0	0	2	4	0	1	0	0	2	0	1	1	0	1	1	0	0	0	1	0	1	0	2	0	1	-	1	0	1	1	1	0	1	1	1	0	1
Laphystia aegyptiaca	0	0	2	4	0	1	0	0	2	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1
Laphystia tolandi	0	0	2	4	0	1	0	0	2	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1

APPENDIX 1

(Continued, extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Dicolonus simplex	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	3	2	0	0	0	1	0	0	0	2	1	1	1	1	0	1	1	3
Eudioctria albius	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	2	1	0	3	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	3
Andrenosoma cyrtoxys	1	1	1	0	1	0	0	0	0	0	0	1	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	2	1	0	1	1	1
Hyperechia nigripennis	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	1	0	4	3	-	0	0	1	0	0	2	2	0	1	1	1	0	1	1	1
Pilica formidolosa	1	1	1	0	1	0	0	0	1	0	0	1	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	2	1	0	1	1	1
Dasyllis funebris	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	2	1	0	1	1	1
Proagonistes praeceps	1	1	1	0	1	0	0	0	0	0	0	1	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	1
Atomosia puella	1	1	2	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	5	3	-	0	0	2	0	0	0	2	0	1	2	1	0	1	1	0
Aphestia annulipes	1	1	2	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	5	3	-	0	0	2	0	0	0	2	0	1	2	1	0	1	1	0
Cerotainia albipilosa	1	1	2	0	1	0	0	0	1	0	1	0	1	1	1	1	1	0	0	5	3	-	0	0	1	0	0	0	2	0	1	2	1	0	1	1	0
Goneccalypsis argenteoviridis	1	1	2	0	1	0	0	2	1	0	0	0	1	1	1	0	1	0	0	5	3	-	0	0	2	0	0	0	2	0	1	2	0	0	1	1	0
Loewinella nigripes	1	1	2	0	1	0	0	0	1	0	0	0	1	1	1	0	1	0	0	5	3	-	0	0	2	0	0	0	2	0	1	1	0	0	1	1	0
Lamyra gulo	1	1	1	0	1	0	0	0	1	1	0	1	0	1	1	0	2	1	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	2	1
Stiphrolamyra angularis	1	1	1	0	1	0	0	0	1	1	0	1	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	1
Orthogonis scapularis	1	1	2	0	1	0	0	2	1	0	0	0	0	1	1	0	1	1	0	5	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	1
Smeryngolaphria numitor	1	1	1	0	1	0	0	3	1	0	0	0	0	1	1	0	1	0	0	5	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	0
Laphria flava	1	1	2	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0	0	4	3	-	0	0	2	0	0	0	2	1	1	1	1	0	1	1	1
Laphria aktis	1	1	2	0	1	0	0	1	0	0	0	1	0	1	1	1	2	0	0	4	3	-	0	0	2	0	0	0	2	1	1	2	1	0	1	1	1
Choerades bella	1	1	2	0	1	0	0	1	1	0	0	0	0	1	1	1	2	0	0	4	3	-	0	0	2	0	0	0	1	0	1	1	1	0	1	1	1
Lampria clavipes	1	1	2	0	1	0	0	1	1	0	0	0	0	1	1	1	2	0/1	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	1
Laxenecera albicincta	1	1	1	0	1	0	0	0	1	0	0	1	0	1	1	0	2	1	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	1
Maira aenea	1	1	2	0	1	0	0	1	1	0	0	0	0	1	1	1	2	1	0	4	3	-	0	0	2	0	0	0	2	0	1	1	1	0	1	1	0
Nusa infumata	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	2	0	0	0	2	0	1	2	2	0	1	1	1
Hoplistomerus nobilis	1	1	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	0	1	2	0	0	0	2	0	0	0	2	0	1	1	1	0	1	2	0
Laphystia aegyptiaca	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	0
Laphystia tolandi	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	1	0	1	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	0

APPENDIX 1
(Continued, extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Dicolonus simplex	1	1	0	1	1	0	0	1	2	0	1	0	0	3	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Eudioctria albius	0	1	0	0	2	0	0	0	2	0	0	0	0	1	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	1	1	0	-	0	1	2	0
Andrenosoma cyrtoxys	1	1	0	1	1	1	0	0	2	0	1	1	0	2	1	1	1	1	1	1	0	1	1	2	1	1	0	0	0	1	1	0	-	0	0	2	0
Hyperechia nigripennis	1	1	0	1	1	1	0	0	1	0	1	1	0	3	1	1	0	0	1	1	0	1	1	1	1	1	1	0	0	1	1	0	-	0	0	0	0
Pilica formidolosa	1	1	0	1	1	1	0	1	2	0	1	1	0	1	1	1	1	1	1	1	0	1	1	2	1	1	1	1	0	1	1	0	-	0	0	2	0
Dasyllis funebris	1	1	0	1	1	1	0	1	2	0	1	1	0	1	1	1	1	1	1	1	0	1	1	2	1	1	1	1	0	1	1	0	-	0	0	2	0
Proagonistes praeceps	1	1	0	1	1	1	0	0	2	0	1	1	0	1	1	1	1	1	1	1	0	1	1	2	1	1	1	1	0	1	1	0	-	0	0	2	0
Atomosia puella	1	1	0	1	1	1	0	2	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	2	1	0	0	3	0	1	1	0	-	0	1	2	0
Aphestia annulipes	1	1	0	1	1	1	0	1	2	0	1	0	0	1	1	1	1	0	1	1	1	1	1	2	1	0	1	3	0	1	1	0	-	0	1	2	0
Cerotainia albipilosa	1	1	0	1	1	0	0	2	1	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	3	0	1	1	0	-	0	1	2	0
Goneccalypsis argenteoviridis	1	1	0	1	1	1	0	2	2	0	1	0	1	1	1	1	1	1	0	1	1	2	1	2	1	0	0	3	0	1	1	0	-	0	1	2	0
Loewinella nigripes	1	1	0	1	1	1	0	2	2	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	3	0	1	1	0	-	0	1	2	0
Lamyra gulo	1	1	0	1	1	1	0	0	2	0	1	1	0	2	1	1	1	0	1	0	0	1	1	2	1	1	1	0	0	1	1	0	-	0	0	2	0
Stiphrolamyra angularis	1	1	0	1	1	1	0	0	2	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	0	-	0	0	2	0
Orthogonis scapularis	1	1	0	1	1	1	0	0	2	0	1	0	0	1	1	1	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0
Smeryngolaphria numitor	1	1	0	1	1	1	0	0	2	0	1	1	0	1	1	1	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0
Laphria flava	1	1	0	1	1	1	0	0	2	0	1	0	0	1	1	1	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	-	0	0	0	0
Laphria aktis	1	1	0	1	1	1	0	1	2	0	1	0	0	2	1	1	1	1	1	1	0	3	1	2	1	1	0	1	0	1	1	0	-	0	0	0	0
Choerades bella	1	1	0	1	1	1	0	0	2	0	1	0	0	1	1	1	1	1	1	1	0	3	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0
Lampria clavipes	1	1	0	1	1	1	1	0	2	0	1	1	0	1	1	1	1	1	1	1	0	3	1	1	1	1	0	1	0	1	1	0	-	0	0	2	0
Laxenecera albicincta	1	1	0	1	1	1	0	0	2	0	1	1	0	3-Feb	1	1	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0
Maira aenea	1	1	0	1	1	1	0	0	2	0	1	1	0	1	1	1	1	1	1	1	0	3	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0
Nusa infumata	1	1	0	1	1	1	0	0	2	0	1	1	0	3	1	1	1	0	1	1	0	1	1	2	1	1	0	0	0	1	1	0	-	0	0	2	0
Hoplistomerus nobilis	1	1	0	1	1	0	0	0	2	0	1	0	0	0	1	1	1	0	1	0	1	1	1	1	1	1	0	0	0	1	1	0	-	0	0	2	0
Laphystia aegyptiaca	1	1	0	1	1	0	0	0	2	0	1	1	0	3	1	1	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0
Laphystia tolandi	1	1	0	1	1	0	0	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	2	1	1	0	1	0	1	1	0	-	0	0	2	0

APPENDIX 1

(Continued, extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Dicolonus simplex	1	0	1	0	0	0	2	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Eudioctria albius	1	2	1	0	0	0	2	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Andrenosoma cyrtoxys	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Hyperechia nigripennis	1	0	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Pilica formidolosa	1	0	2	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Dasyllis funebris	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Proagonistes praeceps	2	0	2	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Atomosia puella	1	0	1	0	0	0	2	0	0	0	1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	4	0	0	3	0	0	0	0	1	0	1	0
Aphestia annulipes	1	0	2	0	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	4	0	0	3	0	0	0	0	1	0	1	0
Cerotainia albipilosa	1	0	1	0	0	0	2	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	1	4	1	0	3	0	0	0	0	1	0	1	0
Goneccalypsis argenteoviridis	1	0	1	0	0	0	2	0	0	0	1	1	1	0	0	1	0	0	2	1	0	1	0	1	1	4	0	0	0	0	0	0	0	1	0	1	0
Loewinella nigripes	1	0	2	0	0	0	2	0	0	0	1	1	1	0	0	0	0	0	2	1	0	1	0	1	1	4	1	0	0	0	0	0	0	1	0	1	0
Lamyra gulo	1	0	2	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Stiphrolamyra angularis	1	0	2	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	1	1	0	1	0
Orthogonis scapularis	1	0	1	0	0	0	2	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	4	0	0	0	1	0	0	0	1	0	1	0
Smeryngolaphria numitor	1	0	1	0	0	0	2	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Laphria flava	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Laphria aktis	1	0	2	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Choerades bella	1	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Lampria clavipes	1	0	1	1	2	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	0	1	0
Laxenecera albicincta	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0	1	0	1	0
Maira aenea	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Nusa infumata	2	0	2	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	1	1	0	0	0	1	0	1	0
Hoplistomerus nobilis	1	0	1	0	2	0	0	1	0	0	1	1	1	0	0	0	0	0	0	2	0	1	1	1	1	2	0	0	2	1	1	0	1	1	0	1	0
Laphystia aegyptiaca	1	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	2	0	1	0	1	1	2	0	0	2	0	0	0	1	1	0	1	0
Laphystia tolandi	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	2	0	1	0	1	1	2	0	0	2	0	0	0	1	1	0	1	0

APPENDIX 1

(Continued, extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Dicolonus simplex	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	4	-	0	2	0	0	0	0	1	1	0	1	1	0	0	0
Eudioctria albius	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	-	0	2	0	0	0	0	1	1	0	1	0	0	1	0
Andrenosoma cyrtoxys	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	3	2	0	0	0	0	0	1	2	2	0	1	0	1
Hyperechia nigripennis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	3	2	0	0	0	0	1	1	2	1	0	1	0	1
Pilica formidolosa	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	3	2	0	0	0	0	0	1	2	2	0	1	0	1
Dasyllis funebris	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	3	2	0	0	0	0	0	1	2	2	0	1	0	1
Proagonistes praeceps	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	3	2	0	0	0	0	1	1	2	1	0	1	0	1
Atomosia puella	1	1	1	0	0	0	0	0	0	1	0	2	2	0	0	0	0	1	1	0	0	0	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Aphestia annulipes	1	1	1	0	0	0	0	0	0	0	0	2	2	2	2	2	0	1	1	0	0	0	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Cerotainia albipilosa	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	-	5	2	0	0	0	0	1	1	2	0	0	0	1	0
Goneccalypsis argenteoviridis	1	1	1	0	0	0	0	0	0	0	0	2	2	2	2	2	2	0	0	0	0	0	-	0	2	0	0	0	0	1	1	1	1	0	0	1	0
Loewinella nigripes	1	1	1	0	0	0	0	0	0	0	0	2	2	2	2	2	2	0	0	0	0	0	-	2	2	0	0	0	0	1	1	2	1	0	0	1	0
Lamyra gulo	1	0	0	0	1	0	0	1	0	0	0	2	2	2	0	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Stiphrolamyra angularis	1	0	1	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Orthogonis scapularis	1	0/1	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Smeryngolaphria numitor	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Laphria flava	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	0	2	0	0	0	0	1	1	2	2	0	0	0	0
Laphria aktis	1	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Choerades bella	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Lampria clavipes	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Laxenecera albicincta	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Maira aenea	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	1	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Nusa infumata	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	1	-	5	2	0	0	0	1	1	1	0	1	1	0	0	0
Hoplistomerus nobilis	1	0	1	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Laphystia aegyptiaca	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	0	-	5	2	0	0	0	1	1	1	0	1	0	0	0	2
Laphystia tolandi	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	0	-	5	2	0	0	0	1	1	1	2	1	0	0	0	0

APPENDIX 1

(Continued, extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Dicolonus simplex	0	0	0	0	0	0	0	4	-	0	0	0	0	1	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Eudioctria albius	0	0	0	0	0	0	0	4	-	1	0	0	0	0	-	0	1	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Andrenosoma cyrtoxys	2	2	2	2	0	0	0	5	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Hyperechia nigripennis	0	0	0	0	0	0	0	5	0	1	0	0	0	2	0	0	1	0	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Pilica formidolosa	2	2	2	2	0	0	0	5	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	1	0	0	0	2	2	1	0	1	1	1	0
Dasyllis funebris	2	2	2	2	0	0	0	5	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Proagonistes praeceps	2	2	0	0	0	0	0	5	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Atomosia puella	2	2	2	2	0	0	0	6	-	1	0	0	0	1	-	0	1	0	0	1	1	0	0	0	0	0	0	1	2	0	0	1	1	0	0
Aphestia annulipes	2	2	2	2	2	0	0	1	-	1	0	0	0	1	-	0	1	0	1	1	2	0	0	1	0	0	0	3	2	0	0	1	1	0	0
Cerotainia albipilosa	0	0	0	0	0	0	0	6	-	1	0	0	0	1	-	0	1	0	0	1	1	0	0	0	0	0	0	2	2	0	0	1	1	0	0
Goneccalypsis argenteoviridis	2	2	2	2	2	2	0	1	-	1	0	0	0	2	0	0	1	0	0	1	2	0	0	0	0	0	0	2	2	0	0	1	1	0	0
Loewinella nigripes	2	2	2	2	2	2	0	1	-	1	0	0	0	2	0	0	1	0	0	1	2	0	0	0	0	0	0	2	2	0	0	1	1	0	0
Lamyra gulo	2	2	2	2	0	0	0	3	0	1	0	0	0	1	-	0	1	1	0	1	2	0	0	0	0	0	0	3	2	1	0	1	1	1	0
Stiphrolamyra angularis	2	2	2	0	0	0	0	3	0	1	0	0	0	2	1	1	1	1	1	1	1	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Orthogonis scapularis	2	2	2	2	0	0	0	5	0	1	0	0	0	2	0	0	1	0	0	1	1	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Smeryngolaphria numitor	2	2	2	2	0	0	0	5	0	1	0	0	0	1	-	0	1	1	1	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	2
Laphria flava	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0	1	1	0	1	1	0	0	0	0	0	0	3	2	1	0	1	1	1	0
Laphria aktis	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0	1	1	0	1	1	0	0	0	0	0	0	2	2	1	0	1	0	0	0
Choerades bella	2	0	0	0	0	0	0	5	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	0	0	0	0	3	2	1	0	1	1	1	0
Lampria clavipes	2	2	0	0	0	0	0	5	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Laxenecera albicincta	2	2	0	0	0	0	0	3	0	1	0	0	0	2	0	0	0	1	0	1	1	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Maira aenea	2	2	2	2	0	0	0	5	0	1	0	0	0	2	1	0	1	1	0	1	2	0	0	0	0	0	0	2	2	0	0	1	1	1	0
Nusa infumata	2	2	2	2	2	0	0	5	0	1	0	0	0	2	0	0	0	1	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	2
Hoplistomerus nobilis	2	2	2	2	2	0	0	3	0	1	0	0	0	2	1	0	0	1	0	1	2	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Laphystia aegyptiaca	2	2	2	2	2	0	0	3	0	1	0	0	0	2	1	0	1	0	0	1	2	0	0	0	0	0	0	2	0	1	0	0	0	1	0
Laphystia tolandi	2	2	2	2	2	0	0	3	0	1	0	0	0	2	0	0	1	0	0	1	1	0	0	0	0	0	0	2	0	1	0	0	0	1	0

APPENDIX 1
(Continued, extended)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Perasis transvaalensis	0	0	2	4	0	1	0	0	2	0	1	0	0	1	1	0	0	0	1	0	1	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Protometer sp. (El Tuparro)	0	0	2	4	0	1	0	0	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1
Psilocurus modestus	0	0	2	2	0	1	1	0	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1
Trichardis testacea	0	0	2	4	0	1	0	0	2	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1
Zabrops tagax	0	0	2	3	0	1	2	0	2	0	1	0	0	2	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1	0	1	1	1	0	1
Leptogaster cylindrica	0	0	1	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	2	1	2	0	0
Leptogaster arida	0	0	1	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	2	1	2	0	0
Beameromyia bifida	0	0	1	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	2	1	2	0	2
Euscelidia pulchra	0	0	1	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	2	1	2	0	0
Lasiocnemus lugens	0	0	2	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	2	1	2	0	0
Tipulogaster glabrata	0	0	2	1	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	2	0	0	1	1	0	1	1	1	0	2	1	2	0	0
Afroestricus chiastoneurus	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Cophinopoda chinensis	0	0	2	4	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	0	0	1
Emphysomera conopsoides	0	0	2	1	0	1	3	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Emphysomera pallidapex	0	0	2	2	0	1	3	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Michotamia aurata	0	0	2	1	0	1	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Ommatius incurvatus	0	0	2	3	0	1	2	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	0
Ommatius tibialis	0	0	2	2	0	1	3	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	2	0	1
Acronyches maya	0	0	2	2	0	1	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	2	1	1	0	1
Bathypogon nigrinus	0	0	1	3	0	1	2	0	2	0	0	0	0	2	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	2	0	1
Ceraturgus fasciatus	0	0	2	4	0	1	2	0	2	0	1	1	0	1	1	0	0	2	1	0	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1
Myelaphus melas	0	0	2	1	0	1	0	0	2	0	1	0	0	2	1	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	1
Cyrtopogon lateralis	0	0	2	4	0	1	3	0	2	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1
Cyrtopogon rattus	0	0	2	4	0	1	3	0	2	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1
Afroholopogon peregrinus	0	0	2	0	0	1	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1
Dasycyrton gibbosus	0	0	2	3	0	1	2	0	2	0	1	0	0	0	1	0	0	0	2	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1

APPENDIX 1

(Continued, extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Perasis transvaalensis	1	1	1	0	1	0	0	2	0	0	0	1	0	1	1	0	1	0	0	1	2	0	0	0	2	0	0	0	2	0	1	2	2	0	1	1	0
Protometer sp. (El Tuparro)	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	0
Psilocurus modestus	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	0
Trichardis testacea	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	1	0	1	2	0	0	0	2	0	0	0	2	0	1	2	1	0	1	2	0
Zabrops tagax	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	2	0	0	0	2	0	1	1	1	0	1	1	0
Leptogaster cylindrica	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	0	2	1	0
Leptogaster arida	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	0	2	1	0
Beameromyia bifida	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0
Euscelidia pulchra	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0
Lasiocnemus lugens	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0
Tipulogaster glabrata	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	1	0	0	0	2	1	3
Afroestricus chiastoneurus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	5	0	0	0	2	1	0	0	2	0	0	0	2	0	1	2	1	0	1	1	4
Cophinopoda chinensis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	5	1	0	0	2	1	0	0	2	0	0	0	2	0	1	2	1	0	1	1	3
Emphysomera conopsoides	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	5	1	0	0	2	1	0	0	2	0	0	0	2	1	1	2	1	0	1	1	1
Emphysomera pallidapex	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	5	0	0	0	2	1	0	0	2	0	0	0	2	1	1	2	1	0	1	1	1
Michotamia aurata	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	1	0	0	2	0	0	0	2	0	1	2	1	0	1	1	3
Ommatius incurvatus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	5	0	0	0	2	1	0	0	2	0	0	0	2	1	1	2	1	0	1	1	4
Ommatius tibialis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	5	0	0	0	2	1	0	0	2	0	0	0	2	0	1	2	1	0	1	1	4
Acronyches maya	1	1	1	0	0	0	0	0	1	0	2	0	0	1	1	0	1	0	0	0	2	0	0	0	0	0	0	0	2	0	1	2	1	0	1	1	3
Bathypogon nigrinus	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	0	2	0	0	0	2	0	0	0	2	0	1	2	1	0	1	1	3
Ceraturgus fasciatus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	3	1	0	0	0	2	0	0	0	2	0	1	1	1	0	1	1	2
Myelaphus melas	1	1	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	3	1	0	0	0	2	0	0	0	2	0	1	1	1	0	1	1	3
Cyrtopogon lateralis	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Cyrtopogon rattus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	1	3
Afroholopogon peregrinus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	2	0	1	2	1	0	1	1	2
Dasycyrton gibbosus	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	0	3

APPENDIX 1
(Continued, extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Perasis transvaalensis	1	1	0	1	1	0	0	0	2	0	1	0	0	1	1	1	1	0	1	0	0	1	1	0	1	1	0	0	0	1	1	0	-	0	0	2	0
Protometer sp. (El Tuparro)	1	1	0	1	1	0	0	0	2	0	1	0	0	2-Jan	1	1	1	0	1	0	0	1	1	0	1	1	0	1	0	1	1	0	-	0	0	2	0
Psilocurus modestus	1	1	0	1	1	0	0	0	2	0	1	0	0	1	1	1	1	1	1	1	0	1	1	2	1	0	0	1	0	1	1	0	-	0	0	2	0
Trichardis testacea	1	1	0	1	1	1	0	0	2	0	1	1	0	2	1	1	1	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	-	0	0	2	0
Zabrops tagax	1	1	0	1	1	0	0	0	2	0	1	0	0	2	1	1	1	1	1	1	0	2	1	2	1	1	0	0	0	1	1	0	-	0	0	2	0
Leptogaster cylindrica	1	1	0	2	2	0	0	0	1	0	0	0	0	1	1	1	1	0	1	1	0	2	1	1	1	0	0	1	0	0	1	0	-	0	1	0	1
Leptogaster arida	1	1	0	2	2	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	2	1	1	0	0	0	1	0	0	1	0	-	0	1	0	1
Beameromyia bifida	1	1	0	2	2	0	0	0	1	0	0	0	0	1	1	1	0	1	1	1	0	1	1	1	1	0	0	1	0	0	1	0	-	0	1	0	1
Euscelidia pulchra	1	1	0	2	2	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	1	2	1	1	1	0	0	2	0	0	1	0	-	0	1	0	1
Lasiocnemus lugens	1	1	0	2	2	0	0	0	2	0	0	1	0	2	1	1	0	0	1	1	0	2	1	1	1	0	0	2	0	0	1	0	-	0	1	0	1
Tipulogaster glabrata	0	1	0	2	2	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	2	1	1	1	0	0	1	0	0	1	0	-	0	1	0	1
Afroestricus chiastoneurus	0	1	0	1	1	0	1	0	2	0	1	2	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	3	0	1	1	0	-	0	1	2	0
Cophinopoda chinensis	0	1	0	1	1	0	1	0	2	0	1	1	0	2	1	1	1	0	1	1	0	1	1	2	1	0	1	3	0	1	1	0	-	0	1	2	0
Emphysomera conopsoides	0	1	0	1	1	0	1	0	2	0	2	2	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	3	0	1	1	0	-	0	1	2	0
Emphysomera pallidapex	0	1	0	1	1	0	1	0	2	0	2	2	0	2	1	1	1	1	1	1	0	1	1	2	1	0	1	3	0	1	1	0	-	0	1	2	0
Michotamia aurata	0	1	0	1	1	1	1	0	2	0	2	2	0	3	1	1	1	0	1	1	0	1	1	0	1	0	1	3	0	1	1	0	-	0	1	2	0
Ommatius incurvatus	0	1	0	1	1	0	1	0	2	0	2	1	0	2	1	1	1	0	0	1	0	1	1	2	1	0	1	3	0	1	1	0	-	0	1	2	0
Ommatius tibialis	0	1	0	1	1	0	1	0	2	0	2	1	0	2	1	1	1	0	1	1	0	1	1	1	1	0	1	3	0	1	1	0	-	0	1	2-Jan	0
Acronyches maya	0	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	0	1	1	0	2	1	1	1	1	0	0	0	0	1	0	-	0	1	0	0
Bathypogon nigrinus	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Ceraturgus fasciatus	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	0	1	1	0	1	1	1	1	0	0	0	0	1	1	0	-	0	0	2	0
Myelaphus melas	0	1	0	2	2	0	0	0	2	0	0	0	0	0/1	1	1	0	0	1	0	0	1	1	0	1	0	0	0	0	1	1	0	-	0	1	0	0
Cyrtopogon lateralis	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Cyrtopogon rattus	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Afroholopogon peregrinus	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	1	0	0	-	0	1	2	0
Dasycyrton gibbosus	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	0	0	1	1	1	0	1	1	1	0	0	0	0	0	1	1	0	-	0	1	2	0

APPENDIX 1
(Continued, extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Perasis transvaalensis	1	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	2	0	1	1	1	1	2	0	0	0	0	1	0	1	1	0	1	0
Protometer sp. (El Tuparro)	1	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	2	0	1	0	1	1	2	0	0	2	0	1	0	1	1	0	1	0
Psilocurus modestus	1	0	2	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Trichardis testacea	1	0	1	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	1	0	1	0	1	1	0	1	0
Zabrops tagax	1	0	2	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	2	0	1	1	1	1	2	0	0	0	0	1	0	1	1	0	1	0
Leptogaster cylindrica	1	0	1	0	0	0	0	0	0	0	0	0	-	1	0	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0
Leptogaster arida	1	0	1	0	0	0	0	0	1	1	0	0	-	1	0	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0
Beameromyia bifida	1	0	1	0	0	0	0	0	1	1	1	0	-	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	1	0
Euscelidia pulchra	0	0	1	0	0	0	0	0	1	0	1	0	-	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0
Lasiocnemus lugens	1	0	1	0	0	0	0	0	0	0	0	0	-	1	0	1	0	0	2	0	0	0	0	0	1	1	0	0	0	0	0	2	0	1	0	1	0
Tipulogaster glabrata	0	0	1	0	0	0	0	0	1	1	1	0	-	1	0	1	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0
Afroestricus chiastoneurus	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Cophinopoda chinensis	2	0	2	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Emphysomera conopsoides	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Emphysomera pallidapex	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Michotamia aurata	2	0	2	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Ommatius incurvatus	1	0	2	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Ommatius tibialis	2	0	2	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	1	0	1	0
Acronyches maya	1	0	1	0	0	0	0	0	1	1	1	0	-	1	0	2	0	0	2	0	0	0	0	0	1	0	0	0	0	1	0	2	0	1	0	1	0
Bathypogon nigrinus	2	1	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	0	0	0	0	1	0	1	1	0	1	0
Ceraturgus fasciatus	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Myelaphus melas	1	0	2	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	0	1	0	1	0
Cyrtopogon lateralis	1	0	1	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Cyrtopogon rattus	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Afroholopogon peregrinus	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	2	0	0	0	0	1	0	1	0
Dasycyrton gibbosus	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1	2	0	0	2	0	0	0	0	1	0	1	0

APPENDIX 1
(Continued, extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Perasis transvaalensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	5	2	0	0	0	1	1	1	0	1	0	0	0	2
Protometer sp. (El Tuparro)	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	0	-	5	2	0	0	0	1	1	1	2	1	0	0	0	0
Psilocurus modestus	1	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	1	1	0	0	0	0
Trichardis testacea	1	0	1	0	0	0	0	0	0	0	0	2	2	2	2	2	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Zabrops tagax	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	2	1	0	0	0	0
Leptogaster cylindrica	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	0	1	0	1	1	1	0	0	1	0
Leptogaster arida	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	0	1	0	1	1	2	0	0	0	0
Beameromyia bifida	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	2	0	0	1	1	2	0	0	1	0
Euscelidia pulchra	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	1	0	0	1	1	1	0	0	0	0
Lasiocnemus lugens	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	1	1	0	1	1	2	0	0	0	0
Tipulogaster glabrata	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	0	1	0	1	1	2	0	0	0	0
Afroestricus chiastoneurus	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	-	0	2	0	0	0	0	1	1	1	0	0	0	0	1
Cophinopoda chinensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	1	1	1	1	0	0	0	0	1
Emphysomera conopsoides	1	0	0	0	1	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Emphysomera pallidapex	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	-	4	2	0	0	0	0	1	1	1	0	0	0	0	2
Michotamia aurata	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	1	0	0	0	0	2
Ommatius incurvatus	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	2	0	0	0	0	1	1	1	0	0	0	0	1
Ommatius tibialis	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	-	0	2	0	0	0	0	1	1	1	0	0	0	0	1
Acronyches maya	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6	-	4	2	0	0	0	0	1	1	1	2	0	0	1	0
Bathypogon nigrinus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	2	1	0	0	0	1	1	0	1	0	0	0	1
Ceraturgus fasciatus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	?	0	1	1	?	?	0	0	0	1
Myelaphus melas	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	-	0	2	0	0	?	0	1	1	?	?	0	0	0	0
Cyrtopogon lateralis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	1	2	0	0	0	2
Cyrtopogon rattus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	2
Afroholopogon peregrinus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	0
Dasycyrton gibbosus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	1

APPENDIX 1

(Continued, extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Perasis transvaalensis	0	0	0	0	0	0	0	3	0	0	0	0	0	1	-	0	1	1	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0
Protometer sp. (El Tuparro)	2	2	2	2	0	0	0	3	0	1	0	0	0	1	-	0	1	0	0	1	2	0	0	0	0	0	1	2	0	1	0	1	1	1	0
Psilocurus modestus	2	2	2	0	0	0	0	3	0	1	0	0	0	0	-	0	1	0	0	1	2	0	1	0	0	0	1	1	2	1	0	1	1	1	0
Trichardis testacea	2	2	2	2	2	0	0	3	0	1	0	0	0	2	0	0	0	1	0	1	1	0	0	0	0	0	0	2	2	1	0	1	1	1	0
Zabrops tagax	2	0	0	0	0	0	0	3	0	1	0	0	0	0	-	0	1	0	0	1	2	0	0	0	0	0	1	2	0	1	0	1	1	1	0
Leptogaster cylindrica	0	0	0	0	0	0	0	0	0	0	0	1	1	1	-	1	1	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	1	0	0
Leptogaster arida	0	0	0	0	0	0	0	0	0	0	0	1	1	0	-	1	1	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	1	0	0
Beameromyia bifida	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2	2	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	1	0	0
Euscelidia pulchra	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2	2	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	1	0	0
Lasiocnemus lugens	0	0	0	0	0	0	0	0	0	0	0	1	1	1	-	1	1	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	1	0	0
Tipulogaster glabrata	0	0	0	0	0	0	0	0	0	0	0	1	1	0	-	1	1	1	0	1	2	1	0	0	0	0	0	2	0	0	0	1	1	0	0
Afroestricus chiastoneurus	0	0	0	1	1	1	0	0	0	0	0	1	0	0	-	1	1	0	1	1	2	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Cophinopoda chinensis	0	0	0	0	0	0	0	0	0	0	0	2	0	0	-	1	1	0	1	1	2	0	0	0	0	1	0	0	0	1	0	1	1	-	0
Emphysomera conopsoides	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	0	1	1	-	0
Emphysomera pallidapex	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	-	0
Michotamia aurata	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	0	0	1	0	1	0	-	0
Ommatius incurvatus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	-	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	1	1	-	0
Ommatius tibialis	0	1	1	1	1	1	0	0	0	0	0	2	0	0	-	1	1	1	1	1	2	0	0	0	0	1	0	0	0	1	0	1	1	-	0
Acronyches maya	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	2	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Bathypogon nigrinus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	1	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Ceraturgus fasciatus	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	0	0	0	1	1	2	0	0	0	0	1	1	1	0	0	0	0	1	0	0
Myelaphus melas	0	0	0	0	0	0	0	4	-	0	0	1	0	0	-	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Cyrtopogon lateralis	0	0	0	0	0	0	0	4	0	0	0	1	0	0	-	1	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Cyrtopogon rattus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Afroholopogon peregrinus	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Dasycyrton gibbosus	0	0	0	0	0	0	0	4	0	0	0	1	0	1	-	0	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0

APPENDIX 1

(Continued, extended)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Heteropogon manicatus	0	0	2	0	0	1	0	0	2	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1
Holopogon priscus	0	0	2	0	0	1	3	0	2	0	1	1	0	0	1	0	0	0	2	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	0
Metapogon punctipennis	0	0	2	0	0	1	0	0	2	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1
Nannocyrtopogon lestomyiformis	0	0	2	3	0	1	2	0	2	0	1	1	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	1	1	1	1	0	1	1	1	0	1
Rhabdogaster pedion	0	0	2	1	0	1	1	0	2	0	1	1	0	2	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	1	1	1	1	1	0	1
Archilestris magnificus	0	0	1	2	0	1	0	0	2	0	0	1	0	0	1	0	1	2	2	0	0	1	2	1	1	0	1	1	1	1	1	1	1	1	1	0	1
Creolestes nigribarbis	0	0	2	2	0	1	1	0	2	0	1	1	0	1	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Microstylum sp. (Karkloof)	0	0	1	2	0	1	1	0	2	0	0	0	0	1	1	0	0	2	1	0	0	1	2	1	1	1	1	0	1	1	1	0	1	1	1	0	1
Prolepsis tristis	0	0	1	3	0	1	2	0	2	0	1	1	0	1	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1
Phellus olgae	0	0	1	3	0	1	2	0	2	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1
Obelophorus terebratus	0	0	2	3	0	1	2	0	2	0	1	0	0	2	1	0	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1
Plesiomma sp. (Guanacaste)	0	0	2	4	0	1	0	0	2	0	1	1	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	1	1	1	0	2	1	1	0	1
Stenopogon sabaudus	1	0	2	3	0	1	2	0	2	0	1	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	2	0	0
Stenopogon rufibarbis	1	0	2	4	0	1	3	0	2	0	1	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	2	0	0
Acnephalum cylindricum	0	0	2	4	0	1	3	0	2	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1
Ancylorhynchus fulvicollis	0	0	1	2	0	1	1	0	2	0	1	1	0	0	1	0	2	0	1	0	0	1	1	1	1	1	1	2	1	1	1	0	1	1	1	0	1
Ospriocerus aeacus	1	0	1	2	0	1	1	0	2	0	1	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	2	0	0
Scleropogon subulatus	1	0	1	2	0	1	1	0	2	0	1	1	0	2	1	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	0	1	1	2	0	0
Scylaticus costalis	0	0	1	2	0	1	1	0	2	0	1	1	0	2	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1
Sisyrnodytes sp. (Gamka)	0	0	2	1	0	1	3	0	2	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1
Tillobroma punctipennis	0	0	2	4	0	1	3	0	2	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1
Coleomyia setigera	0	0	2	3	0	1	2	0	2	0	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	1	1	1	1	0	1
Hypenetes stigmatias	0	0	1	3	0	1	2	0	2	0	1	1	0	1	1	0	0	2	0	0	0	0	2	1	1	-	1	0	1	1	1	1	1	1	1	0	1
Willistonina bilineata	0	0	1	1	0	1	0	1	2	0	1	1	0	2	1	0	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	0	1	1	0	0	1
Daspletis stenoura	0	0	2	4	0	1	3	0	2	0	0	0	0	1	1	0	0	2	1	0	0	0	2	1	1	1	1	0	1	1	1	1	1	1	1	0	1
Lycostommyia albifacies	0	0	1	4	0	1	0	0	2	0	1	1	0	1	1	0	0	0	0	0	0	1	2	1	1	-	1	1	1	1	1	1	1	1	1	0	1

APPENDIX 1
(Continued, extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Heteropogon manicatus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	2	2	0	1	2	1	0	1	2	2
Holopogon priscus	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	3
Metapogon punctipennis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	2	0	0	0	2	0	1	1	1	0	1	2	3
Nannocyrtopogon lestomyiformis	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	2	0	0	0	2	1	1	1	1	0	1	1	3
Rhabdogaster pedion	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	2	0	1	1	1	0	1	0	3
Archilestris magnificus	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	0	4	3	-	0	0	2	0	0	0	2	0	1	2	2	0	1	2	3
Creolestes nigribarbis	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	2	0	0	0	2	0	0	0	2	1	1	1	1	0	1	1	2
Microstylum sp. (Karkloof)	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	1	2	0	0	0	1	0	0	0	2	0	1	1	2	0	1	2	3
Prolepsis tristis	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	4	3	-	0	0	2	0	0	0	2	0	1	2	2	0	1	2	3
Phellus olgae	1	1	0	1	0	0	2	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	1	2	1	0	1	1	3
Obelophorus terebratus	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	2
Plesiomma sp. (Guanacaste)	1	1	2	0	0	0	2	0	0	0	2	0	0	1	1	0	1	1	0	1	1	0	0	0	2	0	0	0	2	0	1	2	1	0	1	2	3
Stenopogon sabaudus	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	0	2	0	1	2	2	0	1	2	2
Stenopogon rufibarbis	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	2	1	1	2	2	0	1	1	2
Acnephalum cylindricum	1	1	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	2	2	0	1	2	2	0	1	1	2
Ancylorhynchus fulvicollis	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	2	0	0	0	1	0	0	0	2	0	1	2	2	0	1	2	2
Ospriocerus aeacus	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0/1	0	1	2	0	0	0	2	0	0	0	2	0	1	2	2	0	1	2	2
Scleropogon subulatus	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	2	0	0	0	2	0	1	2	2	0	1	2	2
Scylaticus costalis	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	2	0	0	0	1	0	0	0	2	0	1	2	1	0	1	2	2
Sisyrnodytes sp. (Gamka)	1	1	0	1	0	0	0	3	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	0	0	2	2	0	1	2	1	0	1	2	2
Tillobroma punctipennis	1	1	0	1	0	0	0	0	1	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	2	0	0	0	1	0	1	1	1	0	1	1	3
Coleomyia setigera	1	1	0	1	0	0	0	0	1	0	0	1	0	1	1	0	2	0	0	1	2	0	0	0	2	0	0	0	2	0	1	2	2	0	1	2	3
Hypenetes stigmatias	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	1	2	0	0	0	2	0	0	0	2	0	1	2	1	0	1	1	2
Willistonina bilineata	1	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	2	1	0	1	2	0	0	0	2	0	1	0	2	0	1	2	1	0	1	1	3
Daspletis stenoura	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	2	0	0	4	3	-	0	0	2	0	0	2	2	0	1	2	2	0	1	2	2
Lycostommyia albifacies	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	0	0	2	2	0	1	1	1	0	1	1	2

APPENDIX 1
(Continued, extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Heteropogon manicatus	0	1	0	1	1	0	0	0	2	0	1	0	0	2	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	0	0	-	0	1	2	0
Holopogon priscus	0	1	0	1	1	0	0	0	1	0	1	0	0	2	1	0	1	1	1	1	0	1	1	1	1	0	0	0	0	1	1	0	-	0	1	2	0
Metapogon punctipennis	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Nannocyrtopogon lestomyiformis	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Rhabdogaster pedion	0	1	0	1	1	0	0	0	1	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	3	0	1	1	0	-	0	1	2	0
Archilestris magnificus	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Creolestes nigribarbis	0	1	0	1	1	0	0	0	2	0	1	0	0	3	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	0	2	0
Microstylum sp. (Karkloof)	0	1	0	1	1	0	0	1	2	0	1	1	0	3	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	0	0	-	0	1	2	0
Prolepsis tristis	0	1	0	0	1	0	0	0	2	0	1	0	0	3	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Phellus olgae	0	1	0	1	1	0	0	0	1	0	1	1	0	3	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Obelophorus terebratus	0	1	0	1	1	0	0	0	2	0	0	0	0	3	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Plesiomma sp. (Guanacaste)	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	-	0	1	2	0
Stenopogon sabaudus	0	1	0	0	1	0	0	0	0	0	0	0	0	3	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Stenopogon rufibarbis	0	1	0	0	1	0	0	0	0	0	0	0	0	3	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Acnephalum cylindricum	0	1	0	1	1	1	0	0	2	0	0	0	0	3	1	1	1	1	1	1	0	1	1	2	0	0	0	0	1	1	0	0	-	0	1	2	0
Ancylorhynchus fulvicollis	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	2	1	2	0	0	0	0	0	1	0	0	-	0	1	2	0
Ospriocerus aeacus	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	0	0	-	0	1	2	0
Scleropogon subulatus	0	1	0	0	1	0	0	0	1	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	0	0	-	0	1	2	0
Scylaticus costalis	0	1	0	0	1	0	0	0	2	0	0	0	0	3-Feb	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	0	0	-	0	1	2	0
Sisyrnodytes sp. (Gamka)	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	0	1	1	1	0	-	0	1	2	0
Tillobroma punctipennis	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	0	2	0
Coleomyia setigera	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	0	1	1	0	0	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Hypenetes stigmatias	1	1	0	1	1	0	0	0	2	0	0	0	0	3	1	1	1	1	1	1	0	2	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Willistonina bilineata	0	1	0	0	1	0	0	0	2	0	0	0	0	3	1	1	1	0	1	1	0	1	1	2	0	0	0	0	0	1	0	0	-	0	1	2	0
Daspletis stenoura	0	1	0	1	1	0	0	1	2	0	2	1	0	3	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Lycostommyia albifacies	0	1	0	1	1	0	0	0	2	0	1	1	0	3-Feb	1	1	1	0	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0

APPENDIX 1
(Continued, extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Heteropogon manicatus	1	0	2	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Holopogon priscus	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Metapogon punctipennis	1	1	2	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Nannocyrtopogon lestomyiformis	1	1	1	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Rhabdogaster pedion	1	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	2	0	0	1	0	1	0	1	0
Archilestris magnificus	2	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	1	0	1	0
Creolestes nigribarbis	1	1	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	1	0	1	0
Microstylum sp. (Karkloof)	1	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	1	0	0	1	0	0	0	1	0	1	0
Prolepsis tristis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Phellus olgae	1	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	0	0	0	1	0	0	0	1	1	1	0
Obelophorus terebratus	1	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	1	2	1	0	0	2	0	0	0	1	1	1	0
Plesiomma sp. (Guanacaste)	2	0	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	2	1	0	0	0	0	0	0	1	0	1	0
Stenopogon sabaudus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	1	0	0	1	0	1	0
Stenopogon rufibarbis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	1	1	0	1	0
Acnephalum cylindricum	1	0	2	0	0	0	0	0	0	0	1	0	-	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	2	0	0	0	0	1	1	1	0
Ancylorhynchus fulvicollis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Ospriocerus aeacus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	0	0	0	0	1	0	0	1	0	1	0
Scleropogon subulatus	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	2	0	0	0	0	1	0	0	1	0	1	0
Scylaticus costalis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0
Sisyrnodytes sp. (Gamka)	1	0	1	0	0	0	0	0	0	0	1	0	-	1	0	0	0	0	0	0	0	1	1	1	1	2	0	0	1	2	1	0	0	1	0	1	0
Tillobroma punctipennis	1	1	2	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0
Coleomyia setigera	0	1	2	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Hypenetes stigmatias	1	1	2	0	2	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	1	0	0	1	0	1	0
Willistonina bilineata	2	1	2	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Daspletis stenoura	2	0	2	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	2	1	0	0	0	0	0	0	1	0	1	0
Lycostommyia albifacies	1	0	2	0	2	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0

APPENDIX 1

(Continued, extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Heteropogon manicatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	2	1	0	0	2
Holopogon priscus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	4	0	2	1	1	0	0	0	1	1	0	0	0	0	0	2
Metapogon punctipennis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	1	1	0	0	2
Nannocyrtopogon lestomyiformis	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	1	0	0	0	2
Rhabdogaster pedion	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	1	1	0	0	0
Archilestris magnificus	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	1	1	0	0	0	1	1	1	2	0	0	0	2
Creolestes nigribarbis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	3	2	0	0	0	3
Microstylum sp. (Karkloof)	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	1	2	0	0	0	3
Prolepsis tristis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	3	2	0	0	0	2
Phellus olgae	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	3	0	2	1	1	0	0	0	1	1	0	1	0	0	0	1
Obelophorus terebratus	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	3	0	2	1	1	0	0	0	1	1	?	?	?	0	0	1
Plesiomma sp. (Guanacaste)	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	1	1	1	2	1	1	0	0	2
Stenopogon sabaudus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	1	0	0	2
Stenopogon rufibarbis	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	2	1	1	0	0	0	1	1	0	1	0	0	0	2
Acnephalum cylindricum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	2	1	1	0	0	0	1	1	0	1	0	0	0	0
Ancylorhynchus fulvicollis	1	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ospriocerus aeacus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	2	1	1	0	0	2
Scleropogon subulatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	2	1	1	0	0	2
Scylaticus costalis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	1	0	0	2
Sisyrnodytes sp. (Gamka)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	2
Tillobroma punctipennis	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	1	0	0	2
Coleomyia setigera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	1	1	0	0	2
Hypenetes stigmatias	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	3	2	0	0	0	2
Willistonina bilineata	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	2
Daspletis stenoura	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	3	2	0	0	0	2
Lycostommyia albifacies	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	2	1	1	0	0	0	1	1	2	1	0	0	0	2

APPENDIX 1

(Continued, extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Heteropogon manicatus	0	0	0	0	0	0	0	4	0	0	0	0	0	1	-	0	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Holopogon priscus	0	0	0	0	0	0	0	0	0	0	0	2	0	1	-	2	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Metapogon punctipennis	0	0	0	0	0	0	0	0	0	1	0	1	0	0	-	1	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	1	0	0
Nannocyrtopogon lestomyiformis	0	0	0	0	0	0	0	0	0	1	0	0	0	1	-	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Rhabdogaster pedion	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Archilestris magnificus	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Creolestes nigribarbis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	1	1	2	0	0	1	0	0	0	0
Microstylum sp. (Karkloof)	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Prolepsis tristis	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0
Phellus olgae	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	1	0	1	1	1	0	0	0	0	0	0	2	0	0	0	0	1	0	1
Obelophorus terebratus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	1	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	1
Plesiomma sp. (Guanacaste)	0	0	0	0	0	0	0	0	0	1	0	1	0	0	-	1	0	0	1	1	2	0	0	0	0	0	0	2	0	0	0	0	1	0	0
Stenopogon sabaudus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Stenopogon rufibarbis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	1	0	1	0	0	0	0	2	0	0	0	0	1	0	0
Acnephalum cylindricum	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	0	0	1	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ancylorhynchus fulvicollis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	0	0	1	1	1	0	0	0	0	0	1	3	0	0	0	0	0	0	0
Ospriocerus aeacus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	0	1	0	0
Scleropogon subulatus	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Scylaticus costalis	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	0	0	1	1	2	0	0	0	0	0	1	3	0	0	0	0	0	0	0
Sisyrnodytes sp. (Gamka)	0	0	0	0	0	0	0	1	0	0	0	0	0	1	-	0	0	0	1	1	2	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Tillobroma punctipennis	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	0	0	1	1	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0
Coleomyia setigera	0	0	0	0	0	0	0	0	0	1	0	1	0	0	-	1	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Hypenetes stigmatias	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0
Willistonina bilineata	0	0	0	0	0	0	0	0	0	0	0	2	0	0	-	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1
Daspletis stenoura	1	1	1	1	0	0	0	1	0	1	0	1	0	1	-	1	0	0	1	1	2	0	0	1	0	0	0	1	0	0	1	0	1	0	0
Lycostommyia albifacies	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1	1	0	1	1	1	0	0	1	0	0	1	2	0	0	1	0	0	0	0

APPENDIX 1

(Continued, extended)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Gonioscelis ventralis	1	0	1	3	0	1	2	0	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1	0	1	1	0	0	1
Trichoura sp. (Tierberg)	0	0	1	1	0	1	0	1	2	0	1	1	0	2	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	2	1	1	0	1
Ablautus coquilletti	0	0	1	1	0	1	2	0	2	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1
Oligopogon sp. (Cape Recife)	0	0	1	3	0	1	2	0	2	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1
Connomyia varipennis	0	0	1	2	0	1	3	0	2	0	1	1	0	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1
Stichopogon elegantulus	0	0	1	1	0	1	0	1	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0
Stichopogon punctum	0	0	1	1	0	1	0	1	2	0	1	1	0	2	1	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0
Stichopogon trifasciatus	0	0	1	1	0	1	0	1	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0
Lasiopogon aldrichii	0	0	1	3	0	1	2	0	2	0	1	1	0	2	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0
Lasiopogon cinctus	0	0	1	3	0	1	2	0	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0
Lissoteles aquilonius	0	0	1	1	0	1	0	1	2	0	1	1	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0
Townsendia albomacula	0	0	1	1	0	1	0	0	2	0	0	1	0	2	1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	0
Damalis monochaetes	0	0	1	2	0	1	1	0	2	0	0	0	0	0	1	0	0	2	0	0	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Damalis annulata	0	0	1	3	0	1	2	0	2	0	0	0	0	0	1	0	0	2	0	0	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Damalis sp. (Palatupana)	0	0	1	0	0	1	0	0	2	0	0	0	0	0	1	0	0	2	0	0	0	1	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Trigonomima sp. (anamaliensis)	0	0	2	0	0	1	1	0	2	1	0	1	0	0	1	0	0	0	0	0	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Holcocephala abdominalis	0	0	2	0	1	1	0	0	2	0	0	0	0	0	1	0	0	2	0	0	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Holcocephala calva	0	0	2	0	1	1	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	2	1	1	-	1	0	1	1	1	0	1	1	1	0	1
Rhipidocephala sp. (Harold Johnson)	0	0	1	0	0	1	1	0	2	1	1	0	0	0	1	0	0	0	0	0	0	0	2	2	1	-	1	0	1	1	1	0	1	1	1	0	1

APPENDIX 1

(Continued, extended)

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Gonioscelis ventralis	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	2	0	0	0	2	1	1	2	1	0	1	2	2
Trichoura sp. (Tierberg)	1	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	2	0	0	0	1	0	1	0	2	0	1	2	2	0	1	1	2
Ablautus coquilletti	1	1	1	0	0	0	0	3	1	0	0	0	0	1	1	0	2	1	0	0	2	0	0	0	2	0	1	0	2	0	1	2	2	0	1	2	2
Oligopogon sp. (Cape Recife)	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	2	2	0	0	2	0	0	0	2	0	1	2	1	0	1	0	1
Connomyia varipennis	1	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	2	0	0	0	2	0	0	0	2	0	1	2	2	0	1	2	3
Stichopogon elegantulus	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	2	0	0	0	1	0	2	0	2	0	1	1	1	0	1	1	0
Stichopogon punctum	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	2	0	0	0	2	0	2	0	2	0	1	1	1	0	1	1	0
Stichopogon trifasciatus	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	2	0	0	0	1	0	2	0	2	0	1	1	1	0	1	1	0
Lasiopogon aldrichii	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	2	0	0	0	1	0	2	0	2	1	1	1	1	0	1	1	0
Lasiopogon cinctus	1	1	1	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	2	0	0	0	1	0	2	0	2	1	1	1	1	0	1	1	0
Lissoteles aquilonius	1	1	1	0	0	0	0	3	1	0	1	0	0	1	1	0	5	0	0	0	2	0	0	0	1	0	2	0	2	0	1	1	1	0	1	1	0
Townsendia albomacula	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	3	2	0	0	0	1	0	2	0	2	0	1	1	1	0	1	0	0
Damalis monochaetes	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	4	0	0	2	3	-	0	0	1	0	0	0	2	0	1	1	1	0	1	0	1
Damalis annulata	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	4	0	0	2	3	-	0	0	1	0	0	0	1	0	1	1	1	0	1	0	1
Damalis sp. (Palatupana)	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	4	0	0	2	3	-	0	0	1	0	0	0	1	0	1	2	1	0	1	0	1
Trigonomima sp. (anamaliensis)	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	4	3	-	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1
Holcocephala abdominalis	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1
Holcocephala calva	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1
Rhipidocephala sp. (Harold Johnson)	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	0	1	1	0	3	2	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	1

The dataset may be downloaded in MacClade and NONA format from the TreeBase database (URL: http://www.treebase.org/; Matrix accession #: S1958) as well as the following URL: http://www.tdvia.de/research/research_data.html. Inapplicable characters are illustrated with a hyphen (-) and missing data with a question mark (?). State numbers in square brackets ([]) and separated by a slash (/) indicate polymorphisms.

APPENDIX 1
(Continued, extended)

	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111
Gonioscelis ventralis	0	1	0	1	1	0	0	0	0	0	0	0	0	3	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Trichoura sp. (Tierberg)	0	1	0	0	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	0	1	1	0	0	-	0	1	2	0
Ablautus coquilletti	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	0	1	2	0	0	0	0	1	1	0	0	-	0	1	2	0
Oligopogon sp. (Cape Recife)	1	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	1	0	-	0	1	2	0
Connomyia varipennis	0	1	0	1	1	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	1	0	0	0	0	1	0	0	-	0	1	2	0
Stichopogon elegantulus	1	1	0	0	1	0	0	0	2	0	0	0	0	1	1	1	1	1	0	1	0	2	1	1	0	0	0	1	0	1	0	0	-	0	0	2	0
Stichopogon punctum	1	1	0	1	1	0	0	0	2	0	0	0	0	1	1	1	1	1	1	1	0	2	1	1	1	0	0	1	0	1	0	0	-	0	0	2	0
Stichopogon trifasciatus	1	1	0	0	1	0	0	0	2	0	0	0	0	1	1	0	1	0	1	0	0	2	1	1	0	0	0	1	0	1	0	0	-	0	0	2	0
Lasiopogon aldrichii	0	1	0	0	0	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Lasiopogon cinctus	0	1	0	0	0	0	0	0	2	0	0	0	0	3-Feb	1	1	1	1	1	1	0	1	1	2	0	0	0	0	0	1	1	0	-	0	1	2	0
Lissoteles aquilonius	1	1	0	1	1	0	0	0	2	0	0	0	0	1	1	0	1	1	1	1	0	2	1	1	1	0	0	1	0	1	0	0	-	0	0	2	0
Townsendia albomacula	1	1	0	0	0	0	0	0	2	0	0	0	0	2	1	1	1	1	1	1	0	1	1	1	0	0	0	2	0	1	1	0	-	0	1	2	0
Damalis monochaetes	1	1	0	1	1	0	0	0	2	0	1	0	0	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	-	0	1	2	0
Damalis annulata	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0	0	0	1	0	1	1	0	-	0	1	2	0
Damalis sp. (Palatupana)	1	1	0	1	1	0	0	0	2	0	1	0	0	1	1	0	0	1	1	1	0	1	1	1	1	0	0	3	0	1	1	0	-	0	1	2	0
Trigonomima sp. (anamaliensis)	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	1	0	-	0	1	2	0
Holcocephala abdominalis	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0	2	1	0	1	0	0	0	0	1	1	0	-	0	1	2	0
Holcocephala calva	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	0	2	1	0	1	0	0	0	0	1	1	0	-	0	1	2	0
Rhipidocephala sp. (Harold Johnson)	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	1	1	1	0	2	1	0	1	0	0	0	0	1	1	0	-	0	1	2	0

APPENDIX 1
(Continued, extended)

	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Gonioscelis ventralis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	2	0	0	0	1	1	0	0	1	0	1	0
Trichoura sp. (Tierberg)	2	1	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	2	1	0	2	0	0	0	0	1	0	1	0
Ablautus coquilletti	2	0	2	0	1	0	0	0	0	0	0	0	-	1	0	2	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0
Oligopogon sp. (Cape Recife)	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Connomyia varipennis	2	0	2	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Stichopogon elegantulus	1	1	2	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Stichopogon punctum	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
Stichopogon trifasciatus	1	1	2	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
Lasiopogon aldrichii	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
Lasiopogon cinctus	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
Lissoteles aquilonius	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0
Townsendia albomacula	0	0	2	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	2	0	0	1	0	0	1	5	0	0	0	0	0	0	0	1	0	1	0
Damalis monochaetes	1	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	2	1	0	2	0	0	0	0	1	0	1	0
Damalis annulata	1	0	2	1	2	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	2	1	0	2	0	0	0	0	1	0	1	0
Damalis sp. (Palatupana)	1	0	2	1	2	0	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	2	1	0	2	0	0	0	0	1	0	1	0
Trigonomima sp. (anamaliensis)	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0/1	5	0	0	0	0	0	1	0	1	0	1	0
Holcocephala abdominalis	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Holcocephala calva	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Rhipidocephala sp. (Harold Johnson)	1	0	1	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0

APPENDIX 1
(Continued, extended)

	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185
Gonioscelis ventralis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	2	1	1	0	0	0	1	1	0	1	0	0	0	2
Trichoura sp. (Tierberg)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	6	0	2	1	1	0	0	0	1	1	0	0	0	0	1	0
Ablautus coquilletti	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	2	1	1	0	0	0	1	1	0	0	0	0	0	2
Oligopogon sp. (Cape Recife)	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	0	2	1	1	0	0	0	1	1	2	0	0	0	0	2
Connomyia varipennis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	7	0	2	1	1	0	0	0	1	1	2	1	0	0	0	3
Stichopogon elegantulus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	6	0	2	1	1	0	0	0	1	1	0	1	0	0	0	2
Stichopogon punctum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	2	1	1	0	0	0	1	1	0	1	0	0	0	2
Stichopogon trifasciatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	2	1	1	0	0	0	1	1	2	1	1	0	0	2
Lasiopogon aldrichii	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	6	0	2	1	1	0	0	0	1	1	0	0	0	0	1	2
Lasiopogon cinctus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	6	0	2	1	1	0	0	0	1	1	0	0	0	0	0	2
Lissoteles aquilonius	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	6	0	2	1	1	0	0	0	1	1	0	1	0	0	0	2
Townsendia albomacula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	6	0	2	1	1	0	0	0	1	1	0	1	1	0	0	0
Damalis monochaetes	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	0	1	1	0	0	1
Damalis annulata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	2	1	1	0	0	1
Damalis sp. (Palatupana)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	5	2	0	0	0	0	1	1	2	1	1	0	0	1
Trigonomima sp. (anamaliensis)	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	0	0	1	1	0	1	1	0	1	2
Holcocephala abdominalis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	0	0	1	1	0	1	1	0	0	2
Holcocephala calva	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	4	2	0	0	0	0	1	1	0	1	1	0	0	2
Rhipidocephala sp. (Harold Johnson)	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	-	0	2	0	0	0	0	1	1	0	1	1	0	0	2

APPENDIX 1

(Continued, extended)

	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
Gonioscelis ventralis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	1	1	1	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Trichoura sp. (Tierberg)	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	2	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ablautus coquilletti	0	0	0	0	0	0	0	0	0	0	0	1	0	1	-	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Oligopogon sp. (Cape Recife)	1	1	1	1	1	1	0	0	0	1	0	1	0	1	-	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	-	0
Connomyia varipennis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	0	0	0	1	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Stichopogon elegantulus	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	3	1	0	1	1	2	0	0	2	0	0	1	0	0	1	0	1	0	-	1
Stichopogon punctum	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	3	1	0	1	1	2	0	0	2	0	0	1	0	0	1	0	1	0	-	1
Stichopogon trifasciatus	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	3	1	0	1	1	2	0	0	2	0	0	1	0	0	1	0	1	0	-	1
Lasiopogon aldrichii	0	0	0	0	0	0	0	1	0	1	0	1	0	1	-	1	1	0	1	1	2	0	0	0	1	0	0	1	0	0	0	1	0	0	1
Lasiopogon cinctus	0	0	0	0	0	0	0	1	0	1	0	1	0	1	-	1	1	0	1	1	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Lissoteles aquilonius	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	3	1	0	1	1	2	0	0	2	0	0	0	0	0	1	0	1	0	-	1
Townsendia albomacula	0	0	0	0	0	0	0	4	0	0	0	0	0	2	0	1	1	0	1	1	2	0	0	0	0	0	0	0	0	1	0	1	0	-	1
Damalis monochaetes	0	0	0	0	0	0	0	1	0	1	0	2	0	2	0	1	2	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Damalis annulata	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	1	2	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Damalis sp. (Palatupana)	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	2	2	0	0	1	2	0	0	0	0	0	1	1	0	0	0	1	0	0	0
Trigonomima sp. (anamaliensis)	0	0	0	0	0	0	0	2	-	0	0	1	0	2	0	2	2	1	1	1	2	0	0	0	0	0	0	1	2	0	0	1	0	0	0
Holcocephala abdominalis	0	0	0	0	0	0	0	4	-	0	0	2	0	2	0	2	2	1	1	1	2	0	1	0	0	0	0	1	2	0	0	1	0	0	0
Holcocephala calva	0	0	0	0	0	0	0	4	-	0	0	2	0	2	0	2	2	1	1	1	2	0	1	0	0	0	0	1	2	0	0	1	0	0	0
Rhipidocephala sp. (Harold Johnson)	0	0	0	0	0	0	0	2	-	0	0	1	0	1	-	1	1	0	1	1	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0

APPENDIX 2

Character description and character matrix of Papavero (1975: table 2) for phylogenetic relationships of Megapodini (19 characters for 8 genera plus a single outgroup taxon)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pegesimallus	1	1	0	1	0	0	0	1	1	1	0	1	0	1	1	1	1	1	0
Lagodias	1	0	0	1	0/1	0	0/1	1	1	1	0	1	0	0	1	1	2	1	0
Cyrtophrys	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0
Deromyia	1	1	1	0	1	1	0	1	1	1	0	1	0	0	0	0/1	0	1	0
Senobasis	1	1	1	0	0	2	0/1	0	1	1	0	0	0	2	0	1	0	1	0
Megapoda	1	1	1	0	0	3	0	0	0	0	1	1	1	3	1	2	2	1	0
Pronomopsis	1	1	1	0	0	3	0	0	0	0	1	1	1	0	1	2	2	0	1
Pseudorus	1	1	1	0	0	3	0	0	0	0	1	1	0/1	0	2	0/1	0	0	2

1. Epandrium fused to hypandrium: (0) absent; (1) present.
2. Cell cup (anal cell): (0) closed; (1) open.
3. Cell m3 (fourth posterior cell): (0) closed; (1) open.
4. Acrostichal setae: (0) absent; (1) present.
5. Number of abdominal tergites in males: (0) 7 tergites; (1) 8 tergites.
6. Shape of hypandrium: (0) mammiform; (1) tongue; (2) triangle or tongue; (3) concave.
7. Number of maxillary palpomeres: (0) one; (1) two.
8. Bullae of tergites: (0) absent; (1) present. See character 154 of present analysis.
9. Number of abdominal tergites in females: (0) 7 tergites; (1) 8 tergites.
10. Female terminalia formed by segment: (0) segment 8; (1) segment 9.
11. Anatergite setation (postscutellar callosities): (0) bare; (1) pilose.
12. Antennal style: (0) absent; (1) present.
13. Cell r1 (marginal cell): (0) open; (1) closed.
14. Width of face (in relation to width of head): (0) one third; (1) two fifths; (2) one fifth; (3) one fourth.
15. Shape of face in profile: (0) plane; (1) prominent; (2) concave.
16. Lateral bristles on abdominal tergite 1: (0) absent; (1) present; (2) reduced.
17. Pilosity of scutellum: (0) absent; (1) developed; (2) reduced.
18. Dorsocentral setae: (0) reduced; (1) present.
19. Postmetacoxal area: (0) membrane; (1) narrowly membranous; (2) partially sclerotized.

The matrix may be downloaded in MacClade and NONA format from the following URL: http://www.asilidaedata.tdvia.de/matrices.html. Papavero's nomenclature is indicated in parentheses in cases where confusion might occur. State numbers separated by a slash (/) indicate polymorphisms. Note: *Lagodias* has been synonymized with *Pegesimallus* by Londt (1980).

APPENDIX 3

Character description and character matrix of Karl (1959: fig. 47) for phylogenetic relationships of Asilidae (18 characters for 11 taxa plus a single outgroup taxon)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ommatiini	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Asilus-group	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0
other Asilini	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptogastrini	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
other Dasypogoninae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lasiopogon	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0
Damalis	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Stichopogon	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0
Hoplistomerini	0	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0
Laphriini	0	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Atomosia	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	1

1. Maxillary palpus one-segmented: (0) no; (1) yes.
2. R2 reaches R1 and not C: (0) no, cell r1 open; (1) yes, cell r1 closed.
3. M3 reaches CuA1 and not C: (0) no, cell m3 open; (1) yes, cell m3 closed.
4. Cell cup (anal cell) closed: (0) no; (1) yes.
5. Lateral ejaculatory processes (“Querapodeme”) absent: (0) yes; (1) no.
6. Epandrium entirely divided medially: (0) no; (1) yes.
7. Gonostyli (referred to as dististyli) situated proximally: (0) no; (1) yes.
8. Hypandrium more or less rectangular: (0) no; (1) yes.
9. Pulvilli absent: (0) no; (1) yes.
10. Alula absent (“Anallappen”): (0) no; (1) yes.
11. Epandrium with separated surstyli: (0) no; (1) yes.
12. Postpedicel (“3. Fühlerglied”) without stylus (“Endborste”): (0) no, stylus present; (1) yes, stylus absent.
13. Epandrium secondarily fused: (0) no; (1) yes.
14. Abdominal tergite 8 largely or entirely reduced: (0) no; (1) yes.
15. Gonocoxites (referred to as basistyli) more or less strongly fused: (0) no; (1) yes.
16. Hypandrium entirely reduced: (0) no; (1) yes.
17. Hypopygium rotated by 180° angle: (0) no; (1) yes.
18. Gonostyli entirely reduced: (0) no; (1) yes.

The matrix may be downloaded in MacClade and NONA format from the following URL: http://www.asilidaedata.tdvia.de/matrices.html. Karl’s nomenclature is indicated in parentheses in cases where confusion might occur.