

**SYSTEMATICS AND PHYLOGENY OF THE DOLICHOPODINAE
(DIPTERA: DOLICHOPODIDAE)**

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May 2004

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements of the degree of Doctor of Philosophy

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ABSTRACT. The phylogenetic relationships of the subfamily Dolichopodinae were investigated based on the examination of over 340 species from all zoogeographic regions. Sixty-five exemplar species were included in cladistic analysis based on 74 morphological characters of adult specimens. Twenty genera are recognized in the Dolichopodinae: *Allohercostomus* Yang, Saigusa and Masunaga, *Anasyntormon* Parent, *Argyrochlamys* Lamb, *Cheatomyia* Dyte, *Dolichopus* Latreille, *Ethiomyia* **gen. nov.**, *Gymnopternus* Loew, *Hercostomus* Loew, *Metaparaclius* Becker, *Muscidideicus* Becker, *Ortochile* Latreille, *Paraclius* Loew, *Parahercostomus* Yang, Saigusa and Masunaga, *Pelastoneurus* Loew, *Platyopsis* Parent, *Poecilobothrus* Mik, *Prohercostomus* Grichanov, *Stenopygium* Becker, *Sybistroma* Meigen, and *Tachytrechus* Stannius. Eleven genera are newly synonymized: *Halaiba* Parent (= *Argyrochlamys* Lamb); *Lichtwardtia* Enderlein (= *Dolichopus* Latreille); *Phalacrosoma* Becker (= *Hercostomus* Loew); *Steleopyga* Grootaert and Meuffels (= *Hercostomus* Loew); *Proarchus* Aldrich (= *Pelastoneurus* Loew); *Sarcionus* Aldrich (= *Pelastoneurus* Loew); *Pterostylus* Mik (= *Poecilobothrus* Mik); *Ludovicius* Rondani (= *Sybistroma* Meigen); *Nodicornis* Rondani (= *Sybistroma* Meigen); *Gonioneurum* Becker (= *Tachytrechus* Stannius); *Syntomoneurum* Becker (= *Tachytrechus* Stannius). Eighty-one new generic combinations are established and one new name is proposed for a secondary homonym. Four genera that were sometimes included in the subfamily are excluded, namely *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg and *Vetimicrotes* Dyte. A key to the world genera of Dolichopodinae is provided. The *Tachytrechus alatus* species group (formerly the genus *Syntomoneurum*) is revised. This species group includes five Neotropical species, all of which are redescribed. A key to the species of the *T. alatus* species group is provided. The new genus *Ethiomyia* is also described, including two Nearctic and one Palearctic species. All species are redescribed and a key is provided to facilitate their identification.

RÉSUMÉ. Une étude phylogénétique de la sous-famille des Dolichopodinae, incluant 349 espèces provenant de toutes les régions biogéographiques, ainsi qu'une analyse cladistique, basée sur 74 caractères morphologiques des adultes de 65 espèces exemplaires, ont été réalisées. Vingt genres appartenant à cette sous-famille sont reconnus: *Allohercostomus* Yang, Saigusa and Masunaga, *Anasyntormon* Parent, *Argyrochlamys* Lamb, *Cheiromyia* Dyte, *Dolichopus* Latreille, *Ethiomyia* **gen. nov.**, *Gymnopternus* Loew, *Hercostomus* Loew, *Metaparaclius* Becker, *Muscidideicus* Becker, *Ortochile* Latreille, *Paraclius* Loew, *Parahercostomus* Yang, Saigusa and Masunaga, *Pelastoneurus* Loew, *Platyopsis* Parent, *Poecilobothrus* Mik, *Prohercostomus* Grichanov, *Stenopygium* Becker, *Sybistroma* Meigen, et *Tachytrechus* Stannius. De plus, 11 genres sont mis en synonymie: *Halaiba* Parent (= *Argyrochlamys* Lamb); *Lichtwardtia* Enderlein (= *Dolichopus* Latreille); *Phalacrosona* Becker (= *Hercostomus* Loew); *Steleopyga* Grootaert and Meuffels (= *Hercostomus* Loew); *Proarchus* Aldrich (= *Pelastoneurus* Loew); *Sarcionus* Aldrich (= *Pelastoneurus* Loew); *Pterostylus* Mik (= *Poecilobothrus* Mik); *Ludovicius* Rondani (= *Sybistroma* Meigen); *Nodicornis* Rondani (= *Sybistroma* Meigen); *Gonioneurum* Becker (= *Tachytrechus* Stannius); *Syntomoneurum* Becker (= *Tachytrechus* Stannius). En outre, l'auteur établit 81 nouvelles combinaisons au niveau générique et propose un nouveau genre en remplacement d'un homonyme secondaire. Quatre genres, parfois inclus dans la sous-famille, sont ici exclus: *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg et *Vetimicrotes* Dyte. Une clef d'identification des genres, à l'échelle mondiale, est présentée. Le groupe d'espèces *Tachytrechus alatus* (autrefois le genre *Syntomoneurum*) est révisé et de nouvelles descriptions des 5 espèces néotropicales qu'il comprend sont incluses. Une clef d'identification des espèces de ce groupe est également présentée. Finalement, le nouveau genre *Ethiomyia* est révisé. Ce genre comprend 2 espèces néarctiques et 1 espèce paléarctique. De nouvelles descriptions de ces espèces sont produites et une clef facilitant leur identification est incluse.

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ACKNOWLEDGEMENTS

Many people have contributed to this thesis over the past several years. First and foremost I want to thank my wife Carole. I wouldn't have been able to complete this project without her continued love, support, encouragement, advice and patience. I am truly a lucky boy.

I am extremely grateful to my supervisor, Dr. Terry Wheeler, for his guidance, support, critical evaluation of my work, patience, generosity and comradeship throughout the duration of this project. I would also like to thank Terry for making it possible for me to take part in several dipterological excursions to California, Europe, Washington, D.C. and Australia which have made my Ph.D. a truly rewarding and unforgettable experience.

Dr. Jeff Cumming played a major role in this project and I want to thank him for his advice, critical evaluation of this thesis, empirical expertise, encouragement, friendship, and more than the occasional moment of absurdity along the way.

Thanks to Dr. Bob Anderson, Dr. Jeff Cumming, Dr. Stephen Gaimari, Dr. David Green, Dr. A.L. Padjen, Dr. Manfred Rau and Dr. Terry Wheeler for serving on my thesis examination committee.

Thanks to Dr. Marc Pollet for his continued enthusiasm and interest in this project, for the countless discussions and emails on dolichopodids, and for all the great times on collecting trips in Quebec, Ontario, Belgium and Costa Rica over the course of this project.

Throughout my time at the Lyman I had the pleasure to interact with a great group of people including: Stéphanie Boucher, Jade Savage, Marjolaine Giroux, Rebecca Zeran, Duncan Selby, Cyrena Riley, Fred Beaulieu, Eleanor Fast, Vanessa Crecco, Jessica Forrest, Beth Wright, Patrice Bouchard, Cory Keeler, Sonia Murray, Joanne Mudd, Joëlle Péruse, Hironnelle Varady-Szabo, Shauna Hawkins and Terry Wheeler. I thank them for making the Lyman a great place to work. I will miss it.

I would like to extend a special thanks to Dr. Jade Savage. Jade played an essential role in the day to day development of this thesis and I am grateful for her sound advice, critical opinion, moral support and friendship.

Thanks to the following people who provided additional advice, assistance and information: Dan Bickel, Bruce Cooper, Brian Driscoll, Peter Dyte, Neal Evenhuis,

Patrick Grootaert, David Lewis, Harold Robinson, Jeff Skevington, Chris Thompson, Hans Ulrich, Dick Vockeroth, Ding Yang and Lili Zhang. Thanks to Marjolaine Giroux for providing the french translation of the abstract.

Financial Support for this thesis was provided by the Federal Biosystematics Group Fellowship, Dipterology Fund (2000, 2002), McGill University Margaret Duporte Fellowship (2000, 2001) and a Natural Sciences and Engineering Research Council of Canada research grant to T.A. Wheeler.

PREFACE

This thesis is composed of five chapters, three of which are original manuscripts that have been published or will be submitted for publication in refereed journals.

Chapter 1.

This chapter constitutes a general introduction and literature review of the current knowledge and previous research on dolichopodid flies with a focus on the subfamily Dolichopodinae.

Chapter 2.

This chapter is a manuscript in preparation for submission:
Brooks, S.E. Systematics and phylogeny of the Dolichopodinae (Diptera: Dolichopodidae).

Chapter 3.

This chapter is a version of a manuscript which has been published in *Insect Systematics and Evolution* under the title:
Brooks, S.E. and T.A. Wheeler. 2002. Revision of the Neotropical genus *Syntomoneurum* Becker (Diptera: Dolichopodidae). *Insect Systematics and Evolution* 33: 311-324.

Chapter 4.

This chapter is a manuscript in preparation for submission:
Brooks, S.E. and T.A. Wheeler. Revision of *Ethiomyia* Brooks (Diptera: Dolichopodidae).

Chapter 5.

This chapter is a general discussion and conclusion.

CONTRIBUTION OF AUTHORS

Scott Edward Brooks designed and executed the research in all three manuscripts and conducted all specimen-based work, data collection, analysis and writing. Terry Wheeler was responsible for the supervision of the thesis research and editing of the manuscripts.

CLAIM TO ORIGINALITY

The work presented in this thesis is considered to be an original contribution to knowledge in the following respects:

1. First phylogenetic analysis of Dolichopodinae.
2. The limits of Dolichopodinae are redefined and four genera are excluded from the subfamily including *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg and *Vetimicrotes* Dyte
3. First key to the dolichopodine genera of the world.
4. Standardized redescrptions of dolichopodine genera are presented incorporating numerous features overlooked in previous studies.
5. First detailed and comprehensive study of the morphology of male and female genitalia of Dolichopodinae.
6. First detailed illustrations of male and female genitalia of dolichopodine genera.
7. Eleven genera are newly synonymized: *Halaiba* Parent (= *Argyrochlamys* Lamb); *Lichtwardtia* Enderlein (= *Dolichopus* Latreille); *Phalacrosuma* Becker (= *Hercostomus* Loew); *Steleopyga* Grootaert and Meuffels (= *Hercostomus* Loew); *Proarchus* Aldrich (= *Pelastoneurus* Loew); *Sarcionus* Aldrich (= *Pelastoneurus* Loew); *Pterostylus* Mik (= *Poecilobothrus* Mik); *Ludovicius* Rondani (= *Sybistroma* Meigen); *Nodicornis* Rondani (= *Sybistroma* Meigen); *Gonioneurum* Becker (= *Tachytrechus* Stannius); *Syntomoneurum* Becker (= *Tachytrechus* Stannius)
8. One new genus, *Ethiomyia* **gen. nov.**, is described and its three included species are redescrbed and figured. A key is also provided to identify species.
9. Eighty-one new generic combinations are established and one new name is proposed.
10. The *Tachytrechus alatus* species group (= *Syntomoneurum* Becker) is defined and revised for the first time.

CHAPTER 1. GENERAL INTRODUCTION AND LITERATURE REVIEW

The order Diptera is one of the most diverse and economically important groups of insects. Worldwide it is estimated that there are about 200,000 species of flies (McAlpine et al., 1979), of which about 124,000 species have been described (Brown, 2001). Along with Tipulidae (14,000 species) and Tachinidae (9200 species) (Brown, 2001), the Dolichopodidae, or long-legged flies, are one of the most diverse families of Diptera with over 6600 described species (Grichanov, unpublished data) comprising about five percent of the known species of flies. Dolichopodids are extremely widespread and are found in all zoogeographic regions (Robinson, 1970b; Dyte, 1975; Dyte and Smith, 1980; Bickel and Dyte, 1989; Negrobov, 1991; Pollet et al., 2004).

Characteristics of Dolichopodidae

Adult dolichopodids range in size from about 1-9 mm in length (Robinson and Vockeroth, 1981) and can be recognized by their elongate legs, reduced wing venation, aristate antennae, and relatively slender build. Most species are metallic greenish-blue to greenish-bronze, while some others are non-metallic yellowish (e.g., some species of *Achalcus* Loew, *Argyrochlamys* Lamb, *Neurigona* Rondani, *Xanthochlorus* Loew and *Xanthina* Aldrich), brown or blackish (e.g. several species of *Micromorphus* Mik and *Medetera* Fischer von Waldheim). Males are known for their wide array of secondary sexual characteristics which have been invaluable features for recognizing species. Male secondary sexual characteristics often include modifications of the antennae, palps, wings and, typically, the legs. The male genitalic capsule or hypopygium is either somewhat small and partially enclosed by preceding abdominal segments, or large, permanently exerted and supported by a pedunculate abdominal segment 7. Snodgrass (1904), Buchmann (1961) and Ulrich (1974) have provided detailed morphological studies of the dolichopodid hypopygium.

Larvae are whitish, cylindrical and relatively slender with distinct creeping welts on segments 4-11. The anterior end is tapered and the posterior end is truncate with four or more lobes on segment 12 (Robinson and Vockeroth, 1981; Corpus, 1986a,b, 1988). The larval head is modified posteriorly into two apically expanded or spatulate

metacephalic rods and two tentorial arms, and the larval mandible is composed of four components (Woodley, 1989; Sinclair, 1992). Dolichopodid pupae are characterized by the possession of a pair of long, dorsal prothoracic respiratory horns and a pair of frontofacial sutures. Most known species also possess spiniferous transverse bands on the abdominal tergites (Dyte, 1967; Robinson and Vockeroth, 1981; Corpus, 1986a,b, 1988).

Natural History of Dolichopodidae

In general, adults and larvae prefer moist environments including stream and lake margins, humid forests, saltmarshes, seashores, and freshwater seepages, where they often occur in large numbers. Some species are closely associated with tree trunks or vertical surfaces (e.g. *Medetera*, *Neurigona*, *Sciapus* Zeller), whereas others occur in drier habitats such as agricultural fields and grasslands (e.g., some species of *Medetera*) (Bickel, 1985) or urban gardens (e.g., some species of *Condylostylus* Bigot) (Robinson and Vockeroth, 1981). Larvae occur in mud, damp soil, leaf litter, moss, algal mats, decaying seaweed, sap wounds, under bark, in tree hole debris and within plant tissues (Dyte, 1959). Before pupation the final instar spins a protective cocoon incorporating soil particles and other environmental debris, which completely encapsulates the pupa, except for the tips of the respiratory horns, which protrude from a small aperture (Dyte, 1959; Corpus, 1986a,b, 1988). Recent studies (Pollet, 1992, 2000, 2001; Pollet and Grootaert, 1991, 1996) demonstrate that dolichopodids have very specific habitat requirements and react quickly to environmental alterations, making them potentially useful as bioindicators for site quality assessment and conservation purposes.

Adults are predacious, feeding primarily on small, soft-bodied insects and other invertebrates such as Diptera larvae (e.g., mosquitoes and chironomid midges), thrips, spingtails, aphids, spiders, mites (see references in Satô, 1991) and annelid worms (Ulrich and Schmelz, 2001). Although the adults of some dolichopodid genera (e.g., *Hydrophorus* Fallén, *Scellus* Loew, *Hydatostega* Phillipi, *Thinophilus* Wahlberg, *Aphrosylus* Haliday) are known to use their forelegs to hold and manipulate their prey (Roubaud, 1903; Doane, 1907; Williams, 1939; Harmston, 1948; Peterson, 1960), most “graze” in areas where slow moving or confined prey are abundant, typically grabbing and crushing prey directly with their labellum (Fischer von Waldheim, 1819; Ulrich and Schmelz, 2001; Brooks,

2002). Adults of some Dolichopodinae have elongate mouthparts (e.g. *Ortochile* Latreille, some species of *Hercostomus* Loew) and are known to be anthophilous and feed on nectar (Dyte, unpublished manuscript) and pollen (see “Remarks” under the generic treatment of *Ortochile* in Chapter 2). The morphology of the mouthparts of adult dolichopodids has been studied in detail by Cregan (1941) and Satô (1991).

In general, little is known about the activities of dolichopodid larvae; however, most are thought to be predators or scavengers. Larvae of many species of *Medetera* are known to be significant predators of bark beetle larvae (DeLeon, 1935). In contrast, larvae of *Thrypticus* Gerstacker are phytophagous and feed as stem-miners in grasses, sedges and rushes (Dyte, 1959).

Many dolichopodids, especially those of the subfamily Dolichopodinae, show complex mating behaviour. Males of this subfamily often engage in mating dances which usually involve wing displays, or displays of secondary sexual characteristics (Steyskal, 1938, 1946). Males of some species, e.g., *Poecilobothrus nobilitatus* (Linnaeus), also establish territories which they defend from conspecific males and other intruders (Lunau, 1992). Males of some Hydrophorinae, e.g., *Hydrophorus oceanus* (Macquart), engage in mate guarding and hold on to the female with their fore legs following copulation, thus preventing other males from mating with her (Dyte, 1988).

Systematic position and monophyly of Dolichopodidae

The Dolichopodidae are classified in the superfamily Empidoidea, the sister group to the Cyclorrhapha (Cumming et al., 1995; Collins and Wiegmann, 2002), along with the paraphyletic family Empididae. Dolichopodidae are part of a monophyletic lineage that also includes the empidid subfamily Microphorinae (Cumming et al., 1995; Grimaldi and Cumming, 1999; Cumming and Brooks, 2002). In all microphorines and dolichopodids the male genitalia and pregenital segments 7 and 8 are rotated and lateroflexed to the right (Cumming et al., 1995). As a result of this modification, the ejaculatory duct has become twisted around the hind gut similar to the Cyclorrhapha; however, the condition observed in the Dolichopodidae + Microphorinae lineage is not homologous to that of Cyclorrhapha in which there has been a complete 360° circumversion of the hypopygium (Cumming et al., 1995). The monophyly of the Dolichopodidae + Microphorinae is also

supported by the possession of rod-like extensions of the subepandrial sclerite that reach beyond the base of the phallus to fuse directly with the hypandrium of the male genitalia (Cumming et al. 1995), and by the long, rod-shaped lower metapleural arm of the thoracic skeleton (Ulrich, 1984, 1990).

The subfamily Microphorinae as currently recognized, including the tribes Microphorini and Parathalassiini (Chvála, 1981, 1983, 1986, 1987, 1988), is paraphyletic with respect to Dolichopodidae, and the dolichopodids form a well-supported monophyletic group with the Parathalassiini. The monophyly of this clade is supported by the possession of an incomplete or evanescent crossvein bm-cu (Chvála, 1983; Ulrich, 1991; Grimaldi and Cumming, 1999; Cumming and Brooks, 2002), as well as several features of the mouthparts (i.e. clypeal ridge perpendicular and broad, lacinia of mouthparts absent, palpus short, six geminately sclerotized pseudotrachea) (Sinclair and Cumming, pers. comm), and thorax (i.e. broad ventral portion of presternum, intersegmental ridge between the meso- and metapleuron forming two pockets, upper metapleural arm rod-shaped) (Ulrich, 1990). Preliminary cladistic analyses of the Microphorinae + Dolichopodidae lineage (Cumming and Brooks, 2002; Shamshev and Grootaert, 2002) indicate that the Parathalassiini may also be paraphyletic with respect to the Dolichopodidae. As such, Cumming and Sinclair's (2000) proposal to include all the microphorine genera within the Dolichopodidae seems justified.

Woodley (1989) listed two synapomorphies supporting the monophyly of the Dolichopodidae sensu stricto. The first is a reduction in wing venation characterized by the first branch of the radial vein originating near the wing base just below the humeral crossvein, a feature that is also present in microphorines, and by the position of the r-m crossvein which is located near the wing base. The second apomorphy is the presence of paired tooth-like structures of the mouthparts termed the epipharyngeal armature (Cregan, 1941; McAlpine, 1981; Satô, 1991). These structures are unique to the dolichopodids and are presumably utilized in tearing the bodies of their prey. The mouthparts of dolichopodids are also characterized by the possession of an enlarged carina which projects vertically into the head capsule (Cregan, 1941; McAlpine, 1981; Satô, 1991, Sinclair and Cumming, pers. comm). The monophyly of Dolichopodidae is further

supported by the possession of an epandrial foramen which is positioned on the left lateral side of the male hypopygium.

Classification and phylogeny of Dolichopodidae

Fundamental works on the classification and systematics of Dolichopodidae include Loew (1864), Lundbeck (1912), Becker (1917-1918, 1922a,b, 1923), Stackelberg (1930, 1933, 1934, 1941, 1971), Parent (1938), Negrobov and Stackelberg (1971-1977), Robinson (1964, 1975), Negrobov (1977-1979), Assis Fonseca (1978) and Robinson and Vockeroth (1981). Although new species of dolichopodids continue to be described at relatively rapid rate, it has long been recognized that there are many problems with the higher-level classification of Dolichopodidae and a comprehensive review of world subfamilies and genera is badly needed (Robinson and Vockeroth, 1981). Most subfamilies have not been studied in a phylogenetic context and many have uncertain limits and are questionably monophyletic (e.g., Diaphorinae, Hydrophorinae, Peloropecodinae, Rhaphiinae, Sympycninae). Furthermore, virtually nothing is known about the phylogenetic relationships of the genera within these subfamilies.

Several subfamily classifications have been proposed for the dolichopodids over the past 150 years (Lioy, 1863-1864; Schiner, 1864; Aldrich, 1905; Kertész, 1909; Becker, 1917-1918, 1922a,b, 1923; Robinson, 1970a,b; Ulrich, 1980; Negrobov, 1986). The earliest classification was that of Lioy (1863-1864), whose concept of the Dolichopodidae included the Scenopinidae (Famiglia Scenopiniti), Lonchopteridae (Famiglia Lonchopteriti), Platypezidae (Famiglia Platypeziti) and Pipunculidae (Famiglia Cephalopsiti) in addition to the dolichopodids (which he divided into two groups: Famiglia Hydrophoriti and Famiglia Medeteriti). Lioy's classification was apparently ignored by subsequent workers. Several months following Lioy (1863-1864), Schiner (1864) published his catalogue of European Diptera, in which he recognized four subfamilies of Dolichopodidae (Rhaphinae, Dolichopinae, Hydrophorinae and Diaphorinae). Aldrich (1905) was the first to treat the Nearctic fauna and recognized 12 subfamilies, including Agonosominae, Diaphorinae, Rhaphiinae, Sympycninae, Neurigoninae, Xanthochlorinae, Thinophilinae, Medeterinae, Hydrophorinae, Plagioneurinae, Aphrosylinae and Dolichopinae. Kertész (1909), subsequently followed

Schiner's (1864) classification in his catalog of the Palaearctic species, but also recognized Aldrich's New World subfamily Plagioneurinae. Lundbeck (1912) adopted the classification of Kertész (1909) in his treatment of the Danish fauna, but considered Aldrich's (1905) system to be a more natural arrangement of the genera.

Becker's series of monographs of the of the world fauna of Dolichopodidae (Becker, 1917-1918, 1922a,b, 1923) provided the most comprehensive treatment of the family available at the time and remains the foundation of modern dolichopodid systematics. Becker recognized 11 subfamilies including: Dolichopodinae, Plagioneurinae, Hydrophorinae, Aphrosylinae, Medeterinae, Rhaphiinae, Neurigoninae, Diaphorinae, Stolidosomatinae, Sympycninae (as Campsicnemininae) and Sciapodinae (as Chrysosomatinae). Becker's system was similar to that of Aldrich (1905); however, he did not recognize Xanthochlorinae, and divided the genera assigned to that group among Rhaphiinae (*Achalcus*), Sympycninae (*Chrysotimus* Loew and *Xanthochlorus*) and Diaphorinae (*Xanthina*). Becker also synonymized the Thinophilinae within the Hydrophorinae, and placed *Teuchophorus* Loew and *Campsicnemus* Haliday in the Sympycninae, *Eutarsus* Loew and *Peloropecodes* Wheeler in the Rhaphiinae, and *Argyra* Macquart, *Nematoproctus* Loew and *Coeloglutus* Aldrich in the Diaphorinae. Becker's subfamily classification was widely adopted by most subsequent workers (Stackelberg, 1930, 1933, 1934, 1941, 1971; Parent, 1938; Foote et al., 1965; Dyte, 1975, Dyte and Smith, 1980).

Robinson (1970a,b) proposed a revised subfamily classification based on the Nearctic and Neotropical fauna arguing that Becker's (1917-1918, 1922a,b, 1923) treatment put too much emphasis on extreme forms and that not enough attention was given to intermediate members of the family. Robinson (1970a) also criticized Becker and followers for lumping most of the smaller dolichopodids into ill-defined subfamilies such as the Sympycninae. Robinson's classification recognized 14 subfamilies and incorporated characters of the mouthparts (Cregan, 1941), genitalia (Buchmann, 1961) and immature stages (Dyte, 1967). Robinson (1970a) dismantled Becker's concept of the Rhaphiinae and split it into three subfamilies, namely Peloropecodinae, Systeminae (containing the single genus *Systemus* Loew) and a more restricted Rhaphiinae (composed solely of the nominal genus *Rhaphium* Meigen). Robinson (1970a,b) also recognized the

Xanthochlorinae of Aldrich (1905) (exclusive of *Chrysotimus* which he placed in the subfamily Peloropeodinae), erected Enliniinae for the genera *Enlinia* Aldrich and *Harmstonia* Robinson, and synonymized Aphrosylinae within the Hydrophorinae. Although no phylogenetic hypothesis was provided, Robinson (1970a) suggested close relationships between Rhaphiinae and Diaphorinae, *Systemus* and Medeterinae, Medeterinae and Neurigoninae, and Stolidosomatinae and Sympycninae.

Ulrich (1981) modified Robinson's (1970a,b) classification to encompass the world fauna and recognized 10 subfamilies. Ulrich expanded Systeminae to include *Achalcus* and *Xanthina* from Robinson's Xanthochlorinae, as well as *Epithalassius* Mik and *Euxiphocerus* Parent. Ulrich also added Stolidosomatinae, Peloropeodinae and *Xanthochlorus* Loew to Sympycninae, and expanded Rhaphiinae to include *Plagioneurus* Loew (i.e. Plagioneurinae), *Argyra*, *Keirosoma* Van Duzee, *Nematoproctus*, *Pseudargyra* Van Duzee and *Somillus* Brèthes from Robinson's Diaphorinae, as well as *Pinacocerus* Van Duzee from Robinson's Sympycninae. In addition, Ulrich transferred several Old World genera into Sympycninae and Dolichopodinae that had previously been assigned to other subfamilies by previous authors. Ulrich's (1981) classification was subsequently adopted (with some modifications) by Bickel and Dyte (1989).

Negrobov (1986) rejected Ulrich's (1981) system and proposed a classification similar to that of Robinson (1970a,b) which recognized 14 subfamilies and included tribal classifications for Diaphorinae, Dolichopodinae, Hydrophorinae, Medeterinae and Sympycninae. Negrobov assigned Robinson's Stolidosomatinae tribal status within the Sympycninae and erected the subfamily Coeloglutinae for the Neotropical genera *Coeloglutus* and *Neotonnoiria* Robinson, which Robinson placed in the Neurigoninae. Bickel (1998) questioned the validity of the Coeloglutinae and considered it a synonym of Neurigoninae. More recently, Naglis (2001) assigned this group tribal status (Coeloglutini) within the Neurigoninae and recognized two additional tribes, i.e. Dactylomyiini and Neurigonini (Naglis, 2002a,b). Like Robinson (1970a,b), Negrobov (1986) recognized a monogeneric subfamily concept of Systeminae; however, Bickel (1986) included *Systemus* within Medeterinae.

Since Negrobov's (1986) classification, two additional subfamilies have been erected, i.e. Babindellinae (Bickel, 1987) and Achalcinae (Grootaert and Meuffels, 1997).

Bickel (1987) erected Babindellinae for the Australian genus *Babindella* Bickel, which is characterized by the possession of a symmetrical male postabdomen. The Achalcinae was erected following the discovery of the genus *Scepastopyga* Grootaert and Meuffels from Papua New Guinea. Grootaert and Meuffels (1997) also included *Achalcus* and *Xanthia* (from Robinson's Xanthochlorinae and Ulrich's Systeminae) within the Achalcinae and suggested a close relationship to the Sciapodinae and Medeterinae.

Despite the various subfamily classifications proposed for the Dolichopodidae, most of the differences of opinion have focused on certain subfamilies, such as Sympycninae and Rhamphiinae, which have been repeatedly redefined. In contrast, the classification of other subfamilies, such as Sciapodinae and Dolichopodinae, has remained relatively stable.

Besides passing comments on the affinities of certain subfamilies (Robinson, 1970a; Grootaert and Meuffels, 1997), very little has been written about their phylogenetic relationships. Most discussions regarding subfamily relationships are based primarily on the morphology of the male hypopygium and the pregenitalic segments (Negrobov, 1986; Bickel, 1994). There are two main morphological forms of the dolichopodid hypopygium, the "encapsulated" condition and the "pedunculate" condition. In the encapsulated condition (e.g., Diaphorinae, Sympycninae, Plagioneurinae) the hypopygium (when at rest) is partially covered by tergite 6 and segment 7 acts as a short lever to roll the genital capsule ventrally and anteriorly (Negrobov, 1986; Bickel, 1987). In the pedunculate condition (e.g., Sciapodinae, Medeterinae, Neurigoninae, Babindellinae, Dolichopodinae) the hypopygium is permanently exserted, although it may rest partially enfolded by the venter of the preabdomen, and segment 7 is modified into a peduncle or external arm on which the genital capsule is supported (Negrobov, 1986; Bickel, 1987). The pedunculate condition is also present in the Microphorinae (Chvála, 1986, 1987, 1988; Ulrich, 1988), and is part of the dolichopodid groundplan, whereas the encapsulate hypopygium has been derived within the family.

The subfamily Dolichopodinae

Members of the subfamily Dolichopodinae are distinguished by the possession of a distinct patch of setae on the dorsal surface of the first antennal segment, one or more

distinct anterior or anterodorsal preapical setae on the mid and hind femora, male abdominal tergite 6 usually bare, and by the large pedunculate genital capsule of males which projects forward under the preceding abdominal segments. The subfamily includes about 1700 described species worldwide, but is most diverse in the Holarctic. Most species are classified in six large genera, including *Dolichopus* Latreille, with about 600 species, *Hercostomus*, with about 470 species (not including species of *Gymnopternus* Loew which are sometimes included within *Hercostomus* in Old World classifications), *Tachytrechus* Stannius, with about 140 species, and *Paraclius* Loew, *Gymnopternus* and *Pelastoneurus* Loew, with over 100 species each.

Becker's (1917-1918, 1922a,b, 1923) classic series of revisions of the world fauna of Dolichopodidae laid the foundation for the modern day concept of the subfamily Dolichopodinae. Becker recognized the following genera of Dolichopodinae worldwide: *Dolichopus*, *Gonioneurum* Becker, *Hercostomus* (including *Ortochile* Latreille and *Muscidideicus* Becker as subgenera, and *Gymnopternus* as a synonym), *Hypophyllus* Haliday, *Leptocorypha* Aldrich, *Ludovicius* Rondani, *Macellocerus* Mik (which was synonymized with *Tachytrechus* by Greene (1922)), *Metaparaclius* Becker, *Paraclius*, *Pelastoneurus*, *Poecilobothrus* Mik, *Polymedon* Osten Sacken, *Psilischium* Becker, *Pterostylus* Mik, *Sarcionus* Aldrich, *Stenopygium* Becker, *Sybistroma* Meigen and *Tachytrechus*. Although Becker and many subsequent Old World workers treated *Gymnopternus* as a synonym (e.g., Negrobov, 1991) or subgenus (Pollet, 1990; Chandler, 1998) of *Hercostomus*, dolichopodologists working on the New World fauna continue to recognize *Gymnopternus* as a separate genus (e.g., Curran, 1933; Robinson, 1964, 1970a; Foote et al., 1965; Robinson and Vockeroth, 1981; Pollet et al. 2004).

The decade following Becker's work saw the establishment of three new genera, i.e. *Vaalimyia* Curran (1926), *Cheirocerus* Parent (1930) (now *Cheiromyia* Dyte), *Pseudohercostomus* Stackelberg (1931), one new subgenus of *Hercostomus*, i.e. *Platyopsis* Parent (1929a), which was subsequently treated as a genus by Parent (1929b), and one new subgenus of *Dolichopus*, i.e. *Macrodolichopus* Stackelberg (1933). In addition, Stackelberg (1933) also elevated *Ortochile* and *Muscidideicus* to generic status. Curran (1926) and subsequent authors (e.g., Parent 1929b; Vanschuytbroeck, 1951), were apparently unaware that *Vaalimyia* had been previously described by Enderlein (1912)

under the name *Lichtwardtia* Enderlein, which was treated as a synonym of *Dolichopus* by Becker (1922b). Dyte (1975) synonymized *Vaalimyia* with *Lichtwardtia* and recognized the latter as a genus.

Parent's (1938) treatment of the Dolichopodinae of France largely followed the classifications of Becker and Stackelberg; however, he elevated *Macrodolichopus* and *Hygroceleuthus* to generic status. This classification was not adopted by subsequent workers who have treated these taxa as subgenera of *Dolichopus* following Stackelberg (1931, 1933) (e.g., Negrobov, 1991), or as synonyms of *Dolichopus* (e.g. Foote et. al., 1965; Pollet et al., 2004).

Robinson's (1970a,b) concept of the Dolichopodinae was similar to that of Becker (1922a); however, he transferred the monotypic Neotropical genus *Proarchus* Aldrich (formerly *Phylarchus* Aldrich) into the subfamily from the Hydrophorinae. Robinson also synonymized *Gongophora* Philippi, *Polymedon* and *Psilischium* with *Tachytrechus* and *Leptocorypha* with *Paraclius*. In contrast, Dyte (1975) retained the generic status of *Polymedon* and this has been followed in recent papers dealing with the Oriental (Yang and Grootaert, 1999; Yang et al., 2001) and Afrotropical fauna (Grichanov, 2004). Dyte (1975) also included *Argyrochlamys* in the Dolichopodinae.

Negrobov (1980) provided a brief discussion of subfamily limits and generic relationships and recommended that *Gymnopternus* should be synonymized with *Hercostomus*, *Ortochile* should be considered a subgenus of *Hercostomus*, *Lichtwardtia* should be considered a subgenus of *Pterostylus*, and *Phalacrosoma* Becker, *Syntomoneurum* (Hydrophorinae), *Anasyntormon* and *Katangaia* (Rhaphiinae) should be transferred to the Dolichopodinae. Shortly thereafter, Ulrich (1981) proposed a revised worldwide classification of the Dolichopodidae, in which he transferred seven genera to the Dolichopodinae including *Anasyntormon*, *Katangaia*, *Phalacrosoma* and *Syntomoneurum* in agreement with Negrobov (1980), as well as *Colobocerus* Parent and *Vetimicrotes* Dyte from the Sympycninae and *Halaiba* Parent from the Rhaphiinae.

Negrobov (1986) proposed a revised classification for the Dolichopodinae in which he recognized two tribes: Tachytrechini, including *Tachytrechus*, *Paraclius* and *Pelastoneurus*, and Dolichopodini comprising the remaining genera. However, Negrobov did not explicitly define the features characterizing each tribe, particularly the

Dolichopodini and his classification was primarily restricted to the Palaearctic fauna, leaving several genera without a tribal assignment. Negrobov (1991) followed a similar classification in his Palaearctic catalogue, but reduced *Poecilobothrus* to subgeneric rank within *Hercostomus*.

The last decade has seen the establishment of four new dolichopodine genera, including the fossil genus *Prohercostomus* Grichanov (1997, 2000), *Allohercostomus* Yang, Saigusa and Masunaga (2001), *Parahercostomus* Yang, Saigusa and Masunaga (2001), *Steleopyga* Grootaert and Meuffels (2001), and one new subgenus of *Hercostomus*, i.e. *Ahercostomus* Yang and Saigusa, 2001. The most recent contribution to dolichopodine systematics is Grichanov's (2004) review of the Afrotropical fauna.

Objectives

Like most subfamilies of Dolichopodidae, the limits of the Dolichopodinae have never been tested using cladistic methods. Furthermore, the phylogenetic relationships of the genera are unknown and the monophyly of several genera is in question. The primary objective of this study was to examine the limits and monophyly of the Dolichopodinae, reconstruct the phylogenetic relationships of the genera using cladistic methods, and provide redescriptions and a key to the dolichopodine genera to facilitate their identification on a world basis (Chapter 2). In the course of this phylogenetic analysis, a number of monophyletic groups of species were identified. Of these groups, one of the best supported is the *Tachytrechus alatus* species group (= *Syntomoneurum* Becker). This species group is revised in Chapter 3. The phylogenetic analysis in Chapter 2 also led to the recognition of a new Holarctic genus of Dolichopodinae, *Ethiromyia* **gen. nov.** In Chapter 4, all three species of *Ethiromyia* are redescrbed and a key is provided to facilitate their identification.

It should be noted that all new taxon names, new synonyms and new combinations proposed in this thesis are not valid within the meaning of the International Code of Zoological Nomenclature, Fourth Edition (Article 8.2) until they are published.

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CHAPTER 2. SYSTEMATICS AND PHYLOGENY OF DOLICHOPODINAE (DIPTERA: DOLICHOPODIDAE)

ABSTRACT. The phylogenetic relationships of the subfamily Dolichopodinae was investigated based on the examination of over 340 species of Dolichopodinae from all zoogeographic regions. Sixty-five exemplar species were included in a cladistic analysis based on 74 morphological characters of adult specimens. Twenty genera are recognized in the Dolichopodinae: *Allohercostomus* Yang, Saigusa and Masunaga, *Anasyntormon* Parent, *Argyrochlamys* Lamb, *Cheiromyia* Dyte, *Dolichopus* Latreille, *Ethiromyia* **gen. nov.**, *Gymnopternus* Loew, *Hercostomus* Loew, *Metaparaclius* Becker, *Muscidideicus* Becker, *Ortochile* Latreille, *Paraclius* Loew, *Parahercostomus* Yang, Saigusa and Masunaga, *Pelastoneurus* Loew, *Platyopsis* Parent, *Poecilobothrus* Mik, *Prohercostomus* Grichanov, *Stenopygium* Becker, *Sybistroma* Meigen, and *Tachytrechus* Stannius. Eleven genera are newly synonymized: *Halaiba* Parent (= *Argyrochlamys* Lamb); *Lichtwardtia* Enderlein (= *Dolichopus* Latreille); *Phalacrosona* Becker (= *Hercostomus* Loew); *Steleopyga* Grootaert and Meuffels (= *Hercostomus* Loew); *Proarchus* Aldrich (= *Pelastoneurus* Loew); *Sarcionus* Aldrich (= *Pelastoneurus* Loew); *Pterostylus* Mik (= *Poecilobothrus* Mik); *Ludovicus* Rondani (= *Sybistroma* Meigen); *Nodicornis* Rondani (= *Sybistroma* Meigen); *Gonioneurum* Becker (= *Tachytrechus* Stannius); *Syntomoneurum* Becker (= *Tachytrechus* Stannius). The following new generic combinations are established: *Argyrochlamys cavicola* (Parent), *Argyrochlamys breviseta* (Parent), *Cheiromyia maculipennis* (Van Duzee), *Dolichopus emelyanovi* (Grichanov), *Dolichopus fractinervis* (Parent), *Dolichopus hollisi* (Grichanov), *Dolichopus minusculus* (Parent), *Dolichopus mironovi* (Grichanov), *Dolichopus nigrotorquatus* (Parent), *Dolichopus sukharevae* (Grichanov), *Dolichopus tikhonovi* (Grichanov), *Ethiromyia chalybea* (Wiedemann), *Ethiromyia purpurata* (Van Duzee), *Ethiromyia violacea* (Van Duzee), *Hercostomus amoenus* (Becker), *Hercostomus argyreus* (Wei and Lui), *Hercostomus briarea* (Wei and Lui), *Hercostomus dactylocera* (Grootaert and Meuffels), *Hercostomus fulgidipes* (Becker), *Hercostomus hubeiensis* (Yang), *Hercostomus imperfectus* (Becker), *Hercostomus postiseta* (Yang and Saigusa), *Hercostomus zygolipes* (Grootaert and Meuffels), *Poecilobothrus aberrans* (Loew), *Poecilobothrus chrysozygos*

(Wiedemann), *Prohercostomus bickeli* (Evenhuis), *Prohercostomus vulgaris* (Meunier), *Prohercostomus interceptus* (Meunier), *Prohercostomus intremulus* (Meunier), *Prohercostomus meunierianus* (Evenhuis), *Prohercostomus notabilis* (Meunier), *Prohercostomus monotonus* (Meunier), *Prohercostomus negotiosus* (Meunier), *Prohercostomus noxialis* (Meunier), *Stenopygium punctipennis* (Say), *Sybistroma acutatus* (Yang), *Sybistroma apicicrassus* (Yang and Saigusa), *Sybistroma apicilarius* (Yang), *Sybistroma biaristatus* (Yang), *Sybistroma biniger* (Yang and Saigusa), *Sybistroma bogoria* (Grichanov), *Sybistroma brevidigitatus* (Yang and Saigusa), *Sybistroma crinicauda* (Zetterstedt), *Sybistroma curvatus* (Yang), *Sybistroma digitiformis* (Yang, Yang and Li), *Sybistroma dorsalis* (Yang), *Sybistroma emeishanus* (Yang), *Sybistroma eucerus* (Loew), *Sybistroma fanjingshanus* (Yang, Grootaert and Song), *Sybistroma flavus* (Yang), *Sybistroma golanicus* (Grichanov), *Sybistroma henanus* (Yang), *Sybistroma impar* (Rondani), *Sybistroma incisus* (Yang), *Sybistroma inornatus* (Loew), *Sybistroma israelensis* (Grichanov), *Sybistroma longiaristatus* (Yang and Saigusa), *Sybistroma longidigitatus* (Yang and Saigusa), *Sybistroma lorifer* (Mik), *Sybistroma luteicornis* (Parent), *Sybistroma miricornis* (Parent), *Sybistroma neixianganus* (Yang), *Sybistroma qinlingensis* (Yang and Saigusa), *Sybistroma sciophillus* (Loew), *Sybistroma sheni* (Yang and Saigusa), *Sybistroma sichuanensis* (Yang), *Sybistroma sinaiensis* (Grichanov), *Sybistroma spectabilis* (Parent), *Sybistroma sphenopterus* (Loew), *Sybistroma transcaucasicus* (Stackelberg), *Sybistroma yunnanensis* (Yang), *Tachytrechus alatus* (Becker), *Tachytrechus analis* (Parent), *Tachytrechus beckeri* (Parent), *Tachytrechus giganteus* (Brooks), *Tachytrechus varus* (Becker). *Pelastoneurus lineatus* de Meijere, 1916, junior secondary homonym of *Pelastoneurus lineatus* Aldrich, 1896, is given the new replacement name *Pelastoneurus neolineatus* **nom. nov.** Four genera are excluded from the subfamily including *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg and *Vetimicrotes* Dyte. A key to the world genera of Dolichopodinae is provided.

INTRODUCTION

Dolichopodidae are one of the most abundant, widespread and diverse families of Diptera. Recent estimates indicate that there are over 6600 described species in 200 genera (Grichanov, 1999b and unpublished data). Dolichopodids are found in all terrestrial habitats from forests to agricultural fields; however, they are particularly diverse and abundant in wet habitats such as humid forests and shores of water bodies. Both larvae and adults of most species are predators on a variety of small insects and other invertebrates. Over the last century the Dolichopodidae has been variously divided into subfamilies both regionally and at a world scale (Aldrich, 1905; Kertész, 1909; Becker, 1917-1918, 1922a; Robinson, 1970a,b; Ulrich, 1981; Negrobov, 1986).

The Dolichopodinae are one of the most diverse subfamilies of Dolichopodidae. Dolichopodines occur worldwide and currently there are about 1700 described species, comprising approximately 25 percent of the species in the entire family. Depending on which of the previously proposed classifications is followed, the number of valid genera included in the subfamily ranges from about 23 to 37. Most of the dolichopodine diversity is divided among the six genera *Dolichopus* Latreille, *Hercostomus* Loew, *Tachytrechus* Stannius, *Paraclius* Loew, *Pelastoneurus* Loew and *Gymnopternus* Loew. These genera together comprise about 90% of described dolichopodine species. Dolichopodines are recognized by the possession of setae on the dorsal surface of the antennal scape, one or more anterior or anterodorsal preapical setae on the mid and hind femora, male abdominal tergite 6 usually bare, and by the typically large, pedunculate male genitalia.

Becker's (1917-1918, 1922a,b, 1923) series of revisions of the world fauna of Dolichopodidae laid the foundation for the modern day concept of the Dolichopodinae. Although there have been a number of subsequent regional treatments of the subfamily (e.g., Stackelberg, 1930, 1933, 1934, 1941, 1971; Parent, 1938; Robinson, 1964), very little has been written about the Dolichopodinae on a world scale since Becker's work. Similarly, generic keys are available for most regions (e.g., Robinson and Vockeroth, 1981; Becker, 1922a; Stackelberg, 1930; Parent, 1929c; Yang et al., 2001), but many are now out of date and a comprehensive key to the world genera is lacking.

Negrobov (1980) provided a brief discussion of generic relationships and limits on a world scale and recommended the transfer of several genera to the Dolichopodinae including *Phalacrosoma* Becker and *Syntomoneurum* Becker from Hydrophorinae, as well as *Anasyntormon* Parent and *Katangaia* Parent from the Rhabhiinae. Shortly thereafter, Ulrich (1981) proposed a revised worldwide classification of the Dolichopodidae, in which he transferred seven genera to the Dolichopodinae including *Anasyntormon*, *Katangaia*, *Phalacrosoma* and *Syntomoneurum* in agreement with Negrobov (1980), as well as *Colobocerus* Parent and *Vetimidrotus* Dyte from the Sympycninae and *Halaiba* Parent from the Rhabhiinae. Negrobov (1986) proposed a tribal classification for the Dolichopodinae and recognized two tribes: Tachytrechini, including *Tachytrechus*, *Paraclius* and *Pelastoneurus*, and Dolichopodini comprising the remaining genera. However, Negrobov did not explicitly define the features characterizing each tribe, particularly the Dolichopodini. His classification was also mainly restricted to the Palaearctic fauna and, as a result, many genera were not assigned to a tribe. Recently, Yang et al. (2001) assigned *Argyrochlamys*, *Lichtwardtia*, *Phalacrosoma* and *Polymedon* to the Tachytrechini, and *Allohercostomus*, *Parahercostomus* and *Pseudohercostomus* to the Dolichopodini in their key to the Oriental genera.

Like most subfamilies of Dolichopodidae, the generic relationships within the Dolichopodinae are unknown and the monophyly of many of these genera is in question. In this study, the phylogenetic relationships of the dolichopodine genera are examined based on a study of over 340 species and an analysis of 59 exemplar species including representatives of nearly all dolichopodine genera *sensu* Ulrich (1981), as well as those newly described in the interim. In addition, each genus of Dolichopodinae is redescribed, and a key to the world genera is provided. The phylogenetic analysis presented here is the first attempt to unravel the relationships of this diverse subfamily and represents a starting point in the study of dolichopodine phylogeny; a hypothesis to be tested and built upon in future studies. This study also represents the first detailed morphological study of the male and female terminalia of the Dolichopodinae across the entire subfamily and the first to use genitalic characters in a phylogenetic context.

MATERIAL AND METHODS

Specimens examined in this study were obtained from the following collections.
(Acronyms used in the text precede each collection)

AMNH	Department of Entomology, American Museum of Natural History, New York, NY, USA.
BMNH	Department of Entomology, The Natural History Museum, London, United Kingdom.
CAS	Department of Entomology, California Academy of Sciences, San Francisco, CA, USA.
CMNZ	Canterbury Museum, Christchurch, New Zealand.
CNC	Canadian National Collection of Insects, Ottawa, ON, Canada.
DEI	Deutsches Entomologisches Institut, Eberswalde, Germany.
HNHM	Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary.
ISNB	Department of Entomology, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
LEM	Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada.

MCZ	Entomology Department, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.
MNHN	Museum National d'Histoire Naturelle, Entomologie, Paris, France.
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
MZLU	Museum of Zoology, Lund University, Lund, Sweden.
NMW	Naturhistorisches Museum Wien, Wien, Austria.
SKU	Saigusa collection of Kyushu University, Biosystematics Laboratory, Kyushu University, Fukuoka, Japan.
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany.
USNM	Dept. of Entomology, United States National Museum of Natural History, Washington, DC, USA.
ZISB	Institute of Zoology, Bulgarian Academy of Sciences, Sofia, Bulgaria.
ZMHB	Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany.
ZMUC	Zoologisk Museum, Copenhagen, Denmark.

Morphological terminology mainly follows McAlpine (1981), with the exception of genitalic terminology, which follows Cumming et al. (1995) and Sinclair (2000). Additional male genitalic terms used herein include: *basal sclerite of sperm pump* and *proctiger brushes*. The former refers to the often well-sclerotized region of the hypandrial bridge (e.g., Figs. 9B,C, 10B,C, 22B, 23B) and is equivalent to Ulrich's (1974)

“Aedegeus-Stützrohr”. The latter term refers to a pair of haired appendages present just below the base of the cerci present in some dolichopodines (e.g. Figs. 22B, 23B,C, 28B, 29B). These structures were first described and figured in *Pelastoneurus vagans* Loew by Snodgrass (1904) which he termed “small flat semi-transparent chitinous appendages” in the description and “median posterior appendages” in the figure caption. In some cases (e.g. *Paraclius arcuatus* (Loew) Fig. 20B), these appendages appear to have become fused medially, forming a single lobe or *proctiger brush*.

In order to study male and female genitalic features, the abdomen was removed and macerated in either KOH or lactic acid. Dark coloured, heavily sclerotized terminalia were macerated in 10% KOH which was heated on a hot plate for about 10 minutes. Lighter coloured, more weakly sclerotized terminalia were macerated in 85% lactic acid heated in a microwave oven. Each microwave heating interval comprised 30 seconds and was followed by a 1-2 minute cooling period during which macerated muscle tissue was removed with a fine probe. In general, KOH gives a better result for female terminalia, which are telescopic and withdrawn into the abdomen. Female specimens prepared with KOH are more pliable, allowing the terminalia to be pulled out easily. In contrast, lactic acid causes the sclerites and membranes to become brittle and prone to tearing during handling.

Figures showing the male genitalia in lateral view are oriented as they appear on the intact specimen (rotated 180° and lateroflexed to the right), with the morphologically ventral surface up, dorsal surface down, anterior end facing right and posterior end facing left. Figures showing the male genitalia in ventral view are correspondingly oriented with the anterior end facing right and posterior end facing left. Abbreviations for morphological terms used in the figures are listed in Appendix 3. Abbreviations used in the text include “T” (= abdominal tergite) and “S” (= abdominal sternite).

In the list of material examined following the generic descriptions all valid species names are followed by one or more of the following acronyms in square brackets, indicating the zoogeographic region(s) of distribution: AF: Afrotropical, sensu Crosskey and White (1977), AU: Australasian and Oceanian, sensu Evenhuis (1989), NE: Nearctic (i.e. North America north of Mexico), sensu Pollet et al. (2004), NT: Neotropical, (i.e. the

Americas south of the United states) sensu Robinson (1970b), **OR**: Oriental, sensu Delfinado and Hardy (1973), **PA**: Palaearctic, sensu Soós and Papp (1991).

One of the biggest obstacles in studying the phylogeny of the Dolichopodinae is its diversity. With about 1700 described species, it would be impractical to examine and include all of them. The only realistic way to deal with this diversity is to sample it using the exemplar method (Yeates, 1995). The analysis included 59 ingroup exemplar species (Appendix 2) from all known dolichopodine genera, sensu Ulrich (1981), with the exception of *Anasyntormon* and *Gonioneurum* Becker which were not available for examination. The analysis also included exemplars of the recently described dolichopodine genera *Allohercostomus* Yang, Saigusa and Masunaga, *Parahercostomus* Yang, Saigusa and Masunaga and *Steleopyga* Grootaert and Meuffels. Exemplar species were treated as terminals in the analysis as advocated by Yeates (1995) and Weins (1998).

The type species of all remaining dolichopodine genera were included in the analysis, except *Metaparaclius* Becker and *Lichtwardtia* Enderlein, in order to ensure proper representation of generic concepts. The type species of *Metaparaclius*, *M. subapicalis* Becker was based on a unique holotype deposited in the HNHM which has since been destroyed. No other specimens of this species are known. The type species of *Lichtwardtia*, *L. ziczac* (Wiedemann) was excluded as only the female holotype was available for study. The analysis also included the type species of most currently recognized subgenera as well as the type species of several genera synonymized by previous authors. The remaining exemplars in the analysis were chosen on the basis of the examination of over 340 species of dolichopodines from all zoogeographical regions. In general, large genera were sampled more extensively (e.g., *Paraclius*, *Pelastoneurus*, *Dolichopus*, *Hercostomus*, *Tachytrechus*, *Gymnopternus*) in an attempt to represent different lineages and provide a test of the monophyly of the genus. At least two species per genus were used for many of the smaller genera, but often sampling in these groups was restricted to the type species in order to keep the number of included exemplars in the analysis down to a manageable number.

One of the biggest gaps in our knowledge of the Dolichopodidae is the phylogenetic relationships of the subfamilies, which consequently makes choosing

outgroups for generic level studies problematic. Bickel (1994) hypothesized a close relationship between the Sciapodinae and Dolichopodinae and used the latter as the outgroup for his analysis of the sciapodine genera. More recently, Ulrich (unpublished) hypothesized a relationship between the Sympycninae (including the Peloroepodinae) and Dolichopodinae based on the possession of well-developed anterior to anterodorsal preapical seta on the hind femur. The peloroepodine genera, in particular, appear to be closely related to the Dolichopodinae based on the shared possession of a bare abdominal tergite 6 in males.

The outgroups for this study consisted of six taxa (Appendix 2) including *Heteropsilopus cingulipes* (Walker) from the Sciapodinae, *Sympycnus annulipes* (Meigen) and *Syntormon pallipes* (Fabricius) from the Sympycninae, *Peloroepodes cornutus* (Van Duzee) and *Nepalomyia nigricornis* (Van Duzee), which have been alternatively placed in the Peloroepodinae (Robinson, 1970a,b) or included in the Sympycninae (Ulrich, 1981), and *Parathalassius* sp. 1 of the “microphorine” grade of genera comprising the basal dolichopodids. *Parathalassius* sp. 1 was used to root the trees.

Seventy-four characters were used in the analysis including 62 binary characters, ten three-state characters and two four-state characters, together comprising 162 character states (Appendix 1). Exemplar-level autapomorphies were not included in the analysis. All characters were equally weighted and treated as unordered, and all multistate characters were treated as non-additive. Taxa exhibiting variable state assignments for certain characters were interpreted as polymorphic. Initial character polarity was based on outgroup comparison (Nixon and Carpenter, 1993), but ultimately depended on rooting the tree by using the outgroup taxon, *Parathalassius* sp. 1.

The character state matrix (Appendix 2) was analysed using PAUP* Version 4.0b10 (Swofford, 2002). A heuristic search using stepwise addition, random addition sequence of taxa and tree-bisection-reconnection (TBR) branch swapping was conducted to find the most parsimonious trees. For the analysis, the parsimony reconstruction option was set to collapse branches if the maximum branch length was equal to zero. The procedure was replicated 1000 times with the maximum number of trees saved per replicate constrained to 500. Once the heuristic search was completed, the trees were

condensed by collapsing branches if the minimum branch length was equal to zero in order to simulate parsimony settings in the program NONA (Goloboff, 1999). Character state distribution was examined using MacClade version 4.03 (Maddison and Maddison, 2001). Bremer supports (= BrS) (Bremer, 1994) were determined for the branches supported in all of the equally parsimonious trees using TreeRot.v2c (Sorenson, 1999). For each node, the number of trees saved per replicate was constrained to 100.

RESULTS AND DISCUSSION

Phylogenetic analysis

The parsimony analysis of the matrix using PAUP* found 4463 equally parsimonious cladograms with a length of 235 steps, consistency index of 0.41 and a retention index of 0.69. The strict consensus cladogram is shown in Fig. 1. Collapsing branches with a minimum branch length of zero retained 126 trees from the original set. Characters are plotted on one of the most parsimonious cladograms in Figs. 2-4.

Monophyly and limits of the Dolichopodinae

The analysis indicates that the current world based classification of Dolichopodinae (i.e. sensu Ulrich, 1981) is paraphyletic, with *Colobocerus*, *Katangaia*, *Pseudohercostomus* Stackelberg and *Vetimicrotes* coming out among the outgroup taxa (Figs. 1, 2). These four genera were transferred into the Dolichopodinae by Ulrich (1981), but they should be excluded from the subfamily (see “GENERA REMOVED FROM THE DOLICHOPODINAE”).

On all of the equally parsimonious cladograms, the monophyly of the Dolichopodinae is supported, albeit weakly (BrS 1, Fig. 1), by the possession of a dorsally haired antennal scape (character 1:1, Fig. 2). *Katangaia longifacies* Parent also possesses this feature, but it appears to have evolved independently as that genus lacks numerous groundplan features of the Dolichopodinae as defined here. A dorsally setose scape is also known to occur outside the Dolichopodinae in the Hydrophorinae (e.g. *Hypocharassus* Mik, *Diostracus* Loew) and some species of *Argyra* Macquart

(Diaphorinae), *Symbolia* Becker (Diaphorinae) and *Stolidosoma* Becker (Stolidosomatinae).

Dolichopodine relationships

The following genera have been synonymized based on the cladistic analysis (Fig. 1): *Halaiba* is synonymized with *Argyrochlamys* Lamb; *Lichtwardtia* is synonymized with *Dolichopus*; *Phalacrosoma* and *Steleopyga* are synonymized with *Hercostomus*; *Proarchus* Aldrich and *Sarcionus* Aldrich are synonymized with *Pelastoneurus*; *Pterostylus* Mik is synonymized with *Poecilobothrus* Mik; *Ludovicus* Rondani and *Nodicornis* Rondani are synonymized with *Sybistroma* Meigen and *Syntomoneurum* Becker is synonymized with *Tachytrechus*. The monotypic genus *Gonioneurum* Becker is also synonymized with *Tachytrechus* based on Becker's (1922a) generic description (see "Remarks" under generic treatment of *Tachytrechus*). One new genus, *Ethiromyia*, is established and described below.

The tribal classification of Negrobov (1986) is not corroborated by the analysis. Although there is a clade that approximates the Tachytrechini (i.e. the *Tachytrechus* genus group; Figs. 1, 2), support for the monophyly of Dolichopodini is lacking. As such, it seems advisable to discontinue use of Negrobov's classification until further studies can resolve the basal relationships within this subfamily. Based on the results of the analysis, four informal genus groups are recognized. Although the monophyly of each genus group is supported in all equally parsimonious trees (Fig. 1), branch support for each is low (BrS 1).

***Allohercostomus* genus group**

This group forms the basal lineage of the Dolichopodinae and includes the single genus *Allohercostomus*, which is known from China and Nepal. The monophyly of *Allohercostomus* is based primarily on the possession of ventrally contiguous eyes, an autapomorphy of the genus. Unlike most dolichopodines *Allohercostomus* possesses a prescutellar depression (character 12:0), a plesiomorphy which appears to be part of the ground plan of the Dolichopodidae, and is present in the Microphorinae, as well as several dolichopodid subfamilies (i.e. Enliniinae, Medeterinae, Neurigoninae,

Peloropectinae, Xanthochlorinae). Although the prescutellar depression is a consistent feature in *Allohercostomus*, it is polymorphic in some species of Dolichopodinae (e.g., *Argyrochlamys* sp. 1) and some species of *Sympycnus*. The remaining dolichopodines are considered a monophyletic group based on the loss of this feature (character 12:1, Fig. 2). This clade is further subdivided into the *Tachytrechus*, *Dolichopus* and *Ortochile* genus groups which are placed in an unresolved trichotomy (Fig. 1).

***Tachytrechus* genus group**

The *Tachytrechus* genus group includes *Argyrochlamys*, *Cheiromyia* Dyte, *Metaparaclius*, *Paraclius*, *Pelastoneurus*, *Platyopsis* Parent, *Stenopygium* Becker and *Tachytrechus*, and is considered to be monophyletic based on the possession of a strong anterior bend in wing vein M (character 34:2, Fig. 2). This character displays homoplasy within *Tachytrechus*, *Cheiromyia* and in the clade including *Platyopsis*, *Stenopygium* and *Pelastoneurus*.

The Old World genus *Argyrochlamys* comprises the basal lineage of this genus group and its limits are expanded here to include the two species formerly placed in *Halaiba*. The monophyly of *Argyrochlamys* is supported by the possession of an undivided, V-shaped T10 of the female terminalia (characters 72:1 and 74: 1, Figs. 6D and 7D). A somewhat similar development has evolved independently in *Ortochile nigrocoerulea* Latreille (Fig. 19E). *Argyrochlamys* sp. 1, from Sri Lanka, forms the sister group to the clade including *A. impudicus* Lamb and *A. cavicola* (Parent). The monophyly of this clade is well-supported (BrS 4, Fig. 1) and is based on the possession of a comma-shaped posterobasal projection on the hind basitarsus of males (character 30:1), a greatly swollen phallus (character 55:1, Figs. 6B, 7B), an apical projection on T8 of the female terminalia (character 71:1, Figs. 6D,E, 7D,E) and the separation of the hypandrial arms from the hypandrium (character 66:1, Figs. 6B, 7B). The first three character states are uniquely derived, whereas the latter has independently arisen in *Pelastoneurus*, *Metaparaclius australiensis* Parent and some species of *Paraclius* and *Hercostomus* (Figs. 16C, 17B, 22B, 23B, 24B). *Argyrochlamys* sp. 1 is part of an undescribed species group that includes species from Sri Lanka and Thailand (P. Grootaert, pers. comm.) characterized by the possession of a strong dorsal seta on the hind basitarsus (character

29:1), a bifurcate projection on the hind tibia of males (in contrast to the comma-shaped projection on the hind basitarsus of male *A. cavicola* and *A. impudicus*), and very reduced male cerci. Grootaert (pers. comm.) has suggested that this species group deserves generic status.

The sister group to *Argyrochlamys* includes *Cheiromyia*, *Metaparaclius*, *Paraclius*, *Pelastoneurus*, *Platyopsis*, *Stenopygium* and *Tachytrechus* (Fig. 1). These genera are considered a monophyletic group on the basis of a laterally flattened ejaculatory apodeme (character 53:3, Fig. 2). Support for this clade is low and assumes separate subsequent reversals in *Stenopygium*, *Platyopsis* and “*Polymedon*” *inopinatus* Parent, and the development of a T-shaped ejaculatory apodeme in *Tachytrechus* (character 53:1). The possession of a laterally flattened ejaculatory apodeme also occurs in some species of *Gymnopternus* and *Hercostomus*, and is considered synapomorphic for the clade including *Ortochile* Latreille, *Poecilobothrus*, *Parahercostomus* and “*Hercostomus*” *straeleni* Vanschuytbroeck (Figs. 3 and 4). One feature of the *Cheiromyia* + *Metaparaclius* + *Paraclius* + *Pelastoneurus* + *Platyopsis* + *Stenopygium* + *Tachytrechus* clade that is immediately apparent is that *Paraclius*, as currently defined, is polyphyletic (Figs. 1, 2). Of the four exemplars included in the analysis, the Oriental species, *Paraclius abbreviatus* Becker, forms a clade with “*Polymedon*” *inopinatus*, which is also Oriental, and *Metaparaclius australiensis* from Australia, whereas the New World exemplars *P. alternans* (Loew), *P. megalocerus* Robinson and the type species *P. arcuatus*, are included in the corresponding sister clade along with *Tachytrechus*, *Cheiromyia*, *Platyopsis*, *Stenopygium* and *Pelastoneurus* (see “Phylogenetic Relationships” under generic treatment of *Paraclius* for further discussion of *Paraclius* species groups and relationships).

The monophyly of the *Metaparaclius australiensis* + *Paraclius abbreviatus* + “*Polymedon*” *inopinatus* clade is weakly supported by the separation of the hypandrial arms from the hypandrium (character 66:1, Fig. 17B), a homoplasious feature which is discussed above (see section on *Argyrochlamys*). In my opinion the monophyly of this clade should be viewed with caution until it can be corroborated in a more extensive analysis of this lineage. *Paraclius abbreviatus* and “*Polymedon*” *inopinatus* are grouped together based on the possession of an enlarged, spherical sperm pump (character 50:1).

A similar sperm pump also occurs in many New World *Paraclius* (see “Phylogenetic Relationships” under generic treatment of *Paraclius*) and some species of *Tachytrechus*. This clade is also supported by the possession of a patch of fine hair on the posterolateral margin of the metepisternum (character 16:1). This feature is present in all of the Oriental *Paraclius* examined in this study and may be synapomorphic for a larger species group of Oriental *Paraclius* which includes “*Polymedon*” *inopinatus* (see “Phylogenetic Relationships” under generic treatment of *Paraclius*). Character 16:1 has also arisen in some species of *Gymnopternus* and *Parahercostomus*, and outside the Dolichopodinae in *Syntormon* Loew (Figs. 2-4).

The clade including *Cheiromyia*, *Stenopygium*, *Pelastoneurus*, *Platyopsis*, *Tachytrechus* and the Nearctic *Paraclius* exemplars (*P. arcuatus*, *P. alternans*, *P. megalocerus*) is supported by the loss of a distinct hypandrial apodeme (character 67:0, e.g., Figs. 20B, 22B, 34B). However, this character is more homoplasious than indicated by the exemplars included in the analysis, especially within *Pelastoneurus* and *Paraclius*. As such, the monophyly of this lineage should be regarded with caution. *Stenopygium*, *Pelastoneurus*, *Platyopsis* and the Nearctic *Paraclius* exemplars appear to be related based on the fusion of T8 and S8 of the female terminalia into a narrow sclerite (character 70:1, Figs. 20E, 22E, 23F, 24E, 25E, 29E). However, this relationship is currently obscured because females of *Cheiromyia* are unknown. This missing data has resulted in alternate equally parsimonious solutions in which *Cheiromyia* is either included in a clade with the above taxa (e.g., Fig. 2), or excluded from it.

The limits of *Tachytrechus* are newly expanded here to include the species formerly placed in the Neotropical genus *Syntomoneurum*. The generic status of *Syntomoneurum* cannot be retained as it renders *Tachytrechus* paraphyletic (Figs. 1, 2). The monophyly of this revised concept of *Tachytrechus* is well-supported (BrS 3, Fig. 1) and is based primarily on the distinctive upturned and laterally flared postgonite (character 61:1, Figs. 33B,D,E, 34B, 35B, 36B). The genus is also supported by four additional homoplasious features (Fig. 2) including an elongate clypeus with rounded lower margin (characters 8:0 and 9:1), which occurs sporadically within the Dolichopodinae (e.g., “*Polymedon*” *inopinatus*, *Dolichopus diadema* Haliday, *Hercostomus amoenus* (Becker)) and outside the subfamily (e.g., *Katangaia longifacies*),

a T-shaped ejaculatory apodeme (character 53:1, as in Fig. 9C), which has also arisen in *Dolichopus* and *Argyrochlamys* sp. 1, and by the medially divided T6 and T7 of the female terminalia (character 69:1), which also occurs in *Pelastoneurus*.

The species previously included in *Syntomoneurum*, here referred to as the *Tachytrechus alatus* species group, form a well-supported clade (BrS 6, Fig. 1) which is revised in Chapter 3. The monophyly of this group is based on the possession of a single notopleural seta (character 14:2), reduced pulvilli on the mid and hind legs (character 17:1), a strong basiventral seta on the fore femur (character 18:1), a ventral cluster of setae on the male fore femur (character 19:1), a cluster of strong setae on the anterior surface of the male mid coxa (character 24:1), a large membranous region on abdominal T5 of males (character 35:1), which has also arisen in “*Polymedon*” *inopinatus*, and an S-shaped curve in wing vein M (character 34:1). The latter character state has also arisen in *T. laevigatus* (Becker) and *Dolichopus*, and is lost in *T. giganteus* (Brooks) within the *T. alatus* species group (see Chapter 3, Figs. 43C,D). The *T. alatus* species group is closely related to the Nearctic species *T. castus* (Wheeler) based on three homoplasious character states including the possession of a ventral tubercle on the male mid femur (characters 25:1), elongate basal projections of the ejaculatory apodeme (character 52:1, Fig. 36B), and a pair of inner medial acanthophorous spines on T10 of the female terminalia (character 73:1, Fig. 36D).

The type species of *Psilischium* Becker, (*Tachytrechus laevigatus*), and *Polymedon* Osten Sacken (*T. flabellifer* (Osten Sacken)) are here included within *Tachytrechus* (Figs. 1, 2) supporting Robinson’s (1970b) synonymy of these genera. *Tachytrechus laevigatus* forms a well-supported monophyletic group with *T. aldrichi* (Van Duzee) based on the possession of a strongly reduced posterior notopleural seta (character 14:1, a feature which also occurs in *T. flabellifer*), a dorsoventrally flattened male fore tibia (character 21:1), an acute epandrial process (character 45:1, Fig. 35A-C), and 1-2 plumose setae on the dorsal surstylus (character 47:1, Fig. 35B). Robinson’s (1970b) synonymy of *Polymedon* with *Tachytrechus* has not been adopted in subsequent works on the Oriental Dolichopodinae, treating the single Old World species “*Polymedon*” *inopinatus* (Dyte, 1975; Yang and Grootaert, 1999; Yang et al., 2001), and the Afrotropical Dolichopodinae (Grichanov, 2004, see “Remarks” under *Katangaia* in

“GENERA REMOVED FROM DOLICHOPODINAE”). My analysis supports Robinson’s synonymy of *Polymedon*; however, the generic placement of “*Polymedon*” *inopinatus* is problematical. As indicated above (and in “Phylogenetic Relationships” under the generic treatment of *Paraclius*), “*Polymedon*” *inopinatus* is part of a species group of Oriental *Paraclius* that includes *P. emeiensis* Yang and Saigusa, *P. pilosellus* Becker and *P. luculentus* Parent. However, transferring “*Polymedon*” *inopinatus* to *Paraclius* would be inappropriate as this Oriental species group does not appear to be congeneric with the lineage of *Paraclius* that includes the type species, *P. arcuatus*. Similarly, transferring “*Polymedon*” *inopinatus* to *Tachytrechus* would also be inappropriate as this would render *Tachytrechus* paraphyletic. Until a more extensive phylogenetically-based study of the world species of *Paraclius* is completed, the placement of “*Polymedon*” *inopinatus* will remain uncertain, although it, along with *Paraclius abbreviatus* and allied species, may be closely related to *Metaparaclius australiensis* (see above). For the present I have listed it under *Paraclius*, but as “*Polymedon*” *inopinatus*, indicating the problematic generic assignment.

The limits of the Neotropical genus *Cheiromyia* are expanded here to include *Cheiromyia maculipennis* (Van Duzee), which is newly transferred from *Sarcionus*. The monophyly of this clade is based on the unique structure of the sperm pump which is enlarged and folded back on itself (character 51:1, Fig. 8C). I have not seen this feature in any of the other dolichopodids examined in this study and consider it to be strong support for the monophyly of this group, despite the fact that this clade is not supported in all equally parsimonious trees. In the alternate topology, *Sarcionus maculipennis* is placed at the base of the *Stenopygium* + *Pelastoneurus* + *Platyopsis* clade based on the loss of a strong bend in wing vein M (character 34:0). However, the degree of curvature of M is a highly homoplastic feature, which in this case appears to be an artifact of taxon sampling rather than an indicator of relationship. Traditionally, *Cheiromyia* has been recognized by the highly modified antenna of males which possess several pubescent projections on the outer surface of the first flagellomere (Parent, 1930a, 1931). However, it appears that this feature has arisen in only some members of this clade as the antenna of *C. maculipennis* is unmodified. This genus seems to be closely related to the New World species group of

Paraclius including *P. venustus* Aldrich and related species (see “Phylogenetic Relationships” under the generic treatment of *Paraclius*).

My analysis suggests that *Platyopsis* is closely related to *Pelastoneurus* and *Stenopygium* based on the possession of an enlarged bulging clypeus (character 10:1) and a weak anterior bend in wing vein M (character 34:0), assuming subsequent reversals in both characters within *Pelastoneurus* (Fig. 2), in contrast to previous classifications (Parent, 1929b; Stackelberg, 1933; Negrobov, 1986, 1991; Grichanov, 1997) which treat *Platyopsis* as a subgenus of *Hercostomus*. Although branch support for this clade is low (BrS 1, Fig. 1) it is evident that *Platyopsis* is not congeneric with *Hercostomus* in the sense of the type species, *H. longiventris* (Loew), and is here assigned generic rank, in agreement with the classifications of Parent (1929c) and Ulrich (1981).

The limits of the previously monotypic Neotropical genus *Stenopygium* are expanded here to include *Stenopygium punctipennis* (Say), which is newly transferred from *Pelastoneurus*. The type species, *Stenopygium nubeculum* Becker, and *S. punctipennis* possess nearly identical male genitalia (Figs. 28A-C, 29A-C) and form a monophyletic group on the basis of a distinctively wrinkled phallus which is elbowed basally (characters 56:1 and 57:1, Figs. 28B, 29B). A wrinkled phallus has also arisen in *Argyrochlamys* sp. 1, and some species of *Sybistroma* possess an elbowed phallus. I agree with the placement of *Stenopygium* as the sister group to *Pelastoneurus* as hypothesized in some of the equally parsimonious trees (Fig. 2). This relationship is supported by the possession of a pair of well-developed proctiger brushes (character 54:1, Figs. 22B, 23B,C 28B, 29B), which also occur in some New World *Paraclius*, and by a well-sclerotized anteroventral portion of the postgonite (character 62:2, Figs. 22B, 23B, 24B, 28B, 29B), a feature that has also arisen in *Argyrochlamys impudicus* (Fig. 6B), *Metaparaclius australiensis* (Fig. 17B) and *Katangaia longifacies* (Fig. 37E). However, until a consensus is reached regarding the relationship between *Stenopygium*, *Pelastoneurus* and *Platyopsis*, this hypothesis must be considered provisional.

Pelastoneurus is expanded here to include the monotypic Neotropical genus *Proarchus*, as well as most of the species of the Neotropical genus *Sarcionus*. The results of the analysis support Robinson’s (1975) hypothesis of a close relationship between these three New World genera. As noted by Robinson (1975), *Proarchus* has generally

been distinguished from *Pelastoneurus* on the basis of its straight wing vein M. I regard this feature as a species-level variation and do not consider it sufficient to warrant continued generic status for *Proarchus*. Several of the species newly transferred from *Sarcionus*, including *Pelastoneurus acutispina* (Van Duzee), *P. currani* (Van Duzee), *P. pectinicauda* (Van Duzee), *P. rotundicornis* (Van Duzee) and the type species *P. lineatus*, are part of a species group of *Pelastoneurus* that also includes *P. umbripictus* Becker and *P. turbidus* Becker. These species have very similar male genitalia and appear to form a monophyletic group based on the possession of thick blunt setae on the margin of the cercus (Fig. 23A). *Pelastoneurus* and *Sarcionus* have traditionally been distinguished by the narrow, long face and relatively short, weakly bulging clypeus of the latter; however, this feature seems to have arisen secondarily within *Pelastoneurus*. Unlike the species of *Sarcionus* discussed above, *Sarcionus flavicoxa* Aldrich, *Sarcionus intermedius* Van Duzee and *Sarcionus maculatus* Van Duzee do not appear to be congeneric with the type species of *Pelastoneurus*. Instead the male genitalia of these species seem closer to the New World species group of *Paraclius* which includes *P. venustus* and related species. However, until more extensive phylogenetic studies are available, the placement of these species will remain uncertain. For the present I have listed them listed under *Pelastoneurus*, but as “*Sarcionus*” *flavicoxa* Aldrich, “*Sarcionus*” *intermedius* Van Duzee and “*Sarcionus*” *maculatus* Van Duzee, to indicate their problematic generic assignment. Further phylogenetic studies are also required to ascertain the limits of *Pelastoneurus* on a global scale as many species outside the New World seem to be misplaced (see “Phylogenetic Relationships” under generic treatment of *Pelastoneurus*). *Pelastoneurus*, as newly defined here, is considered to be monophyletic based on the separation of the hypandrial arms from the hypandrium (character 66:1, Figs. 22B, 24B, 25B, see section on *Argyrochlamys* above for discussion of this character), the medially divided T6 and T7 of the female terminalia (character 69:1, which has also arisen in *Tachytrechus*), and the possession of a plumose arista with the dorsal and ventral hairs longer than the lateral hairs (character 4:1, see Robinson and Vockeroth, 1981: fig. 10). Although the plumose arista is a distinctive feature of *Pelastoneurus*, it is not restricted to this genus and has also arisen in some species of *Dolichopus* (i.e. those formerly in *Lichtwardtia*, see

below), *Poecilobothrus aberrans* (Loew) (formerly in *Pterostylus*, see below), *Cheiromyia pennaticornis* Parent, and in some females of *Stenopygium punctipennis*.

***Dolichopus* genus group**

The *Dolichopus* genus group includes *Dolichopus*, *Gymnopternus* and the newly established genus *Ethiromyia* (Figs 1 and 3). The monophyly of this clade is based on the possession of a cluster of fine hairs on the pleural surface of the thorax in front of the posterior spiracle (character 15:1). This feature has also independently arisen in some species of *Tachytrechus* and Afrotropical *Pelastoneurus*, and outside the Dolichopodinae in *Syntormon* Loew (Sympycninae) and *Hydatostega* Philippi (Hydrophorinae).

Gymnopternus is the basal taxon of this genus group and is considered monophyletic based on the possession of elongate projections on the base of the ejaculatory apodeme (character 52:1, Fig. 13B) and its distinctive postgonite (character 58:1, Fig. 13C), confirming the hypothesis of Pollet (1990). Some species of *Tachytrechus* also possess well-developed basal projections on the ejaculatory apodeme (see discussion in “*Tachytrechus* genus group”, Fig. 36B), and a similar postgonite has also arisen in *Peloropeodes* Wheeler. The placement of *Gymnopternus* in this clade conflicts with the traditional view that this genus is closely related to *Hercostomus*. In the Palaearctic literature, *Gymnopternus* is treated as either a synonym (Becker, 1917-1918; Negrobov, 1991) or subgenus (Pollet, 1990; Chandler, 1998; Wei, 1997; Yang and Grootaert, 1999; Yang and Saigusa, 1999) of *Hercostomus*; however, that classification is not based on a single synapomorphy or convincing character-based argument. With the exception of Poole (1996), *Gymnopternus* is given generic status in the Nearctic literature (e.g., Robinson, 1964; Robinson and Vockeroth, 1981; Foote et al., 1965; Pollet et al., 2004). My analysis supports the latter classification and not only hypothesizes a sister group relationship between *Gymnopternus* and the *Dolichopus* + *Ethiromyia* lineage, but also demonstrates that *Hercostomus*, as currently recognized, is a polyphyletic assemblage (Fig. 1).

Dolichopus and *Ethiromyia* form a monophyletic group based on the distinctive structure of the dorsal surstylar lobe (character 48:1, Figs. 9B, 10B, 11B), a feature that has also arisen in *Metaparaclius australiensis* Parent (Fig. 17B), and by the possession of

a pair of inner, medial acanthophorous spines on T10 of the female terminalia (character 73:1, Figs. 9E, 10E, 11E). The latter feature has also arisen in *Ortochile*, *Parahercostomus* and *Poecilobothrus* (Figs. 4, 19E, 21D, 26D). *Platyopsis maroccanus* (Parent) (Fig. 25D) and some species of *Tachytrechus* (Figs. 34D, 36D) also possess a pair of inner, medial acanthophorous spines; however, the spines are not as distinctively offset from the marginal row as they are in the other taxa.

Ethiomyia is newly established for the enigmatic species group which includes the Nearctic species *Gymnopternus purpuratus* (Van Duzee) and *G. violaceus* (Van Duzee), and the Palaearctic species *Hercostomus chalybeus* (Wiedemann) (Fig. 1). This clade is based on two synapomorphies (Fig. 2) including the possession of a long apicoventral seta on the fore tibia of males (character 20:1), and the distinctive male cerci (character 68:1, Figs. 11A, 12A,B). Despite the fact that both of these features are homoplasious and have arisen in some species of *Dolichopus* and other, more distantly related dolichopodine genera, they are part of a suite of congruent nested synapomorphies that support the monophyly of this group. Historically, the position of these species has been contentious; however, recent regional classifications (Chandler, 1998; Pollet et al. 2004) have placed them in *Gymnopternus*. Although the monophyly of *Ethiomyia* is weakly supported (BrS 1, Fig. 1), the cladistic analysis indicates that keeping these species in *Gymnopternus* is not a phylogenetically valid option as it would render that genus paraphyletic. Transferring these species into *Dolichopus* is also undesirable as it would only dilute the distinctive concept of this genus. As such, assigning these species to a separate genus is the only viable option.

The limits of *Dolichopus* are expanded here to include the species formerly placed in *Lichtwardtia*. The monophyly of this genus is based on three homoplasious character states (Fig. 3), including the possession of an S-shaped bend in wing vein M (character 34:1), a T-shaped ejaculatory apodeme (character 53:1, Figs. 9C, 10C), and the presence of one or more strong dorsal setae on the hind basitarsus (character 29:1). The latter feature has also arisen in *Argyrochlamys* sp. 1, *Parahercostomus*, *Poecilobothrus regalis* (Meigen) and some species of Afrotropical *Hercostomus* included in Grichanov's (1999a) species group 1 (e.g., *H. congoensis* (Curran)). The distribution of character states 34:1 and 53:1 is discussed above in the "*Tachytrechus* genus group" section. Although

Lichtwardtia is a distinctive, monophyletic group based on the possession of a plumose arista (character 4:1), and an anteroproximal stub vein on wing vein M (character 32:1), recognition of this genus renders *Dolichopus* paraphyletic since no synapomorphies have been found to support the monophyly of *Dolichopus* exclusive of *Lichtwardtia* based on an examination of nearly 90 species of *Dolichopus*.

***Ortochile* genus group**

The *Ortochile* genus group includes *Hercostomus*, *Muscidideicus* Becker, *Ortochile*, *Parahercostomus*, *Poecilobothrus* and *Sybistroma* Meigen. The analysis confirmed that *Hercostomus* is polyphyletic (Fig. 1). This is not surprising as *Hercostomus* has long been a dumping ground for species that do not fit into the other dolichopodine genera. The *Ortochile* genus group is considered to be monophyletic based on the possession of a distinct posterior preapical seta on the mid femur (character 27: 1, Fig. 4), in addition to the terminal posteroventral seta, which is also sometimes developed. This feature is subsequently lost in *Parahercostomus* and *Sybistroma*, and is polymorphic in *Sybistroma impar* (Rondani) and *Ortochile nigrocoerulea*. The presence of a posterior preapical seta on the mid femur has also arisen in some Afrotropical species of *Paraclius* (e.g. *P. microproctus* Parent) and *Pelastoneurus* (e.g. *P. congoensis* Parent, *P. pedunculatus* Parent), some species of *Gymnopternus* and in some Sympycninae (e.g., *Syntormon pallipes* and *Colobocerus alchymicus* Parent). A similar development occurs in *Platyopsis*; however, this genus possesses two strong posteroventral setae (character 27: 2) on the mid femur.

The monotypic Palaearctic genus *Muscidideicus* is the basal taxon of this genus group and forms the sister to the remaining genera, which are considered to be monophyletic based on the fusion of the epandrium and hypandrium near the base of the basiventral epandrial lobe (character 65:1, Figs. 14A,C, 26A,C, 30C). Although branch support for this clade is low (BrS 1, Fig. 1), this feature is uniquely derived in this group (Fig. 4). This clade is further divided into two subgroups, the first of which comprises the genus *Sybistroma* and a lineage which includes the type species of *Hercostomus* (i.e. *H. longiventris*). The second subgroup includes the Old World genera *Ortochile*,

Parahercostomus and *Poecilobothrus*, as well as the Afrotropical species “*Hercostomus*” *straeleni*.

The monophyly of the subgroup that includes the *Hercostomus longiventris* lineage and *Sybistroma* is primarily supported by the position of the basiventral epandrial lobes, which are shifted ventrally and flank the hypandrium, forming a composite tripartite structure (character 63:1, Figs. 14C, 15B,C,D, 30A,C, 31A,C, 32A,C). This feature is uniquely derived in the Dolichopodinae (Fig. 4) and, in my opinion, provides reasonable evidence for the monophyly of this clade despite low branch support (BrS 1, Fig. 1). This result supports Grichanov’s (2000b) hypothesis of a close relationship between *Hercostomus* s. str. and *Sybistroma* (i.e. including *Ludovicus* and *Nodicornis*, see below). The above interpretation of homology differs from that used in recent papers dealing with species in this clade, which interpret the ventrally shifted basiventral epandrial lobes as part of the hypandrium (e.g., Grichanov, 1999a; Grootaert and Meuffels, 2001; Yang, 1996b, 1998a, 1999a; Yang and Saigusa, 1999, 2001a). This subgroup is also supported by the possession of a thick, knob-like apical process on the basiventral epandrial lobe (character 41:1, Figs. 14A-C, 15A,C,D, 31A-C, 32A-C), which appears to be a modified basiventral epandrial seta. Evidence for this interpretation is seen in *Sybistroma obscurellum* (Fallén) which lacks the knob-like process, but instead possesses a weak seta in its place (Fig. 30A-C). The *Hercostomus longiventris* lineage includes some species that lack both a seta and a knob-like process and others in which the process is present but weakly differentiated, appearing partially fused with the basiventral epandrial lobe. These occurrences suggest that the knob-like process has been secondarily lost in some species as a result of fusion with the basiventral epandrial lobe.

Hercostomus longiventris is part of a lineage which also includes the widespread species *Hercostomus chetifer* (Walker), and the type species of the Oriental genera *Phalacrosoma* and *Steleopyga*. This clade is supported by the arrangement of the hypandrium and basiventral epandrial lobes which form an asymmetrical complex (character 64:1, Figs. 14C, 15C,D). Although this feature is uniquely derived in the analysis (Fig. 4), a similar modification has also arisen in some species of *Sybistroma*. This lineage appears to be particularly diverse in China (e.g. Wei, 1997; Yang, 1997a, 1999a; Yang and Grootaert, 1999; Yang and Saigusa, 1999, 2000a,b, 2001c, see

“Remarks” under generic treatment of *Hercostomus*), and also includes Grichanov’s (1999a) Afrotropical *Hercostomus* species group 2, as well as species from the western Palearctic (e.g., *H. fulvicaudis* (Haliday)), Nearctic (e.g., *H. tibialis* (Van Duzee)) and Oriental (e.g. *H. flavicans* Grootaert and Meuffels) regions. Based on the material examined in this study and a survey of descriptions in the literature, I have not found any evidence supporting the monophyly of this lineage exclusive of *Phalacrosona* and *Steleopyga* and consider these genera to be synonymous with *Hercostomus*.

The limits of *Sybistroma* are expanded here to include the species of *Nodicornis* and *Ludovicius*. The latter genera have traditionally been distinguished from *Sybistroma* on the basis of their modified male antennae; however, this generic division is not corroborated by the analysis (Fig. 1). Although the traditional *Sybistroma* is weakly supported in one third of the equally parsimonious trees, based on the possession of slender and elongate surstyli (character 46:1, Fig. 30B), this feature also occurs in some species of the traditional *Ludovicius* (Fig. 31B), and in my opinion, does not constitute a sufficient basis to maintain the old generic limits. The monophyly of *Sybistroma*, in this new sense, is primarily supported by the possession of elongate, symmetrical and digitiform basiventral epandrial lobes (character 40:1, Figs. 30A-C, 31A-C, 32A-C), elongate and setose apicoventral epandrial lobes (character 42:1, Figs. 30A,C, 31A,C), and by the secondary loss of the posterior preapical seta on the mid femur (character 27:0), which is present in most of the other species of the *Ortochile* genus group (see above). Although these features together support the monophyly of *Sybistroma*, each has undergone subsequent reversal within this genus (Fig. 4). Character state 40:1, while unique to the included exemplar taxa, has also been lost in some species of *Sybistroma* (e.g., *Sybistroma miricornis* (Parent)) and has arisen in some species currently placed in *Hercostomus* by Yang and Saigusa (2000a) (e.g., the *Hercostomus longus* group). The analysis also indicates that the limits of *Ludovicius* and *Nodicornis* are flawed. *Ludovicius* has traditionally been distinguished from most other dolichopodines, including *Nodicornis*, on the basis of a thickened antennal scape and a reduced pedicel in males (Parent, 1938; Yang and Saigusa, 2001a). However all of the species of *Nodicornis* examined in this study, including the type species, possess a similar modification of the antennae, which is not clearly different from that of *Ludovicius*. Overlap between these

genera is also seen in the structure of the male genitalia (e.g. *Ludovicicus spectabilis* Parent and *Nodicornis nodicornis* (Meigen)).

The analysis supports the monophyly of both *Sybistroma* and the *Hercostomus longiventris* lineage. However, as noted above, there are some species of *Sybistroma* that possess an asymmetrical arrangement of the basiventral epandrial lobes and hypandrium typical of the *Hercostomus longiventris* lineage (e.g. *Sybistroma miricornis*, *S. brevidigitatus* (Yang and Saigusa), *S. yunnanensis* (Yang)). Likewise, there are some species currently placed in *Hercostomus* which possess digitiform, symmetrical basiventral epandrial lobes, typical of *Sybistroma* (e.g. *H. longus* group, *H. curvativus* Yang and Saigusa). At the present time the position of such apparently intermediate species cannot be ascertained and a phylogenetic analysis of this clade incorporating additional exemplar species such as those mentioned above is required to test the hypothesis of relationships presented here. I suspect that future analyses may reveal that the *Hercostomus longiventris* lineage is paraphyletic with respect to *Sybistroma*, which may necessitate the synonymy of these genera under the older name *Sybistroma*.

The monophyly of the *Ortochile* + *Parahecostomus* + *Poecilobothrus* + “*Hercostomus*” *straeleni* subgroup is based on the possession of a laterally flattened ejaculatory apodeme (character 53:3) and a pair of inner medial acanthophorous spines on T10 of the female terminalia (character 73:1, Figs. 19E, 21E, 26D), assuming a subsequent reversal in “*Hercostomus*” *straeleni* (Fig. 3). Branch support for this clade is low (BrS 1) and both character states are homoplasious (see discussion in “*Tachytrechus* genus group” and “*Dolichopus* genus group”). *Ortochile* forms the basal taxon of this clade and is considered monophyletic on the basis of a greatly elongated proboscis (character 7:1) and the rounded lower margin of the clypeus (character 8:0), of which the latter is extensively homoplasious within the Dolichopodinae (see discussion of *Tachytrechus* above). In previous classifications, *Ortochile* has been treated either as a genus (Stackelberg, 1941; Negrobov, 1986, 1991), or as a subgenus of *Hercostomus* (Becker, 1917-1918; Dyte, 1976; Assis Fonseca, 1978). The results of the analysis support the assignment of full generic status to *Ortochile*. The remaining taxa of this subgroup form a clade based on the possession of well-developed preapical lateroventral lobes on the posterodorsal portion of the postgonite (character 59:1, Figs. 21B, 26B,

27B), a feature first noted by Lundbeck (1912) in his description of *P. nobilitatus* (Linnaeus). A somewhat similar development of the postgonite has independently arisen in *Sybistroma nodicornis* (Fig. 32B).

The limits of *Poecilobothrus* are expanded here to include *Poecilobothrus aberrans*, formerly in the monotypic genus *Pterostylus* Mik, as well as *P. chrysozygos* (Wiedemann) and the related *P. bigoti* Mik, which are transferred from *Hercostomus*. This group is considered to be monophyletic based on the possession of a distinct dark spot on the notum directly above the notopleuron (character 13:1). This feature has arisen independently in *Dolichopus unguatus* (L.), *Metaparaclius austaliensis* and *Pelastoneurus tripartitus* (Figs. 2 and 3). Like *Ortochile*, *Poecilobothrus* has also been assigned either full generic status (Mik, 1878, Becker, 1917-1918; Stackelberg, 1941; Parent, 1938; Dyte, 1969, 1976; Assis Fonseca, 1978; Ulrich, 1981; Chandler, 1998), or subgeneric status within *Hercostomus* (Negrobov, 1991; Evenhuis, 1994). The results of the analysis support full generic status for *Poecilobothrus*.

The sister lineage to *Poecilobothrus* includes the type species of the Oriental genus *Parahecostomus*, *P. zhongdianus* (Yang) and “*Hercostomus*” *straeleni*, one of the species included in Grichanov’s (1999a) Afrotropical *Hercostomus* species group 1. The monophyly of this group is weakly supported (BrS 1) based on the possession of velvety pilosity on the ventral surface of the male fore tarsus (character 22:1). This feature is quite homoplasious within the Dolichopodinae, and in my opinion, this relationship should be regarded with caution until it can be corroborated by additional synapomorphies. The monophyly of *Parahecostomus* is supported by the loss of the sutural, presutural and acrostichal setae, the reduced vertical setae, the thickened wing veins R_{2+3} and R_{4+5} in males, and by the possession of 1-3 dorsal setae on the hind basitarsus (character 29:1). The latter feature also occurs in two species of Afrotropical *Hercostomus* species group 1 (*H. congoensis*, *H. ultimus* Parent). The monophyly of Grichanov’s (1999a) Afrotropical *Hercostomus* species group 1 appears to be based on the possession of long apicoventral seta on the fore tibia (character 20:1) and a modified hind tarsus in males (Grichanov, 1999a). All of the species of this group examined in this study also possess an enlarged abdominal spiracle 7 in males, which may prove to be an additional synapomorphy. This species group may represent a new genus; however, such

a taxonomic decision should wait until the monophyly and relationships of this group can be assessed in a more extensive phylogenetic analysis of the lineage. Several additional species currently placed in *Hercostomus* appear to be referable to the clade that includes *Poecilobothrus*, *Parahercostomus* and Grichanov's (1999a) Afrotropical *Hercostomus* group 1 (see "Remarks" under generic treatment of *Hercostomus*).

SUBFAMILY DOLICHOPODINAE LATREILLE, 1809

Type genus: *Dolichopus* Latreille, 1796

The Dolichopodinae includes the following genera: *Allohercostomus* Yang, Saigusa and Masunaga, *Anasyntormon* Parent, *Argyrochlamys* Lamb, *Cheiromyia* Dyte, *Dolichopus* Latreille, *Ethiomyia* **gen. nov.**, *Gymnopternus* Loew, *Hercostomus* Loew, *Metaparaclius* Becker, *Muscidideicus* Becker, *Ortochile* Latreille, *Paraclius* Loew, *Parahercostomus* Yang, Saigusa and Masunaga, *Pelastoneurus* Loew, *Platyopsis* Parent, *Poecilobothrus* Mik, *Prohercostomus* Grichanov, *Stenopygium* Becker, *Sybistroma* Meigen, and *Tachytrechus* Stannius. Four genera have been removed from the Dolichopodinae as defined here: *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg and *Vetimicrotes* Dyte (see "GENERA REMOVED FROM THE DOLICHOPODINAE").

Recognition. This subfamily is distinguished from other dolichopodid subfamilies based on the following combination of characters: scape setose dorsally; mid and hind femur with 1 or more anterior preapical setae; male abdominal T6 bare, rarely with setae on lateral margin; male segment 7 bare, forming a peduncle; hypopygium folded under abdomen.

Description. Head: Occiput convex; 1 pair of divergent ocellar setae, usually strong; 1 pair of vertical setae; antennae inserted above middle of head; scape dorsally setose, usually with acute medioventral process; pedicel with fine setae on apical margin; pedicel condyle present, well-developed, inserting into base of first flagellomere, occasionally

weakly developed in some males with modified antennae; eyes with ommatrichia, often slightly longer below; postocular setae uniseriate; 1 pair of postvertical setae.

Thorax: Acrostichals usually biserial, sometimes uniserial or absent; 5-7 dorsocentrals; postpronotum with 1 strong mediocline seta and 1 or more weaker outer setae or hairs; 1 outer posthumeral, and usually 1 weaker inner posthumeral; 1-2 notopleurals; presutural seta and sutural seta usually present, occasionally absent; 2 supraalar; 1 postalar; lower part of propleuron with 1 prothoracic seta. Scutellum with 1 strong inner seta and usually 1 small outer seta on lateral margin.

Legs: Mid femur with 1-5 anterior or anterodorsal preapical setae, rarely absent in male; hind coxa with 1 strong lateral seta; hind femur with 1-10 anterior preapical setae.

Wing: Costa continuous to M; M straight or with weak to strong anterior or S-shaped bend, ending near or before wing apex, usually unbranched, occasionally with stub vein.

Abdomen: T1-5 setose. Male: T6 usually bare, rarely with setae on lateral margin; pregenitalic sternites partially to entirely membranous, often forming a concavity for hypopygium; segment 7 bare, tergite and sternite forming ring-like or tubular peduncle; hypopygium usually large, folded under abdomen. Female: Segments 6-10 telescopic, T10 with acanthoporous spines.

KEY TO WORLD GENERA OF DOLICHOPODINAE

This key includes all genera of Dolichopodinae except the fossil genus *Prohercostomus* from Baltic amber. As a result of continuing problems regarding the limits and monophyly of some genera on a world scale and widespread homoplasy within the subfamily, some species may be assigned to incorrect genera according to this key. Superscript numbers refer to supplementary notes that follow the key.

1. Scape setose above; mid and hind femora usually with one or more distinct preapical setae on anterior or anterodorsal surface, preapical on mid femur occasionally reduced in male (e.g., *Hercostomus amoenus*), hind femur occasionally with 4 smaller anteroventral

- preapical setae (e.g., *Hercostomus dactylocera*); vein M reaching wing margin near or before apex; male abdominal tergite 6 usually bare, rarely with setae on lateral margin; male abdominal segment 7 bare, tubular, hypopygium pedunculate, usually large and projecting forward under abdomen2
- Not with the above combination of characters **non-Dolichopodinae**
2. Hind basitarsus with one or more distinct dorsal setae3
- Hind basitarsus without dorsal setae7
3. Pleura with cluster of fine hairs in front of posterior spiracle; vein M beyond crossvein dm-cu with obtuse to angular S-shaped bend, sometimes with anteroproximal and/or posterodistal stub veins arising on corners bend in M, R₄₊₅ and M subparallel beyond bend in M; arista velvety, shortly pubescent or plumose **Dolichopus** Latreille
- Pleura in front of posterior spiracle bare; venation variable4
4. Thorax with distinct dark blackish-purple metallic spot above notopleuron; mid femur with strong posterior preapical setae about even with anterodorsal preapical; arista strongly pubescent or plumose (western Palaearctic) **Poecilobothrus** Mik (in part)
- Thorax without distinct dark purple-black spot above notopleuron; mid femur with or without distinct posterior preapical setae; arista weakly pubescent or bare5
5. Sutural, presutural and acrostichal setae absent; vertical setae weaker than postverticals, male with veins R₂₊₃ and R₄₊₅ thickened in basal part (Oriental China)
..... **Parahercostomus** Yang, Saigusa and Masunaga
- Sutural, presutural and acrostichal setae present; vertical setae stronger than postverticals, R₂₊₃ and R₄₊₅ not thickened in basal part6
6. Body non-metallic, head and thorax grey, abdomen yellowish-brown or grey; vein M beyond crossvein dm-cu with strong anterior bend, strongly convergent with R₄₊₅; hind basitarsus with 1 dorsal seta; hind tibia of males with distinct bifurcate posteroapical projection; male cercus extremely reduced, stub-like; female terminalia with T10

- undivided and distinctly V-shaped (Fig. 7D) (Sri Lanka and Thailand)
 *Argyrochlamys* Lamb (in part)
- Body metallic, vein M straight or with weak, sinuous anterior bend beyond crossvein dm-cu; hind basitarsus with 1-2 dorsal setae; males lacking bifurcate posteroapical projection on hind tibia; male cercus variable, not extremely reduced and stub-like; female terminalia as in Fig. 21D with T10 divided medially, not V-shaped
 *Hercostomus* Loew (in part)
7. Pleura with cluster of fine hairs in front of posterior spiracle8
- Pleura bare in front of posterior spiracle 12
8. Vein M straight and subparallel with R_{4+5} beyond crossvein dm-cu9
- Vein M with distinct anterior bend and convergent with R_{4+5} beyond crossvein dm-cu ...
11
9. Hind femur with anterior preapical seta positioned far from apex, i.e. slightly beyond middle or at distal third; 5 dorsocentrals; arista evenly plumose, hairs long; wing brown, usually with pale transverse stripe just beyond crossvein dm-cu; postgonite narrow (Afrotropical) *Pelastoneurus* Loew (in part)
- Not with above combination of characters; hind femur with anterior preapical seta closer to apex; usually 6 dorsocentrals, if 5, then postgonite broad and complex with several lobes (Fig. 13C); arista with variable pubescence, occasionally subplumose10
10. Fore tibia lacking anterodorsal comb-like row of strong spine-like setae, fore tibia of male with elongate apicoventral seta. Clypeus usually strongly bulging and proboscis greatly enlarged and strongly projecting (especially in females), and/or with dark spots at insertion points of setae on mid and hind tibiae. Cercus of male large, rounded, pale with dark margin, margin with very long, fine setae (Figs. 11A 12A,B); dorsal sustylus notched preapically on dorsal surface with keel-like projection across notch (Fig. 11B); posterodorsal part of postgonite absent or simple and digitiform. Female terminalia with

inner medial pair of acanthoporous spines on T10 (Fig. 11D) (Holarctic).....

.....*Ethiomyia* gen. nov.

- Fore tibia usually with anterodorsal comb-like row of strong spine-like setae, fore tibia of male lacking elongate apicoventral seta. Clypeus usually flat to weakly produced, sometimes strongly produced in female, proboscis not enlarged and strongly projecting; hind tibiae lacking dark spots at insertion points of setae. Cercus of male variable, not as above; dorsal sustylus not notched preapically on dorsal surface; posterodorsal part of postgonite complex, broad, with a pair of dorsolateral lobes, often with secondary dorsal and lateral membranous lobes, and usually with a medioventral lobe (Fig. 13C). Female terminalia lacking inner medial pair of acanthoporous spines on T10 (Fig. 11D)

.....*Gymnopternus* Loew

11. Arista bare, clypeus usually rounded below; male with apex of postgonite dorsally upturned and flared laterally (Fig. 33D,E)..... *Tachytrechus* Stannius (in part)

- Arista strongly pubescent or plumose; clypeus with lower margin usually straight, male postgonite not as above..... *Pelastoneurus* Loew (in part, some Afrotropical species)

12. Seven dorsocentrals; abdomen dorsoventrally flattened; veins R_{4+5} and M subparallel and sinuous beyond crossvein dm-cu, male wing with pronounced convex curve in R_{4+5} and M and darkened apex; clothing setae on mid and hind femora well-developed, nearly as strong as preapical setae; upper and lower propleuron with long dense hair, prothoracic seta pale or brown; posterodorsal part of postgonite not developed (Fig. 18B); male and female genitalia as in Fig. 18 (western Palaearctic)..... *Muscidideicus* Becker

- Five or six dorsocentrals, abdomen not distinctly dorsoventrally flattened; veins R_{4+5} and M subparallel or convergent beyond crossvein dm-cu, M straight or with anterior bend; clothing setae on femora usually weak, if strong then vein M with strong anterior bend and convergent with R_{4+5} ; prothoracic seta usually black, male and female genitalia not as above.....**13**

13. Hind femur of male with preapical anteroventral row of four setae; segment 7 elongate and slender; base of sternite 8 with a cluster of thick spines (Fig. 16D); fore

tarsus of male with apical segments flattened laterally; species with brownish-yellow to partly blackish colour (Southeast Asia); male genitalia as in Fig 16.....

.....***Hercostomus longiventris* group** (in part, *H. dactylocera* and *H. zygolipes*)

- Males without the above combination of characters, or females14

14. Eyes contiguous at oral margin; vertical setae shorter than postverticals; scutum with triangular depression in front of scutellum; acrostichals uniserial and strong; vein M straight and parallel or nearly parallel with R_{4+5} beyond crossvein dm-cu (China and Nepal)..... ***Allohercostomus*** Yang, Saigusa and Masunaga

- Eyes separate at oral margin; vertical setae usually distinctly stronger than postverticals; scutum usually evenly convex in front of scutellum; acrostichals biserial or absent, rarely uniserial15

15. Proboscis and palps greatly elongated and slender, proboscis longer than head is high; vein M beyond crossvein dm-cu with weak anterior bend before middle, convergent with R_{4+5} and ending well above wing apex, close to apex of R_{4+5} ; basal segment of foretarsus usually with 3-4 distinct ventral setae (western Palaearctic) ***Ortochile*** Latreille

- Proboscis thick and short, not exceeding height of head; palps usually short, if long then relatively broad; M straight or with anterior bend, R_{4+5} and M subparallel or convergent ...
.....16

16. Males with several slender, digitiform, pubescent projections on outer surface of first flagellomere (Neotropical)..... ***Cheatomyia*** Dyte (in part)

- Males without projections on outer surface of first flagellomere, or females17

17. Body non-metallic; head grey, with whitish pollen, wider than high with frons and face broad in both sexes; thorax pale-grey to dark grey or blackish with whitish-grey pollen; 6 dorsocentrals, fifth pair usually strongly offset medially; vein M beyond crossvein dm-cu usually with strong anterior bend and strongly convergent with R_{4+5} ; abdomen yellowish brown; hind basitarsus of male with elongate comma-shaped posterobasal projection; male genitalia as in Figs. 6A-C and 7A-C; female terminalia with

- T10 undivided and distinctly V-shaped, usually with a pair of rod-like apical projections (Figs. 6D, 7D), if projections absent, then setae of body and legs pale (Palearctic, Afrotropical and Oriental).....*Argyrochlamys* Lamb (in part)
- Body usually metallic; 5-6 dorsocentrals, penultimate posterior pair usually in line or weakly offset medially; venation variable; hind basitarsus of male without comma-shaped posterobasal projection; male and female terminalia not as above.....18
18. Face and clypeus broad in both sexes, clypeus bulging and subequal in height to face; 6 dorsocentral setae, wing with brownish spots or bands, vein M beyond crossvein dm-cu with weak anterior bend before middle, hypopygium distinctive (Figs. 28A-C, 29A-C), subtriangular, phallus strongly wrinkled (Neotropical)*Stenopygium* Becker
- Face and clypeus variable; 5-6 dorsocentrals, wing with or without brownish markings, venation variable, hypopygium not as above.....19
19. Distal segment of arista plumose with dorsal and ventral hairs longer than lateral hairs and often widely spaced, if weakly plumose, then with clypeus strongly bulging and subequal in height to face, 5 dorsocentrals, and hind femur with 1 strong anteroventral preapical seta; vein M beyond crossvein dm-cu usually with strong anterior bend and distinctly convergent with R₄₊₅, M occasionally straight (e.g. *P. tripartatus*), or weakly bent anteriorly; hind coxa usually with lateral seta near apex
-*Pelastoneurus* Loew (in part)
- Distal segment of arista bare or with hairs subequal in length; venation variable; position of lateral seta on hind coxa variable.....20
20. Vein M beyond crossvein dm-cu straight or with weak anterior bend, subparallel to weakly converging with R₄₊₅; or M distinctly S-shaped and subparallel with R₄₊₅ beyond bend.....21
- Vein M with strong anterior bend towards R₄₊₅, veins strongly converging.....33
21. Hind femur with 2 or more anterodorsal preapical setae.....22
- Hind femur with 1 anterior or anterodorsal preapical seta24

- 22.** Clypeus strongly bulging, subequal in height to face, with lower margin straight, ending well-above lower eye margin; face and clypeus broad in both sexes, weakly converging below; palps large; proboscis large and thick; mid femur with 2-4 anterior and 2 strong posteroventral preapical setae in addition to terminal posteroventral preapical seta which is weakly developed; hind femur with 2 anterodorsal preapical setae; Scutum with violet longitudinal stripe along each row of dorsocentrals; male and female genitalia as in Fig. 25A-E (North Africa).....*Platyopsis* Parent
- Clypeus flat, at most weakly produced in some females, lower margin rounded or straight; palps and proboscis usually not enlarged, if large, then clypeus extending well-beyond lower eye margin; mid femur with 1-5 anterior setae, occasionally with 1 strong posteroventral preapical seta; hind femur with 2 or more anterodorsal setae.....**23**
- 23.** Lower margin of clypeus straight, ending above lower eye margin, face narrowed towards clypeus; hind femur with 2 elongate anterodorsal preapical setae; hind tibia with elongate setae; mid and hind tarsi with tarsomeres 4-5 white with dense white hairs; posterior margin of wing distinctly incised near middle; apex of postgonite with preapical lateroventral lobes (China).....“*Hypophyllus*” *sinensis* Yang (males)¹
- Lower margin of clypeus usually rounded or subtriangular and often extending to or beyond lower eye margin, if clypeus not rounded below, then face narrow below antennae and widening towards clypeus or extending well beyond lower eye margin; hind femur with 2 or more normally developed anterodorsal setae; apex of postgonite strongly upturned and flared laterally (Fig. 33D,E)..... *Tachytrechus* Stannius (in part)
- 24.** Scutum with distinct dark spot above notopleuron.....**25**
- Scutum without distinct dark spot above notopleuron**26**
- 25.** Thorax and abdomen metallic green or bluish-green, spot above notopleuron metallic purplish-black; lower margin of clypeus straight; hypandrium short, conical, slightly dorsoventrally flattened, fused to epandrium laterally near basiventral epandrial lobe (Fig.

- 26A,C); postgonite with acute ventrally curved medial lobe and 1-2 preapical lateroventral lobes (Fig. 26B) (western Palaearctic).....*Poecilobothrus* Mik (in part)
- Thorax and abdomen bluish-black, spot above notopleuron dull black, notum with dark medial longitudinal stripe and usually a dark spot in front of scutellum; lower margin of clypeus subtriangular; hypandrium not fused to epandrium laterally near basiventral epandrial lobe; postgonite not as above (Afrotropical).....*Pelastoneurus* Loew (in part)
- 26.** Males with apical third of wing broadly brown; mid tibia with 1 anteroventral seta, seta curved and fine apically, and 1 very fine apicoventral seta; basitarsus of mid leg with strong basiventral seta; sperm pump large, tubular and folded back on itself (Fig. 8C) (Neotropical) *Cheiromyia* Dyte (in part)
- Males without the above combination of characters, or females27
- 27.** Clypeus with lower margin rounded or subtriangular and sometimes extending beyond lower eye margin, if clypeus not rounded below, then face narrow below antennae and widening towards clypeus; vein M beyond crossvein dm-cu with weak anterior bend or with distinct S-shaped bend with M and R₄₊₅ subparallel beyond bend.....28
- Clypeus with lower margin straight and ending above lower eye margin; face narrowed towards clypeus or sides subparallel; vein M beyond crossvein dm-cu with weak anterior bend, not with S-shaped bend30
- 28.** Male genitalia with apex of postgonite strongly upturned and flared laterally (Fig. 33D,E); female terminalia with T6 and T7 divided medially
..... *Tachytrechus* Stannius (in part)
- Male genitalia with apex of postgonite not as above, female terminalia with T6 and T7 undivided (some species of *Hercostomus* from China, India and Nepal).....29
- 29.** Male foretarsus with tarsomeres 3-5, 4-5, or tarsomere 5 flattened; fifth pair of dorsocentrals aligned or, at most, weakly offset medially; mid femur with 1 posterior preapical seta, about even with anterior preapical, in addition to terminal posteroventral preapical seta which is sometimes developed; male cercus relatively small, slender,

tapered apically (Fig. 15A); postgonite with well-developed medioventral projection (Fig. 15A,B); hypandrium laterally flanked by basiventral epandrial lobes forming an asymmetrical complex (Fig. 15B,C,D)

.....*Hercostomus longiventris* group (in part, *H. amoenus* and related species)

- Male foretarsus simple; fifth pair of dorsocentrals strongly offset medially; mid femur without posterior preapical seta, about even with anterior preapical; male cercus large, nearly as long as epandrium, with 90° furcation, with long setae marginal setae, distal margin jagged; apicoventral epandrial lobe spine-like and furcate; basiventral epandrial lobes weakly developed, not flanking hypandrium*Hercostomus* Loew (in part, *Hercostomus* (*Ahercostomus*) *jiangchenganus* Yang and Saigusa)

30. Hind femur with anterior preapical seta positioned far from apex, slightly beyond middle or at distal third; 5 dorsocentrals; arista with long hairs; vein M beyond crossvein dm-cu straight and subparallel to R₄₊₅; wing brown, usually with pale transverse stripe just beyond crossvein dm-cu; postgonite narrow (Afrotropical)

.....*Pelastoneurus* Loew (in part)

- Hind femur with anterior preapical seta positioned close to apex; 6 dorsocentrals; arista usually with short pubescence, or bare; vein M beyond crossvein dm-cu straight and subparallel to R₄₊₅ or with weak sinuous anterior bend and converging with R₄₊₅31

31. Antenna of male with enlarged scape, reduced pedicel, 1-segmented arista usually with one or more lamellae; if antenna not as above, then hypopygium with elongate, setose apicoventral epandrial lobes (Figs. 30A,C, 31A,C); basiventral epandrial lobes usually elongate and digitiform (Figs. 30C, 31C, 32C), usually with pointed or frayed knob-like tip (Figs. 31A,C, 32A,C)*Sybistroma* Meigen (in part, males)

- Scape and pedicel of male normal, arista 2-segmented, rarely with apical lamella; apicoventral epandrial lobes not elongate and setose; basiventral epandrial lobes variably developed with or without knob-like tip; or females32

32. Male genitalia with basiventral epandrial lobes and hypandrium forming a complex of entangled asymmetrical lobes (Fig. 14A,C); mid femur with 1 strong posterior preapical about even with anterior preapical *Hercostomus longiventris* group (in part, males)

- Male genitalia variable, not as above; mid femur with or without strong posterior preapical about even with anterior preapical; or females *Hercostomus* Loew (in part, including females of *H. longiventris* group), *Anasyntormon* Parent, *Sybistroma* Meigen (in part, females)^{2,3}

33. Antenna of male with scape enlarged, usually elongated and thickened, pedicel reduced and funnel-shaped, arista bare with apical lamella, sometimes also with lamella at middle 34

- Antenna of male with scape and pedicel normal-sized, pedicel occasionally reduced, arista usually without apical lamella, or females 35

34. First flagellomere conical or subtriangular, 2-2.5x as long as wide, pointed apically; arista with apex of lamella narrowed to a fine point or notched; face narrowing towards clypeus or nearly parallel-sided (Australia and Papua New Guinea)

..... *Metaparaclius* Becker (in part, males)

- First flagellomere at most 1.5x as long as wide, usually shorter, rounded apically; arista with lamella rounded or pointed apically; face widening towards clypeus (Nearctic)

..... *Tachytrechus* Stannius (in part)

35. Lower margin of clypeus rounded or subtriangular and often extending to or beyond lower eye margin, if clypeus not rounded or subtriangular below, then face narrow below antennae and widening towards clypeus; hind femur with 1 or more anterodorsal preapical setae (Old World species usually with 2 or more); male genitalia with apex of postgonite strongly upturned and flared laterally; (Fig. 33D,E)

..... *Tachytrechus* Stannius (in part)

- Lower margin of clypeus usually straight and ending above lower eye margin; face usually narrowed towards clypeus or sides subparallel, if lower margin of clypeus rounded and extending beyond lower eye margin, then posterolateral margin of

metepimeron with patch of setae, male genitalia with large, dark, shell-like cercus, epandrium with complex, eversible sac adjacent to surstylus, and apicoventral epandrial lobe with 3 fine, branched setae (“*Polymedon*” *inopinatus*, Oriental); hind femur usually with 1 anterodorsal preapical seta; postgonite not as above36

36. Arista plumose*Pelastoneurus* Loew (in part, some Old World species)
- Arista weakly to strongly pubescent.....37

37. Scutum with distinct dark metallic spot above notopleuron; upper propleuron with 2 strong black setae; hind basitarsus with 1-2 short anterior setae (Australia).....
.....*Metaparaclius* Becker (in part, female *M. australiensis*)
- Not with the above combination of characters*Paraclius* Loew^{2, 4}

¹ See “Remarks” under *Sybistroma* regarding the placement of “*Hypophyllus*” *sinensis*.

² Some Old World species currently placed in *Pelastoneurus* may key out here.

³ Female “*Hypophyllus*” *sinensis* Yang keys out here.

⁴ Unplaced species formerly in *Sarcionus* i.e. “*Sarcionus*” *flavicoxa* Aldrich, “*Sarcionus*” *intermedius* Van Duzee, “*Sarcionus*” *maculatus* Van Duzee key out here.

GENERA OF DOLICHOPODINAE

GENUS *ALLOHERCOSTOMUS* YANG, SAIGUSA AND MASUNAGA

(Fig. 5A-E)

Allohercostomus Yang, Saigusa and Masunaga, 2001: 180. Type species: *Hercostomus rotundatus* Yang and Saigusa [Palearctic], by original designation.

Recognition. This genus may be recognized by its ventrally contiguous eyes, vertical setae shorter than postverticals, strong uniserial acrostichals, scutum flattened in front of

scutellum, M straight and parallel or nearly parallel with R_{4+5} beyond crossvein dm-cu, and small size (body length 2.5-3.2 mm, wing length 2.8-3.4 mm).

Description. Head: Vertex not excavated, 1 pair of weak vertical setae, shorter than postverticals. Frons about 3.5-4.0x wider than high, sides converging anteriorly. Face slightly narrowing below. Clypeus laterally detached from eye margin, recessed and narrowed below, subtriangular, lower margin rounded, ending well above lower eye margin. Palp small and narrow, somewhat digitiform. Antenna: scape short, subconical, with distinct medioventral process; pedicel short; first flagellomere about as long as wide, subtriangular to rounded apically; arista dorsal to subapical, 2-segmented, basal segment short, second segment bare. Eyes contiguous at lower margin. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Acrostichals uniserial and strong, posterior acrostichals as strong as anterior dorsocentrals; 6 dorsocentrals, fifth offset medially; 1 strong outer and 1 weak inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper part of propleuron with a few fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum bare (e.g., *A. rotundatus*) or with 2 hairs (e.g., *A. chinensis* Yang, Saigusa and Masunaga). Scutum with triangular, depressed region in front of scutellum. Scutellum with 1 strong inner seta and 1 minute outer seta on lateral margin.

Legs: Pulvilli developed normally on all legs. Foreleg: Tibia with anterodorsal row of strong setae and 1 long apicoventral seta (present in *A. rotundatus*). Midleg: Femur with 1 anterior preapical seta. Hindleg: Coxa with strong lateral seta near middle; femur with 1 anterodorsal preapical seta; tibia of male with apical ridge-like process posterodorsally (present in *A. rotundatus*); basitarsus equal to slightly longer than second tarsomere, with strong basiventral seta, slightly longer than width of basitarsus, male with weak dentiform process posterobasally (present in *A. rotundatus*).

Wing: Hyaline to brownish. R_{2+3} more or less straight; R_{4+5} nearly straight with slight posterior curve in distal section; M straight, ending near wing apex, subparallel with R_{4+5} ; crossvein dm-cu distinctly shorter than distal section of CuA_1 .

Abdomen: Conical, short. Male: T6 bare; S2 and S3 unmodified, S4 weakly sclerotized, emarginate posteriorly; S5 mostly membranous, weakly sclerotized anterolaterally; S6 mostly membranous with thin sclerotized band along anterior margin, fused to T6 laterally; segment 7 forming well-developed peduncle; S8 subtriangular, setose. Hypopygium (Fig. 5A-C): Epandrium about 1.3-1.8x longer than high; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe moderately to well-developed, subquadrate in lateral view, basiventral epandrial seta present on lobe; apicoventral epandrial lobe well-developed, ovoid to elongate and digitiform, with 1 basiventral and 2 apical setae. Surstylus 2-lobed. Ventral lobe with dorsal hump beyond middle, distal portion narrow with thick apical spine. Dorsal lobe about as long as ventral lobe with strong dorsal seta beyond middle, apex acute. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion well-developed, simple, tapering apically. Proctiger brushes absent. Cercus subtriangular. Hyandrium well-developed, broad, extending to or beyond apex of apicoventral epandrial lobe, mainly free laterally, fused to epandrium distinctly anterior to basiventral epandrial lobe; hyandrial apodeme present, well-developed, hyandrial arms connected to hypandrium. Sperm pump weakly sclerotized; ejaculatory duct elongate; ejaculatory apodeme well-developed, laterally flattened; basal sclerite of sperm pump heavily sclerotized, U-shaped in dorsal view. Phallus slender (*A. rotundatus* with preapical dentiform projection). Female (Fig. 5D,E): T6, T7, S6 and S7 undivided; T8 and S8 divided medially, tergite and sternite not fused anterolaterally. T10 divided medially into hemitergites each bearing 2-3 acanthoporous spines; spines rounded and flattened apically. Upper lobe of cercus with strong apical seta.

Geographical Distribution. *Allohercostomus* includes three species: *A. rotundatus* from Palaearctic China, *A. chinensis* from Oriental China, and *A. nepalensis* Yang, Saigusa and Masunaga from Nepal (Yang et al. 2001).

Phylogenetic Relationships. *Allohercostomus* is hypothesized to be the most basal dolichopodine based on the possession of a prescutellar depression (character 12:0), a plesiomorphy which is lost in the remaining dolichopodine genera. Autapomorphies of

Allohercostomus include the possession of ventrally contiguous eyes, short vertical setae and strong uniserial acrostichals.

Remarks. The presence of a prescutellar depression was not mentioned in the original description of *Allohercostomus*. Although I have only seen specimens of *A. rotundatus*, the presence of this feature in the other species has been confirmed by D. Yang (pers. comm.).

Material Examined.

Allohercostomus rotundatus (Yang and Saigusa), [PA]: 2 ♂ ♂ paratypes, 2 ♀ ♀ paratypes (SKU); 1 ♂ paratype, 1 ♀ paratype (LEM).

GENUS *ANASYNTORMON* PARENT

Anasyntormon Parent, 1932: 114. Type species: *Anasyntormon secundus* Parent [Oriental], designation by Dyte, 1975: 245.

Remarks. *Anasyntormon* was erected by Parent (1932) and includes the Oriental type species *A. secundus* and *A. exceptus* (Becker), which was originally described in *Syntormon*. Parent (1932) placed *Anasyntormon* in the Rhapsiinae and indicated that the genus can be distinguished from *Syntormon* by its free hypopygium and convergent wing veins R₄₊₅ and M. In the original description of *A. exceptus* Becker (1922b) noted that the hypopygium and wing venation is similar to that of *Hercostomus*. The unique male holotype of *A. exceptus* was deposited in the Hungarian Museum and was destroyed during the Hungarian Revolution of 1956 (M. Foldvari, pers. comm.). Parent (1932) described *A. secundus* based on an undisclosed number of males from Sumbawa, Indonesia collected during the Rensch Expedition. These specimens are apparently at Martin Luther Universität, Halle de Salle, Germany, with the other material from the Rensch Expedition; however, to date, I have not been able to confirm this and have not seen the specimens.

Ulrich (1981) transferred *Anasyntormon* to the Dolichopodinae based on the examination of a male of *A. secundus* in the BMNH. Unfortunately, I was unable to locate this male during a visit to the BMNH in July, 2000 and have not seen any other specimens. Ulrich (1981) made the following comments on *A. secundus* (translated from the original German): “The examined male [*A. secundus* Parent, London] is similar to a typical *Hercostomus* in habitus and examined characters. This similarity is not contradicted by the apical arista. The finger-like projection of the second antennal segment (as seen in *Syntormon*) is absent and in its place is an axial nipple (similar to the “collar-shaped prolongation” of Lundbeck 1912 known from the Dolichopodinae and other subfamilies). *Anasyntormon* is congeneric with *Hercostomus* or at least closely related.” Negrobov (1980) also examined material of *Anasyntormon* and, like Ulrich (1981), concluded that the genus is a dolichopodine.

GENUS *ARGYROCHLAMYS* LAMB

(Figs. 6A-E, 7A-E)

Argyrochlamys Lamb, 1922: 391. Type species: *Argyrochlamys impudicus* Lamb [Oriental], by monotypy.

Halaiba Parent, 1929a: 56. Type species *Halaiba cavicola* Parent, by monotypy. **syn. nov.**

Camptoneura Parent, 1930b: 110. Type species: *Camptoneura decolor* Parent, by monotypy [= *Argyrochlamys impudicus* Lamb]. Preoccupied by *Camptoneura* Fieber 1858; synonymized by Dyte (1975).

New Combinations. The following new combinations are hereby established:

Argyrochlamys cavicola (Parent, 1929a) **comb. nov.** (*Halaiba*); *Argyrochlamys breviseta* (Parent, 1939) **comb. nov.** (*Halaiba*).

Recognition. Species of *Argyrochlamys* can be distinguished by their dull, non-metallic, pale yellowish-brown to dark grey colour and strongly medially offset fifth pair of dorsocentrals. Males can be further distinguished by the distinctive comma-shaped or bifurcate projection near the joint of the hind tibia and basitarsus. Females can be further distinguished by their distinctive terminalia with T10 acutely V-shaped and usually with a pair of well-developed rod-like apical projections on T8 that typically protrude from the abdomen.

Description. Setae of head, thorax and legs entirely or mainly dark to mainly or entirely pale. Head: Slightly to distinctly wider than high in frontal view. Vertex not excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons and face broad in both sexes. Frons about 2.5-3.4x wider than high, sides weakly convergent anteriorly. Face weakly narrowing below. Clypeus slightly produced, wider than high, lower margin straight, ending above or at level of lower eye margin. Palp ovoid with weak setae on outer surface, with or without 2-3 stronger apical setae. Antenna: Scape short, subconical, with weak to distinct medioventral process, dorsal surface with only a few setae; pedicel short, marginal setae often stronger ventrally; first flagellomere ovoid to subtriangular, often longer in male; arista dorsal to apical, normally developed or very short and thick (e.g., male *A. breviseta*), 2-segmented, second segment bare. Uppermost postocular setae stronger than lower setae. Postvertical setae subequal or stronger than uppermost pair of postoculars.

Thorax: Broad, acrostichals biserial; 6 dorsocentrals, fifth pair strongly offset medially; 1 strong outer posthumeral, 1 weaker inner posthumeral; 2 notopleurals; 1-2 presuturals, anterior presutural sometimes not differentiated; 1 sutural; 2 supraalars; 1 postalar. Upper part of propleuron with a few to several fine hairs; lower part of propleuron with 1 strong prothoracic seta, with or without sparse fine hairs; pleural surface in front of posterior spiracle bare; metepisternum bare. Notum sometimes with flattened region in front of scutellum (e.g., *Argyrochlamys* sp. 1). Scutellum with 1 strong inner seta on lateral margin, weak outer seta present or absent.

Legs: Pulvilli developed normally on all legs. Midleg: Femur with 1 anterodorsal preapical seta. Hindleg: Coxa with strong lateral seta near or above middle; femur with

well-developed setae along anterodorsal surface, 1 anterodorsal preapical seta, with or without distinct anteroventral preapical seta; tibia of male sometimes with distinct bifurcate posteroapical projection (e.g., *Argyrochlamys* sp. 1); basitarsus distinctly shorter than second tarsomere, with strong basiventral seta, sometimes with 1 strong dorsal seta (e.g., *Argyrochlamys* sp. 1), male basitarsus often with concavity and elongate comma-shaped projection posterobasally, occasionally absent (e.g., *Argyrochlamys* sp. 1).

Wing: Hyaline, veins pale. R_{2+3} usually straight and ending well beyond middle of wing; R_{4+5} usually curving posteriorly in distal section; distal section of M beyond crossvein dm-cu with strong anterior bend near middle, ending before wing apex, convergent with R_{4+5} ; crossvein dm-cu distinctly shorter than distal section of CuA_1 . Venation of *A. impudicus* aberrant, with R_{2+3} short, reaching wing margin just beyond middle; R_{4+5} running parallel to R_{2+3} in basal section, curving posteriorly to run parallel with costa in apical third; distal section of M with 90° bend beyond middle, strongly curved beyond bend, reaching wing margin distinctly above apex, strongly convergent with R_{4+5} .

Abdomen: Subconical. Male: T6 bare, short, mostly covered by T5; S2-4 weakly sclerotized; S5 mainly membranous, invaginated medially; S6 mainly to entirely membranous; segment 7 forming short peduncle, mostly hidden in normal repose; S8 rounded to subtriangular, setose. Hypopygium (Figs. 6A-C, 7A-C): Epandrium 1.7-2.3x longer than high; foramen positioned laterally, well-separated from base of cerci; basiventral epandrial lobe not developed, basiventral epandrial seta positioned on infolded ventral margin of epandrium; apicoventral epandrial lobe digitiform to bump-like or absent, with 2-3 strong setae. Surstylus 2-lobed. Ventral lobe digitiform or short and blunt. Dorsal lobe about twice as long as ventral lobe, digitiform, with a strong, sometimes thickened, dorsal seta and several apical setae. Postgonite: anteroventral portion weakly or well-sclerotized, with bifurcate base sitting under sperm pump; posterodorsal portion well-developed, simple or bifurcate. Proctiger brushes absent. Cercus variable, digitiform to oval (Figs. 6A, 7A), sometimes very reduced (e.g., *Argyrochlamys* sp. 1). Hypandrium more or less trough-like, apex sometimes with a pair of well-sclerotized dentiform projections (e.g., *A. impudicus*, *A. cavicola*, Figs. 6A,C, 7A,C), free laterally with membranous connection to epandrium basiventrally; hypandrial

apodeme well-developed; hypandrial arms connected to or separated from hypandrium, sometimes with a pair of weakly sclerotized rounded projections apicodorsally (e.g., *A. impudicus*, *A. cavicola*, Figs. 6B, 7B). Sperm pump small; ejaculatory apodeme short, rod-like, apex occasionally dorsoventrally flattened and weakly flared laterally (e.g., *Argyrochlamys* sp. 1); basal sclerite of sperm pump indistinct. Phallus usually swollen in basal three-quarters (e.g., *A. impudicus*, *A. cavicola*, Figs. 6B, 7B), sometimes slender and finely wrinkled (e.g., *Argyrochlamys* sp. 1). Female (Figs. 6D,E, 7D,E): T6,T7, S6 and S7 undivided, well-sclerotized to nearly membranous; T8 and S8 divided medially, tergite and sternite not fused anterolaterally, T8 usually with well-developed rod-like apical projection extending well beyond base of T10 (e.g., *A. impudicus*, *A. cavicola*, Figs. 6D, 7D), S8 weakly sclerotized. Furca present, rod-like or bifurcate apically. T10 acutely V-shaped, not divided medially, bearing 6-8 acanthoporous spines. Cercus weakly sclerotized, upper lobe digitiform with several short apical setae

Geographical Distribution. *Argyrochlamys* is recorded from the Afrotropics (Sudan, Djibouti, Somalia, Ghana, Seychelles, Mauritius) (Dyte and Smith, 1980) and the Oriental region (Chagos Island, Sri Lanka) (Dyte, 1975). Dyte (unpublished manuscript) also records *A. impudicus* and *A. cavicola* from Oman in the southernmost part of the Palaearctic region.

Phylogenetic Relationships. *Argyrochlamys* forms the sister group to the large clade including *Cheiromyia*, *Paraclius*, *Pelastoneurus*, *Platyopsis*, *Tachytrechus* and *Metaparaclius* based on the curvature of wing vein M (character 34:2). See “*Tachytrechus* genus group” section above for discussion of the monophyly of *Argyrochlamys*.

Remarks. Parent (1929a) placed *Halaiba* in the Rhaphiinae, based on the shape of the first flagellomere and the apical arista, but noted the presence of setae on the dorsum of the scape and the *Paraclius*-like wing venation, suggesting placement in the Dolichopodinae. Ulrich (1981) subsequently transferred *Halaiba* to the Dolichopodinae based on an examination of the types of both *H. cavicola* and *H. breviseta*. My cladistic

analysis support Ulrich's classification and further indicates a close relationship between the type species of *Halaiba* and *Argyrochlamys* based primarily on characters of the male and female terminalia. *Argyrochlamys* has traditionally been recognized by its aberrant wing venation; however, this feature is an autapomorphy of *A. impudicus*. I consider *Halaiba* to be congeneric with *Argyrochlamys*.

The male genitalia of *A. breviseta* have a heavily sclerotized, dark, bifurcate, dorsal process which is curved ventrally. Based on my examination of the male syntype, I believe this structure to be the postgonite; however, dissection is required to confirm this interpretation.

Species of *Argyrochlamys* are restricted to ocean beaches and are usually collected in burrows of ghost crabs (*Ocypode* Lamarck, Ocypodidae). At present, their ecological role within these burrows is unknown.

Material Examined.

Argyrochlamys breviseta (Parent), [AF]: 1 ♂ syntype, 1 ♀ syntype (BMNH)

Argyrochlamys cavicola (Parent), [PA, AF]: 1 ♂ syntype, 1 ♀ syntype (MNHN)

Argyrochlamys impudicus Lamb, [PA, AF, OR]: 1 ♂ syntype, 1 ♀ syntype, 1 ♂, 1 ♀ (BMNH); 3 ♀ ♀ (MZLU); 1 ♂, 1 ♀ (LEM); ♂ holotype of *Camptoneura decolor* Parent (MNHN).

Argyrochlamys sp. 1, [OR, Sri Lanka]: 4 ♂ ♂, 5 ♀ ♀ (MZLU)

GENUS *CHEIROMYIA* DYTE

(Fig. 8A-C)

Cheirocerus Parent, 1930a: 13. Type species: *Cheirocerus palmaticornis* Parent [Neotropical], by monotypy. Preoccupied by *Cheirocerus* Eigenmann, 1917.

Cheiromyia Dyte, 1980: 223. Type species: *Cheirocerus palmaticornis* Parent, automatic. N. name for *Cheirocerus* Parent, 1930a.

New Combination. The following new combination is hereby established: *Cheiromyia maculipennis* (Van Duzee, 1934) **comb. nov.** (*Sarcionus*).

Recognition. Two of the three described species, *C. palmaticornis* and *C. pennaticornis* can be easily recognized by the distinctive antennae with several slender pubescent projections on the outer surface of the first flagellomere. *Cheiromyia maculipennis* lacks projections on the first flagellomere and can be identified by characters given in the key. All species share a characteristic sperm pump which is folded back on itself.

Description (male). Head: Usually slightly broader than high, occasionally distinctly broader than high (e.g., *C. pennaticornis*). Occiput convex medially, sometimes slightly concave behind postoculars (e.g., *C. pennaticornis*). Vertex distinctly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2-3x wider than high, sides subparallel to convergent anteriorly. Face very narrow, with sides strongly converging below (e.g., *C. maculipennis*) to quite broad (e.g., *C. pennaticornis*) with sides subparallel; clypeus flat, lower margin straight, ending well above lower eye margin. Palp small, with weak to somewhat elongate setae on outer surface (e.g., *Cheiromyia* sp. 1), with or without distinct apical seta. Antenna: Scape short, subconical, with weak to well-developed acute process medioventrally and ventrally; pedicel unmodified and short (e.g., *C. maculipennis*) to strongly flattened (e.g., *C. pennaticornis*); first flagellomere variable in shape: subtriangular (e.g., *C. maculipennis*), ovoid basally with long, narrow, tapering apex (e.g., *C. palmaticornis*), or greatly elongated and narrowly triangular (e.g., *C. pennaticornis*), outer surface usually with series of 3-9 slender pubescent projections, projections sometimes branched, absent in *C. maculipennis*; arista dorsal, 2-segmented, distinctly pubescent, occasionally plumose (e.g., *C. pennaticornis*). Lowermost postocular seta sometimes stronger. Postvertical setae slightly to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; usually 6 distinct dorsocentrals, anteriormost dorsocentral sometimes small to indistinct (e.g., *C. maculipennis*), aligned; 1 outer posthumeral, 1 weaker inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalar; 1 postalar. Upper part of propleuron with cluster of weak hairs; lower part of

propleuron with 1 strong prothoracic seta and weak hairs; pleural surface in front of posterior spiracle bare; metepisternum with a row of 2-3 fine hairs. Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin.

Legs: Pulvilli developed normally on all legs, small but distinct. Foreleg: Femur usually with distinct posterior preapical seta, or a series of 2-3 progressively longer setae; tibia sometimes thickened (e.g., *Cheiromyia* sp. 1); tarsus sometimes with distinct pile ventrally and enlarged claws (e.g., *C. pennaticornis*). Midleg: Femur with 1 anterior or anterodorsal preapical seta; tibia occasionally with 1 fine apicoventral seta (e.g., *C. maculipennis*); basitarsus with distinct to strong basiventral seta, tarsomeres 2-3 weakly flattened on medial surface and silvery in *C. maculipennis*. Hindleg: Coxa with strong lateral seta slightly to distinctly below middle; femur with 1 anterodorsal preapical seta; tibia lacking posteroapical process; basitarsus distinctly shorter than second tarsomere, with distinct basiventral seta and 1-3 weaker ventral setae, with small hook-like process posterobasally.

Wing: Hyaline or brownish, occasionally with apical third brown (e.g., *C. maculipennis*). R_{2+3} weakly sinuous basally, straight in distal section; R_{4+5} straight, with or without weak posterior curve in distal section; distal section of M beyond crossvein dm-cu usually with strong anterior bend near middle, bend occasionally weak (e.g., *C. maculipennis*), ending before wing apex; crossvein dm-cu subequal to or longer than distal section of CuA_1 .

Abdomen: Subconical. T6 bare; S2 unmodified; S3 unmodified to emarginate and membranous posteromedially; S4 strongly emarginate and membranous posteromedially, sometimes divided; S5 mainly membranous, sometimes with a pair of textured membranous lobes basally (e.g., *C. maculipennis*, *C. palmaticornis*); S6 mainly membranous, weakly sclerotized along anterior margin; segment 7 forming well-developed peduncle; S8 ovoid to teardrop-shaped, setose. Hypopygium (Fig. 8A-C): Epandrium subrectangular in lateral view, about 1.7-2x longer than high; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe usually not developed with basiventral epandrial seta arising on infolded ventral epandrial margin, small lobe occasionally present with basiventral epandrial seta arising on medial surface (e.g., *C. pennaticornis*); apicoventral epandrial lobe well-developed and

projecting ventrally, sometimes distinctly anteroposteriorly flattened (e.g., *C. maculipennis*), with 2 preapical to apical setae, setae often long and fine, *C. palmaticornis* with elongate narrow projection arising from medial surface of left lobe (Fig. 8A,B). Surstylus 2-lobed. Ventral and dorsal lobes more or less digitiform and subequal in length; dorsal lobe often with rounded preapical projection. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion well-developed, digitiform. Proctiger brushes absent. Cercus usually subtriangular or ovoid with weak marginal setae, cercus of *C. palmaticornis* very large, triangular, with strong setae on apical margin (Fig. 8A). Hypandrium long, trough-like (e.g., *C. palmaticornis*, Fig. 8A,B) or bifurcate (e.g., *C. maculipennis*), with membranous connection to epandrium basiventrally, free laterally; hypandrial apodeme absent; hypandrial arms connected to hypandrium. Sperm pump large, tubular and folded back on itself (Fig. 8C); ejaculatory apodeme usually well-developed, laterally flattened; basal sclerite of sperm pump wide, more or less straight in dorsal view, occasionally positioned apicodorsally on sperm pump. Phallus slightly to distinctly thickened, sometimes flared preapically with narrow apex, apex occasionally bifurcate (e.g., *C. maculipennis*).

Female unknown.

Geographical Distribution. This genus is known only from the Neotropical region including Guyana, Brazil, Ecuador and Bolivia.

Phylogenetic Relationships. *Cheiromyia* is part of the clade including *Paraclius*, *Stenopygium*, *Pelastoneurus*, *Platyopsis* and *Tachytrechus*. The discovery of females may help to elucidate the position of this genus within this clade (see “*Tachytrechus* genus-group” section above).

Remarks. The two BMNH specimens determined by H. Oldroyd and J.C. Deeming as *C. palmaticornis* belong to an undescribed species (here referred to as *Cheiromyia* sp. 1) with a thickened fore tibia and shortened tarsomere 2 on the foreleg.

The holotype and paratype of *C. maculipennis* may represent two similar species that differ in the shape of the first antennal flagellomere, hypandrium and phallus;

however, more specimens are required to determine if these differences are discrete or part of a continuum of variation. Curran (in Van Duzee, 1934) noted a possible female of *C. maculipennis* in the AMNH (not examined).

Material Examined.

Cheiromyia maculipennis (Van Duzee), [NT]: ♂ holotype (AMNH), ♂ paratype (CAS)

Cheiromyia palmaticornis Parent, [NT]: 6 ♂ ♂ (USNM)

Cheiromyia pennaticornus Parent, [NT]: ♂ holotype (SMTD)

Cheiromyia sp. 1, [NT]: 2 ♂ ♂ (BMNH)

GENUS *DOLICHOPUS* LATREILLE

(Figs. 9A-F, 10A-F)

Dolichopus Latreille, 1796: 159. Type species: *Musca unguata* Linnaeus [Palearctic], designation by Latreille, 1810: 443.

Ragheneura Rondani, 1856: 144. Type species: *Dolichopus griseipennis* Stannius, by original designation.

Hygroceleuthus Loew, 1857: 10. Type species: *Dolichopus latipennis* Fallén, designation by Coquillett, 1910: 554. Listed as subgenus of *Dolichopus* by Negrobov (1991).

Rhagoneurus Loew, 1864: 346. Unjustified emendation of *Ragheneura* Rondani, 1856, based on Loew's misspelling "*Rhageneura*" (see discussion in Dyte, 1975).

Spathichira Bigot, 1888a: xxiv. Type species: *Dolichopus funditor* Loew, by original designation.

Lichtwardtia Enderlein, 1912: 406. Type species: *Lichtwardtia formosana* Enderlein [= *Dolichopus ziczac* Wiedemann], by original designation. **syn. nov.**

Eudolichopus Frey, 1915: 10 (as subgenus). Type species: *Musca plumipes* Scopoli, designation by Steyskal, 1973: 347 (see discussion in Dyte, 1975).

Leucodolichopus Frey, 1915: 10 (as subgenus). Type species: *Dolichopus remipes* Wahlberg, designation by Steyskal, 1973: 348.

Melanodolichopus Frey, 1915: 10 (as subgenus). Type species: *Dolichopus stenhammari* Zetterstedt, designation by Steyskal, 1973: 348.

Vaalimyia Curran 1926: 398. Type species: *Vaalimyia violacea* Curran [= *Dolichopus angularis* Macquart], by original designation. **syn. nov.**

Macrodolichopus Stackelberg, 1933: 109 (as subgenus). Type species: *Dolichopus diadema* Haliday, by original designation.

Hydroceleuthus, incorrect subsequent spelling by Aldrich, 1921: 8.

Hygrocelenthus, incorrect subsequent spelling by Parent, 1929c: 176.

Rageneura, incorrect subsequent spelling by Bigot, 1890:269

Raghenerura, incorrect subsequent spelling by Dyte, 1975: 232.

Rhageneura, incorrect subsequent spelling by Loew, 1864: 346.

Spatichira, incorrect subsequent spelling by Bigot, 1888b: xxx.

New Combinations and Transfers. The following new combinations are hereby established: *Dolichopus emelyanovi* (Grichanov, 1998) **comb. nov.** (*Lichtwardtia*); *Dolichopus fractinervis* (Parent, 1929c) **comb. nov.** (*Vaalimyia*); *Dolichopus hollisi*

(Grichanov, 1998) **comb. nov.** (*Lichtwardtia*); *Dolichopus minusculus* (Parent, 1934b) **comb. nov.** (*Vaalimyia*); *Dolichopus mironovi* (Grichanov, 1998) **comb. nov.** (*Lichtwardtia*); *Dolichopus nigrotorquatus* (Parent, 1937) **comb. nov.** (*Vaalimyia*); *Dolichopus sukharevae* (Grichanov, 1998) **comb. nov.** (*Lichtwardtia*); *Dolichopus tikhonovi* (Grichanov, 1998) **comb. nov.** (*Lichtwardtia*). The following species are reassigned to *Dolichopus*: *Dolichopus angularis* Macquart, 1842; *Dolichopus aethiopicus* (Bezzi, 1906) (*Rhagoneurus*); *Dolichopus hirsutisetis* (de Meijere, 1916) (*Rhagoneurus*); *Dolichopus ziczac* Wiedemann, 1824.

Recognition. *Dolichopus* can be recognized by the possession of an obtuse to angular S-shaped bend in wing vein M, pleuron with a cluster or row of fine hairs in front of the posterior spiracle and hind basitarsus with 1 or more strong dorsal and anterior setae. Species formerly included in *Lichtwardtia* can be distinguished by the possession of a plumose arista and stub veins anteroproximally and posterodistally arising on the corners of the angular S-shaped bend in wing vein M.

Description. Head: Vertex more or less flat to weakly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 1.6–3.0x wider than high, sides subparallel to distinctly convergent anteriorly. Face and clypeus usually bare, occasionally with weak hairs (e.g., *D. latilimbatus* Macquart, *D. nubilus* Meigen). Face broad to narrow in male with sides convergent, occasionally subparallel, narrowest near or below middle, sometimes distinctly widening below, broader in female with sides subparallel to weakly convergent. Clypeus usually flat to weakly produced, sometimes strongly bulging, lower margin usually straight to weakly emarginate, occasionally rounded to subtriangular (e.g., male *D. latipennis*), usually ending well above lower eye margin, occasionally extending to or beyond lower eye margin (e.g., *D. diadema*). Palp ovoid, rounded to subtriangular apically, sometimes smaller in male, weak setae and/or fine hairs on apical half of outer surface, usually with distinct apical seta. Antenna: Scape usually short, subconical with short dorsal setae, occasionally elongated and flattened, with long dense setae (e.g., *D. latipennis*, *D. consanguineus* (Wheeler), *D. crenatus* (Osten Sacken)), acute medioventral process usually distinct to well-developed, occasionally absent or reduced in species with

elongated scape, ventral acute process often present; pedicel usually short, occasionally elongated and flattened in species with elongate scape (e.g., *D. latipennis*); first flagellomere ovoid to subtriangular, sometimes acute and elongate in male (e.g., *D. acuticornis* Wiedemann, *D. fumosus* Van Duzee); arista dorsal to subapical, usually 2-segmented, rarely 1 segmented (e.g., male *D. dorycerus* Loew), basal segment occasionally thickened and densely pubescent (e.g., *D. consanguineus*), distal segment usually velvety to shortly pubescent, sometimes plumose (e.g., *D. angularis*), rarely glabrous (e.g., male *D. dorycerus*), occasionally with apical lamella in male (e.g., *D. dorycerus*, *D. phyllocerus* Vockeroth). Lower postocular setae often flattened, especially in male (e.g., *D. remipes*, *D. setifer* Loew), lowermost seta sometimes stronger, postgenal area behind lower postoculars occasionally with dense setae (e.g., *D. annulitarsis* Ringdahl, *D. czezanovskii* Stackelberg). Postvertical setae slightly to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 5-6 dorsocentrals, penultimate pair aligned to strongly offset medially; posterior mesonotum in front of scutellum usually bare, occasionally with fine setae (e.g., *D. aldrichi* (Wheeler), *D. latipennis*, *D. latilimbatus*, *D. humilis* Van Duzee, *D. nubilus*); 1 strong outer posthumeral, 1 strong to weak inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Dark metallic spot above notopleuron occasionally present (e.g., *D. unguatus*). Upper and lower part of propleuron with fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle with a cluster or row of fine hairs; metepisternum with a cluster or row of several fine hairs. Scutellum with 1 strong inner seta and usually 1 small outer seta on lateral margin, dorsum and/or posterior margin with fine hairs, occasionally bare.

Legs: Pulvilli developed normally on all legs. Foreleg: Often modified in male. Femur often with 1 well-developed posterior preapical seta, occasionally 2 setae, rarely with strong anterior preapical (e.g., *D. finitus* Walker), male occasionally with long, fine setae ventrally to posteroventrally (e.g., *D. indigenus* Van Duzee, *D. unguatus*); tibia of male sometimes with long, fine apical seta (e.g., *D. diadema*); basitarsus sometimes with strong basiventral seta (e.g., *D. angularis*); tarsus often modified in male, sometimes elongate, tarsomeres variably flattened and/or fringed with setae, occasionally piliferous

ventrally (e.g., *D. consanguineus*), fifth tarsomere often strongly laterally flattened and dark (e.g., *D. dakotensis* Aldrich). Midleg: Usually unmodified in males. Femur with 1-5 strong anterior preapical setae, male occasionally with long, fine setae posteroventrally (e.g., *D. unguatus*); tibia of male occasionally narrow and flattened (e.g., *D. plumipes*), with swollen apex (e.g., *D. fulvipes* Loew), or with elongate setae (e.g., *D. comatus* Loew); basitarsus often with 1 strong dorsal seta usually beyond middle (e.g., *D. lobatus* Loew, *D. stenhammari*), rarely 2-3 dorsal setae (e.g., *D. dasypodus* Coquillett), sometimes with distinct basiventral seta (e.g., *D. angularis*); tarsus occasionally modified in males, usually variably flattened or fringed with modified setae. Hindleg: Often modified in male. Coxa with strong lateral seta near middle to distinctly below, rarely reduced (e.g., *D. exsul* Aldrich); femur with 1-5 strong anterodorsal preapical setae, often with well-developed dorsobasal setae (e.g., *D. unguatus*), male frequently with long ventral to posteroventral setae (e.g., *D. atratus* Meigen, *D. cuprinus* Wiedemann, *D. longimanus* Loew); tibia often thickened in male, ciliolarius (row of minute, closely-set hairs on apicodorsal part of tibia) present or absent, sometimes set inside shallow concavity (e.g., *D. acuticornis*, *D. crassicornis* Aldrich), male often with posterior to posterodorsal bare or minutely-haired stripe or region which is occasionally widened or swollen in basal half (e.g., *D. coercens* Walker, *D. diadema*, *D. stenhammari*, *D. unguatus*), male with posteroapical ridge or lip-like process, often with associated dentiform projection; tarsus rarely modified in males (e.g., *D. remipes*), basitarsus slightly shorter to distinctly longer than second tarsomere, usually with 2 or more strong dorsal and 1 or more anterior setae, sometimes with only 1 dorsal seta (e.g., *D. conspectus* Van Duzee, *D. ziczac*), with several short ventral setae, sometimes with distinct basiventral seta, basitarsus of male with variably developed dentiform to hook-like posterobasal process.

Wing: Greyish or brownish to hyaline; sometimes infuscated, patterns of infuscation variable (see figures in Van Duzee et al., 1921), usually weaker or absent in female. Costa of male often with short to elongate swelling or pterostigma near insertion of R_1 , occasionally flap-like (e.g., *D. costalis* Frey); R_{2+3} usually weakly sinuous basally, becoming straight or weakly curved distally, sometimes with anterior bend at tip; R_{4+5} relatively straight with posterior curve in distal section; distal section of M beyond

crossvein dm-cu with two obtuse to right-angled bends forming a S-shaped bend before middle, sometimes with posterodistal and/or anteroproximal stub veins (e.g., *D. ziczac*), M straight or weakly curved beyond bend, ending slightly to distinctly before wing apex; R_{4+5} and M usually subparallel beyond bend in M, sometimes distinctly convergent or divergent apically; crossvein dm-cu slightly longer to distinctly shorter than distal section of CuA_1 , distal section of CuA_1 straight or curved towards wing margin; males of some species (e.g., *D. lobatus*, *D. plumipes*) with well-developed anal lobe; wing occasionally short and broad in male (e.g., *D. latipennis*); calypter of male occasionally with crimped hairs (e.g., *D. unguatus*).

Abdomen: Subconical. Male: T1 occasionally with large lateral pockets lined with fine hairs or modified setae (e.g., *D. flagellitenens* Wheeler, *D. lobatus*); T1 and T2 occasionally with long fine hairs laterally (e.g., *D. annulitarsis*, *D. compactus* Van Duzee); T2 occasionally with swollen lateral margin (e.g., *D. dorycerus*); T6 bare; S2 unmodified; S3 unmodified to emarginate and membranous posteriorly; S2 and S3 occasionally with long, fine setae (e.g., *D. setifer*); S4 usually deeply emarginate and membranous posteriorly to almost entirely membranous, occasionally divided; S5 sclerotized laterally to mainly membranous, usually with narrow medial sclerotized band fused to S6 posteriorly, lateral sclerotized bands also usually fused to S6 posteriorly, occasionally with a pair of eversible glandular sacs (e.g., *D. plumipes*, *D. popularis* Wiedemann); S6 mainly membranous, sclerotized along anterior margin, sometimes fused to T6 laterally; segment 7 forming well-developed peduncle; S8 heart-shaped to subquadrate, setose. Hypopygium (Figs. 9A-D, 10A-D) usually large. Epandrium ovoid-subtriangular to subrectangular in lateral view, about 1.5-2.0x longer than high, usually with weak to distinct bulge midlaterally on left side posterior to foramen, bulge sometimes well-developed (e.g., *D. latilimbatus*); foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe weak to well-developed, sometimes absent (Fig. 10D), right and left lobes usually asymmetrical (Fig. 9D), left lobe usually bilobate with inner and outer projection, usually larger than right lobe, basiventral epandrial seta present (*D. minusculus* with 3 strong setae along ventral epandrial margin); apicoventral epandrial lobe weak to well-developed, occasionally absent, usually subquadrate or subtriangular in lateral view with acute or keel-like

dorsoapical extension, sometimes digitiform or bifurcate, usually with 2-3 setae, apical seta sometimes thick (e.g., *D. unguatus*, Fig. 9A), apical edge of lobe occasionally with a fringe of setae (e.g., *D. latilimbatus*) or several spine-like setae (e.g., *D. exsul*). Surstylus 2-lobed. Ventral lobe variable, usually digitiform and curved ventrally, often with dorsal hump (Fig. 9B), sometimes short and broad (Fig. 10B), apex sometimes with 1 to several modified setae near apex. Dorsal lobe (Figs. 9B, 10B) flared apically, usually with 1 preapical lateral seta, often with 1-2 strong or modified mediodorsal setae; dorsal surface usually emarginate or notched preapically with keel-like projection near or across notch (i.e. “Segel” sensu Buchmann, 1961); apex (i.e. “Kopfteil” sensu Buchmann, 1961) expanded and often textured. Postgonite with anteroventral portion weakly sclerotized, nearly membranous and usually bifurcate anteriorly; posterodorsal portion usually well-developed, rarely absent or very short (e.g., *D. genualis* Van Duzee, *D. gratiolus* Steyskal, *D. mironovi*), usually simple and slender (Fig. 9B), occasionally broad and swollen with rounded apex in lateral view (e.g., *D. angularis*, Fig. 10B), occasionally bifurcate (e.g., undescribed species from Sri Lanka, Taiwan and Northern Australia), tripartate (e.g., *D. atripes* Meigen), or with weak lateral projections (e.g., *D. harbecki* Van Duzee, *D. lepidus* Staeger), arched and strongly curved ventrally to straight in lateral view. Proctiger brushes absent. Cercus (Figs. 9A, 10A) usually large, sometimes small and short, subrectangular to ovoid or subtriangular, usually pale with dark margin, occasionally entirely dark (e.g., *D. deterrentus* Loew); apical and lateral margin often jagged, with several digitiform projections, the first with a strong, spatulate, apicoventral seta; many species with dense setae on lateral part of ventral surface (e.g., *D. unguatus*, Fig. 9A); margin often with sickle and/or scythe-shaped setae; cercus rarely thickened and fleshy (e.g., *D. finitis* Walker, *D. quadrilamellatus* Loew). Hypandrium short to elongate, usually subtubular with left side extending dorsally over phallus, slit along right side, occasionally trough-like (e.g., *D. genualis*), with or without dentiform process near apex, free laterally with weakly sclerotized to membranous connection to epandrium basally; hypandrial arms connected to hypandrium, occasionally weakly sclerotized near point of connection; hypandrial apodeme present, with knob-like apex. Sperm pump cylindrical; ejaculatory duct sometimes elongate; ejaculatory apodeme rod-like, apex flared and more or less T-shaped in dorsal view (Figs. 9C, 10C), rarely reduced (e.g., *D.*

cruralis Wahlberg); basal sclerite of sperm pump very well-developed, thick and heavily sclerotized, V-shaped to U-shaped in dorsal view (Figs. 9C, 10C), occasionally with elongated, rod-like base. Phallus usually elongate and slender, occasionally thickened, rarely short (e.g., *D. cruralis*), sometimes with 1 to several dentiform projections, rarely serrate (eg. *D. exsul*) or with thin elongate projection (e.g., *D. comatus*). Female (Figs. 9E,F, 10E,F): Terminalia elongate to quite short; T6, T7, S6 and S7 undivided, usually with darkened anterior and lateral margins; T8 and S8 divided medially, tergite and sternite weakly to distinctly fused anterolaterally. Furca present or absent, variable in structure. T10 divided medially into hemitergites each bearing 3-7 acanthoporous spines along outer margin and a single, slightly smaller inner medial spine present (Figs. 9E, 10E), spines rounded or pointed apically, occasionally wide and flattened apically (e.g., *D. crenatus*). Upper lobe of cercus usually with long apical seta.

Geographical Distribution. *Dolichopus*, as newly defined above (i.e including species formerly in *Lichtwardtia*) occurs in the Holarctic, Afrotropical, Oriental and Australasian regions, and also in the Hawaiian Islands (*D. exsul*). The genus is most diverse in the Holarctic. Three of the six species listed in the Afrotropical Catalog (Dyte and Smith, 1980) were transferred to *Hercostomus* by Grichanov (1999a) (*H. congoensis*, *H. directus* (Walker), *H. ultimus*) and the remaining three species are based on dubious records.

Phylogenetic Relationships. *Dolichopus* is the sister group to *Ethiomyia* based on the possession of a pair of inner medial acanthoporous spines on T10 of the female terminalia and by the distinctive structure of the dorsal surstylar lobe of the male genitalia. Buchmann (1961) provided detailed illustrations of the latter feature for several species of Palaearctic *Dolichopus*.

Remarks. Several subgenera have been recognized within *Dolichopus* (Frey, 1915; Stackelberg, 1930). Frey (1915) divided the genus into four admittedly artificial subgenera (i.e. *Dolichopus* s. str., *Eudolichopus*, *Leucodolichopus*, *Melanodolichopus*) based on colour combinations of the femora and postocular setae. Although subsequent authors have used Frey's subgeneric characters to divide *Dolichopus* into groups within keys

(Van Duzee et al., 1921; Stackelberg, 1930; Parent 1938), these groups have not been recognized as subgenera. In his treatment of the Palaearctic fauna Stackelberg (1930) recognized three subgenera of *Dolichopus* (i.e. *Dolichopus* s. str., *Hygroceleuthus* and *Macrodolichopus*), and this classification was followed by Negrobov (1991) and Chandler (1998). I consider these subgenera of no taxonomic value as both *Hygroceleuthus* and *Macrodolichopus* are based on variable characters of the antenna and clypeus, and *Dolichopus* s. str. is nothing more than the paraphyletic residue that is left over. Further phylogenetic studies of *Dolichopus* are required before a meaningful subgeneric classification can be put in place.

As noted above (see “*Dolichopus* genus group”), the generic status of *Lichtwardia* can no longer be maintained, and it is here recognized as a species-group (the *Dolichopus ziczac* group) within *Dolichopus*. Grichanov (1998) revised the Afrotropical species of this group and recognized 11 species including six new species, bringing the number of described species in this group to 13 (i.e. including *D. hirsutisetis*, from the Oriental region and *D. ziczac* from the Oriental and Australasian/Oceanian regions). I have seen an additional nine undescribed species from Sri Lanka, Nigeria, Taiwan and Australia, based on only 24 specimens from the unsorted holdings of the CNC and USNM, suggesting that this species group may be much more diverse than is currently known.

Material Examined.

Dolichopus acuminatus Loew, [NE]: 1♂ (CNC)

Dolichopus acuticornis Wiedemann, [PA]: 2♂♂ (CNC)

Dolichopus adaequatus Van Duzee, [NE]: 5♂♂, 1♀♀ (CNC)

Dolichopus adultus Van Duzee, [NE]: 3♂♂ (CNC)

Dolichopus aeratus Van Duzee, [NE]: 2♂♂, 2♀♀ (CNC)

Dolichopus alacer Van Duzee, [NE]: 2♂♂, 2♀♀ (CNC)

Dolichopus albiciliatus Loew, [NE]: 3♂♂, 3♀♀ (CNC)

Dolichopus albicoxa Aldrich, [NE]: 6♂♂, 4♀♀ (CNC)

Dolichopus aldrichii (Wheeler), [NE]: 1♂ (CNC)

Dolichopus angularis (Macquart), [AF]: 3♂♂, 2♀♀ (ISNB), 1♂ (CAS)

- Dolichopus annulitarsis* Ringdahl, [PA]: 5♂♂, 3♀♀ (CNC)
- Dolichopus atratus* Meigen, [PA]: 7♂♂, 3♀♀ (CNC)
- Dolichopus atripes* Meigen, [PA]: 2♂♂, 1♀♀ (CNC)
- Dolichopus barbicauda* Van Duzee, [NE]: 6♂♂, 4♀♀ (CNC)
- Dolichopus bifractus* Loew, [NE]: 6♂♂, 5♀♀ (CNC); 6♂♂, 3♀♀ (USNM)
- Dolichopus brevimanus* Loew, [NE]: 5♂♂, 2♀♀ (CNC)
- Dolichopus brevipennis* Meigen, [PA, NE]: 10♂♂, 5♀♀ (CNC); 2♂♂, 2♀♀ (LEM)
- Dolichopus bryanti* Van Duzee, [NE]: 3♂♂, 2♀♀ (CNC)
- Dolichopus canadensis* Van Duzee, [NE]: 10♂♂, 6♀♀ (CNC)
- Dolichopus canaliculatus* Thompson, [NE]: 8♂♂, 5♀♀ (CNC)
- Dolichopus chrysostomus* Loew, [NE]: 2♂♂ (CNC)
- Dolichopus cilifemoratus* Macquart, [PA]: 1♂ (CNC)
- Dolichopus coercens* Walker, [NE]: 3♂♂, 3♀♀ (CNC)
- Dolichopus comatus* Loew, [NE]: 2♂♂, 2♀♀ (CNC)
- Dolichopus compactus* Van Duzee, [NE]: 2♂♂, 2♀♀ (CNC)
- Dolichopus completus* Van Duzee, [NE]: 1♂, 1♀ (CNC)
- Dolichopus consanguineus* (Wheeler), [NE]: 2♂♂, 2♀♀ (CNC)
- Dolichopus conspectus* Van Duzee, [NE]: 2♂♂, 2♀♀ (CNC)
- Dolichopus coquillettii* Aldrich, [NE]: 1♂, 1♀ (CNC)
- Dolichopus correus* Steyskal, [NE]: 2♂♂, 1♀ (CNC)
- Dolichopus costalis* Frey, [PA]: 2♂♂, 1♀ (CNC)
- Dolichopus crassicornis* Aldrich, [NE]: 1♂ (CNC)
- Dolichopus crenatus* (Osten Sacken), [NE]: 2♂♂, 2♀♀ (LEM); 1♂, 1♀ (CNC)
- Dolichopus cruralis* Wahlberg, [PA]: 1♂, 1♀ (CNC)
- Dolichopus cuprinus* Wiedemann, [NE]: 3♂♂, 2♀♀ (CNC)
- Dolichopus czekanovskii* Stackelberg, [PA, NE]: 1♂, 1♀ (CNC)
- Dolichopus dakotensis* Aldrich, [NE]: 2♂♂, 2♀♀ (CNC)
- Dolichopus dasyops* Malloch, [NE, PA]: 2♂♂, 2♀♀ (CNC)
- Dolichopus dasypodus* Coquillett, [NE]: 2♂♂, 2♀♀ (CNC)

- Dolichopus detersus* Loew, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus diadema* Haliday, [PA]: 2 ♂♂, 1 ♀ (LEM); 1 ♂, 1 ♀ (BMNH)
- Dolichopus diversipennis* Curran, [NE]: 2 ♂♂ (CNC)
- Dolichopus dorsalis* Van Duzee, [NE, NT?]: 1 ♂, 1 ♀ (CNC)
- Dolichopus dorycerus* Loew, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus efflatouni* Parent, [PA]: 2 ♂♂, 1 ♀ (USNM)
- Dolichopus enigma* Melander and Brues, [NE]: 3 ♂♂, 2 ♀♀ (CNC)
- Dolichopus eudactylus* Loew, [NE]: 2 ♂♂ (CNC)
- Dolichopus exsul* Aldrich, [AU, OR]: 3 ♂♂, 2 ♀♀ (CNC)
- Dolichopus finitus* Walker, [NE]: 25 ♂♂, 3 ♀♀ (LEM)
- Dolichopus flagellitenens* Wheeler, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus flavicoxa* Van Duzee, [NE]: 1 ♂, 1 ♀ (CNC)
- Dolichopus flavilacertus* Van Duzee, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus flavipes* Stannius, [PA, NE]: 1 ♂ (CNC)
- Dolichopus formosus* Van Duzee, [NE]: 1 ♂, 1 ♀ (CNC)
- Dolichopus fortis* Aldrich, [NE]: 2 ♂♂ (CNC)
- Dolichopus fractinervis* (Parent), [AF]: 3 ♂♂, 1 ♀ (ISNB)
- Dolichopus fraterculus* Zetterstedt, [PA]: 3 ♂♂, 2 ♀♀ (CNC)
- Dolichopus fulvipes* Loew, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus fumosus* Van Duzee, [NE]: 1 ♂ (CNC)
- Dolichopus funditor* Loew, [NE]: 2 ♂♂ (CNC)
- Dolichopus genualis* Van Duzee, [NE]: 3 ♂♂, 2 ♀♀ (CNC)
- Dolichopus gladius* Van Duzee, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus gratiolus* Steyskal, [NE]: 1 ♂ (CNC)
- Dolichopus gratus* Loew, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus groenlandicus* Zetterstedt, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus harbecki* Van Duzee, [NE]: 2 ♂♂, 2 ♀♀ (CNC)
- Dolichopus humilus* Van Duzee, [NE]: 3 ♂♂, 2 ♀♀ (CNC)
- Dolichopus incisuralis* Loew, [NE]: 3 ♂♂, 2 ♀♀ (CNC)

- Dolichopus incongruus* Wheeler, [NE]: 1 ♂ (CNC)
- Dolichopus indigenus* Van Duzee, [NE]: 2 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus ivanovi* Stackelberg, [PA, NE]: 3 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus johnsoni* Aldrich, [NE]: 1 ♂ (CNC)
- Dolichopus laciniatus* Coquillett, [NE]: 2 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus laticornis* Loew, [NE]: 3 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus latilimbatus* Macquart, [PA]: 2 ♂ ♂, 1 ♀ (CNC)
- Dolichopus latipennis* Fallén, [PA, NE]: 5 ♂ ♂, 4 ♀ ♀ (CNC)
- Dolichopus latipes* (Loew), [NE]: 2 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus lepidus* Staeger, [PA]: 3 ♂ ♂, 1 ♀ (CNC)
- Dolichopus linearis* Meigen, [PA]: 1 ♂ (CNC)
- Dolichopus lobatus* Loew, [NE]: 2 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus longicornis* Stannius, [PA]: 2 ♂ ♂, 1 ♀ ♀ (CNC)
- Dolichopus longimanus* Loew, [NE]: 2 ♂ ♂, 2 ♀ ♀ (CNC)
- Dolichopus myosotus* Osten Sacken, [NE]: 4 ♂ ♂, 4 ♀ ♀ (USNM)
- Dolichopus nubilus* Meigen, [PA]: 3 ♂ ♂, 1 ♀ (LEM)
- Dolichopus plumipes* (Scopoli), [PA, NE]: 12 ♂ ♂, 7 ♀ ♀ (CNC)
- Dolichopus popularis* Wiedemann, [PA]: 4 ♂ ♂, 2 ♀ ♀ (LEM)
- Dolichopus remipes* Wahlberg, [PA, NE]: 3 ♂ ♂, 1 ♀ (CNC)
- Dolichopus setifer* Loew, [NE]: 5 ♂ ♂ (LEM)
- Dolichopus stenhammari* Zetterstedt, [PA, NE]: 6 ♂ ♂, 5 ♀ ♀ (CNC)
- Dolichopus unguulatus* (Linnaeus), [PA]: 6 ♂ ♂, 8 ♀ ♀ (CNC)
- Dolichopus ziczac* Wiedemann, [OR]: ♀ holotype
- Dolichopus* sp. 1, [OR, Sri Lanka]: 1 ♂ (USNM)
- Dolichopus* sp. 2, [OR, Sri Lanka]: 1 ♂ (USNM)
- Dolichopus* sp. 3, [AF, Nigeria]: 7 ♂ ♂ (CNC)
- Dolichopus* sp. 4, [AF, Nigeria]: 1 ♂ (CNC)
- Dolichopus* sp. 5, [AF, Nigeria]: 1 ♂ (CNC)
- Dolichopus* sp. 6, [AU, Australia]: 1 ♂ (CNC)

Dolichopus sp. 7, [AU, Australia]: 1 ♂ (CNC)

Dolichopus sp. 8, [OR, Taiwan]: 1 ♂ (CNC)

Dolichopus sp. 9, [AU, Australia]: 5 ♂ ♂, 5 ♀ ♀ (CNC)

GENUS *ETHIROMYIA* gen. nov.

(Figs. 11A-E, 12A,B)

Type species: *Hercostomus purpuratus* Van Duzee, 1925: 185 [Nearctic], by present designation.

New Combinations. The following new combinations are hereby established: *Ethiromyia chalybea* (Wiedemann, 1817) **comb. nov.** (*Hercostomus*); *Ethiromyia purpurata* (Van Duzee, 1925) **comb. nov.** (*Gymnopternus*); *Ethiromyia violacea* (Van Duzee, 1921) **comb. nov.** (*Gymnopternus*).

Recognition. *Ethiromyia* is very similar to *Gymnopternus*, with which it shares a straight M, parallel to subparallel R₄₊₅ and M and a cluster of fine hairs on the pleuron in front of the posterior spiracle. Males of *Ethiromyia* are distinguished by their distinctive cerci and by the possession of an elongate apicoventral seta on the fore tibia. Females possess an inner medial pair of acanthoporous spines on T10. *Ethiromyia* also lacks the dorsal setae on the hind basitarsus found in species of *Dolichopus* and the anterodorsal row of strong setae on the fore tibia present in most species of *Gymnopternus*.

Description. Head: Vertex not excavated, 1 pair strong vertical setae, stronger than postverticals. Frons about 2-2.8x wider than high, sides weakly convergent anteriorly. Face, broad in male, sides slightly convergent below or subparallel, broader in female with sides subparallel. Clypeus slightly produced to strongly bulging, especially in female, lower margin straight or slightly emarginate, ending well above lower eye margin. Palp ovoid, with weak setae on apical half of outer surface and a distinct apical seta. Proboscis large and projecting in *E. purpurata* and *E. chalybea*. Antenna: Scape

subconical, with well-developed acute medioventral process; pedicel short; first flagellomere subtriangular to ovoid, about as long as wide; arista dorsal, 2-segmented, second segment weakly pubescent (e.g. *E. purpurata*) to strongly pubescent (e.g. *E. chalybea* and *E. violacea*, especially females). Lowermost postocular seta sometimes stronger. Postvertical setae subequal to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 6 dorsocentrals, fifth pair distinctly offset medially; 1 strong outer posthumeral, 1 weak inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle with a cluster or row of fine hairs; metepisternum with a cluster of several fine hairs. Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin, dorsum with sparse hairs, posterior margin with sparse short hairs or long dense hairs (e.g., *E. chalybea*).

Legs: Pulvilli developed normally on all legs. Foreleg: Tibia of male with long, fine apicoventral seta. Midleg: Femur with 1 anterior preapical seta, male of *E. violacea* with relatively long, fine hairs basoventrally. Hindleg: Coxa with strong lateral seta near or slightly below middle; femur with 1 anterodorsal preapical seta; apical half of femur and basal part of tibia with long, fine hairs posteriorly in male of *E. purpurata*; apex of tibia with weak to indistinct ridge-like process posterodorsally in male, male of *E. chalybea* with dense posterior clothing setae; basitarsus subequal to shorter than second tarsomere, with distinct basiventral seta, males with hook-like process posterobasally.

Wing: Brownish to grey. Costa of male sometimes with pterostigma near insertion of R_1 (e.g., *E. purpurata*); R_{2+3} relatively straight to weakly convex; R_{4+5} straight with posterior curve in apical section; distal section of M beyond crossvein dm-cu with barely discernable sinuous bend before middle, straight, or with slight convex curve in distal section similar to that of R_{4+5} , ending near wing apex; R_{4+5} and M subparallel; crossvein dm-cu subequal to or shorter than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare; S2 unmodified; S3 unmodified or emarginate and mainly membranous posteromedially; S4 strongly emarginate or divided, membranous medially; S5 mainly to entirely membranous; S6 mainly membranous,

sclerotized along anterior margin; segment 7 forming well-developed peduncle; S8 subquadrate to subtriangular, setose. Hypopygium (Figs. 11A-C, 12A,B) large. Epandrium subtriangular in lateral view, about 1.5-2x longer than high, foramen positioned laterally, well-separated from base of cerci; basiventral epandrial lobe weakly developed, left lobe larger than right lobe in *E. purpurata* (Fig 11C), basiventral epandrial seta present; apicoventral epandrial lobe well-developed, subquadrate, rounded or flared apically, with 1 lateral and 2 apical setae. Surstylus 2-lobed. Ventral lobe more or less digitiform with weak dorsal to mediodorsal preapical projection, apex with short, stout seta. Dorsal lobe larger than ventral lobe, with 1-2 strong mediodorsal setae and 1 preapical lateral seta, dorsal surface notched preapically with distinct to weakly developed keel-like projection across notch bearing a short seta (Fig. 11B). Postgonite with anteroventral portion weakly sclerotized, nearly membranous and bifurcate anteriorly; posterodorsal portion vestigial (e.g., *E. chalybea*, *E. violacea*, Fig. 12A,B), or well-developed and digitiform (e.g., *E. purpurata*, Fig. 11B). Proctiger brushes absent. Cercus (Figs. 11A, 12A,B) large, round to ovoid, pale with dark margin; apical and lateral margin jagged, *E. purpurata* and *E. chalybea* with well-developed digitiform projections apicomediaally (Figs. 11A, 12A), *E. chalybea* with strong, spatulate, apicoventral seta on first digitiform projection (Fig. 12A); lateral and/or apical margin with very long, fine setae. Hypandrium elongate and slender, trough-like, free laterally with membranous connection to epandrium basally; hypandrial arms connected to hypandrium; hypandrial apodeme well-developed, with knob-like apex. Sperm pump cylindrical; ejaculatory apodeme rod-like; basal sclerite of sperm pump well-developed, thick and heavily sclerotized, broadly V-shaped in dorsal view. Phallus elongate and slender, apical portion with weak rounded projection (e.g., *E. purpurata*, *E. violacea*, Figs. 11B, 12B), or finely serrate (e.g., *E. chalybea*, Fig. 12A). Female (Fig. 11D,E): T6, T7, S6 and S7 undivided; T8 and S8 divided medially, tergite and sternite fused anterolaterally. Furca narrow and weakly sclerotized or absent. T10 divided medially into hemitergites each bearing 4-5 acanthoporous spines along outer margin and a single inner medial spine (Fig. 11D), spines pointed to blunt apically. Upper lobe of cercus with short apical seta.

Etymology. The generic name is derived from the Greek *etheria* (hair) in reference to the long hairs on the male cercus, and the Greek *myia* (fly). The gender is feminine.

Geographical Distribution. *Ethiomyia* is Holarctic with two species (*E. purpurata* and *E. violacea*) in eastern North America, and *E. chalybea* in Europe.

Phylogenetic Relationships. This genus is the sister group to *Dolichopus*.

Material Examined.

Ethiomyia chalybea (Wiedemann), [PA]: 2♂♂syntypes, 1♀ syntype (ZMHB); 18♂♂,
20♀♀ (LEM)

Ethiomyia purpurata (Van Duzee), [NE]: ♂ holotype, 1♀ paratype, 2♂♂ (CNC); 74♀♀,
59♀♀ (LEM)

Ethiomyia violacea (Van Duzee), [NE]: 6♂♂, 3♀♀ (CNC)

GENUS *GYMNOPTERNUS* LOEW

(Fig. 13A-F)

Gymnopternus Loew, 1857: 10. Type species: *Dolichopus cupreus* Fallén [Palearctic], designation by Coquillett, 1910: 548. Listed as a subgenus (Pollet, 1990; Chandler, 1998) or synonym of *Hercostomus* (Dyte, 1975, 1976; Dyte and Smith, 1980; Negrobov, 1991; Poole, 1996).

Paragymnopternus Bigot, 1888a: xxiv. Unavailable name, genus proposed before 1931 without included nominal species. Listed as a synonym of *Gymnopternus* by Kertész (1909: 248).

Recognition. This genus is distinguished by its nearly straight wing vein M, R₄₊₅ and M parallel to subparallel, pleuron with a cluster of fine hairs in front of the posterior spiracle, fore tibia usually with an anterodorsal comb-like row of strong, often spine-like

setae. *Gymnopternus* is most similar to *Ethiomyia*, but can be distinguished by characters given above in the “Recognition” section for *Ethiomyia* and in the key.

Description. Head: Vertex not excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 1.8-3.0x wider than high, sides subparallel to slightly convergent anteriorly, bare or with 1-3 fine hairs in front of each vertical seta (e.g., *G. annulatus* Van Duzee, *G. barbatulus* Loew, *G. ohioensis* Robinson, *G. proprio facies* Robinson). Face concave, bare or with a few weak hairs, broad to narrow in male, sides strongly to weakly convergent below, narrowest at or above upper clypeal margin, usually broader in female with sides convergent to subparallel. Clypeus pubescent or bare, flat to weakly produced, sometimes strongly produced in female, lower margin straight or slightly emarginate, ending well above lower eye margin. Palp ovoid, rounded to subtriangular apically, with weak setae on apical half of outer surface, usually with distinct apical seta. Antenna: Scape subconical, with distinct acute medioventral process; pedicel short, medial margin occasionally strongly projecting into first flagellomere; first flagellomere variable, subquadrate, ovoid or subtriangular to triangular, sometimes acute and elongate in male (e.g., *G. subulatus* Loew), about as long as wide to over 2x longer than wide, usually more well-developed and elongate in male; arista dorsal, 2-segmented, second segment pubescent, nearly plumose in some species, occasionally bare with apical lamella in male (e.g., *G. nigribarbis* Loew, *G. mirificus* Melander). Lowermost postocular seta occasionally stronger. Postvertical setae slightly to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; usually with 6 dorsocentrals, occasionally with 5 (e.g. *G. flavus* Loew), penultimate pair strongly offset medially, posterior part of mesonotum in front of scutellum bare or with fine setae; 1 strong outer posthumeral, 1 weaker inner posthumeral, sometimes indistinct; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper part of propleuron with fine hairs, outer 2-3 hairs sometimes slightly stronger; lower part of propleuron with 1 strong prothoracic seta and fine hairs; pleural surface in front of posterior spiracle with at least 1 fine hair, usually with a cluster of 2-10 fine hairs; metepisternum with 1 or more fine hairs. Scutellum with 1 strong inner

seta and 1 minute outer seta on lateral margin, dorsal surface and margin bare or with fine hairs.

Legs: Pulvilli developed normally on all legs, occasionally slightly enlarged on fore tarsus of male (e.g., *G. exilis* Loew and *G. subdilatatus* Loew). Foreleg: Tibia usually with distinct anterodorsal comb-like row of strong, often spine-like setae, usually preceded by 1 strong anterodorsal seta; males of some species (e.g., *G. barbatulus*, *G. ohioensis*, *G. proprio facies*) with fine ventral hairs on tarsomeres 2-5. Midleg: Femur with 1 anterior preapical seta, some species with 1 strong posteroventral preapical in addition to terminal posteroventral preapical which is also sometimes developed (e.g., *G. annulatus*, *G. barbatulus*, *G. ohioensis*, *G. proprio facies*). Hindleg: Coxa with strong lateral seta near middle; femur with 1 anterodorsal preapical seta; tibia sometimes with apical, ridge-like or dentiform process posterodorsally in male; basitarsus shorter than second tarsomere, most species with distinct basiventral seta, males of most species with distinct dentiform process and/or sclerotized ridge posterobasally.

Wing: Brownish to hyaline. Costa of male occasionally swollen basally before R_1 (e.g., *G. brevicornis* (Staeger), *G. celer* (Meigen)); R_{2+3} straight to weakly convex; R_{4+5} nearly straight or with slight posterior curve in distal section, usually straightening just before apex; distal section of M beyond crossvein dm-cu usually with barely discernable sinuous bend before middle, nearly straight, or with slight posterior curve in distal section similar to that of R_{4+5} , ending near wing apex; R_{4+5} and M parallel to subparallel; crossvein dm-cu shorter than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare; S2 unmodified or weakly emarginate and membranous anteriorly and posteriorly; S3 weakly to strongly emarginate and membranous posteriorly; S4 strongly emarginate and membranous posteriorly to entirely divided medially; S5 mainly membranous with weakly sclerotized regions, often with weakly sclerotized lateral longitudinal bands, distal portion sometimes with narrow medial sclerotization, pair of eversible of glands often present (e.g. *G. aerosus* (Fallén), *G. assimilus* (Staeger), *G. cupreus*, *G. metallicus* (Stannius), see Couturier (1974)); S6 mainly membranous, weakly sclerotized along anterior and/or lateral margin; segment 7 forming well-developed peduncle; S8 heart-shaped, often with short, narrow stalk-like base, setose. Hypopygium (Fig. 13A-D) large, nearly as large as abdomen in some

species. Epandrium 1.5-1.8x longer than high, ovoid in lateral view; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe absent to moderately developed, basiventral epandrial seta usually present, occasionally absent (e.g., *G. annulatus*, *G. barbatulus*); apicoventral epandrial lobe well-developed, short and broad to elongate and slender, enlarged apically, with 1 strong lateral to lateroventral seta near or slightly beyond middle, 2 smaller preapical to apical setae, occasionally with a cluster of apical setae (e.g., *G. weemsi* Robinson). Surstylus 2-lobed. Ventral lobe variable, more or less digitiform, often with dorsal projections, apex usually tapered bearing a stout seta. Dorsal lobe laterally flattened, apex rounded to acute upcurved, often rugose laterally, usually with 1 strong dorsal to apical seta often on a tubercle, subequal to slightly longer than ventral lobe. Postgonite (Fig. 13B,C) with anteroventral portion usually very reduced to absent, occasionally developed, weakly sclerotized, flat, broad and emarginate anteriorly; posterodorsal portion well-developed and complex, usually broad, with ventral medial lobe and a pair of dorsolateral lobes, often with secondary dorsal and lateral membranous lobes, ventral medial lobe occasionally absent. Proctiger brushes absent. Cercus small to medium-sized, occasionally large, variable in shape ranging from subtriangular to ovoid to subrectangular to crescent-shaped, occasionally bilobate (*G. exilis*). Hypandrium simple, narrow, trough-like, mainly free laterally, fused to epandrium distinctly anterior to basiventral epandrial lobe/seta (Fig. 13D); hypandrial apodeme present, well-developed; hypandrial arms connected to hypandrium, sometimes also narrowly fused to epandrium laterally near basiventral epandrial seta/lobe. Sperm pump large, reniform; ejaculatory apodeme elongate, curved ventrally with acute apex, distinctly flattened laterally to rod-like, often weakly sclerotized and translucent, usually with long basal projections appressed to base of phallus (Fig. 13B), projections occasionally short (e.g., *G. petilus* Yang and Saigusa); basal sclerite of sperm pump variably sclerotized, nearly straight in dorsal view with lateral triangular projections. Phallus elongate and slender, apex weakly serrate and/or with dentiform process. Female (Fig. 13E,F): T6, T7, S6 and S7 undivided, T6 and T7 often with darkened proximal and lateral margins; T8 and S8 divided medially, tergite and sternite weakly fused anterolaterally. T10 divided medially into hemitergites each bearing 4 acanthoporous

spines along outer margin, spines rounded and flattened apically. Upper lobe of cercus usually with long apical seta, seta occasionally reduced (e.g., *G. barbatulus*)

Geographical Distribution. This genus is widespread and occurs in the Nearctic, Palaearctic and Oriental regions.

Phylogenetic Relationships. *Gymnopternus* forms the sister group to the *Dolichopus* + *Ethiomyia* clade based on the possession of a cluster of setae in front of the posterior spiracle. As discussed above (see “*Dolichopus* genus group”), *Gymnopternus* should be regarded as a genus and not placed in *Hercostomus* as a synonym or subgenus, as has been done by most Palaearctic workers.

Remarks. Most species of *Gymnopternus* have a distinctive anterodorsal row of strong setae on the fore tibia. A similar modification has also arisen in some members of the *Hercostomus longiventris* lineage (e.g., *H. fulvicaudis*, *H. tibialis*), *Hercostomus nigriplantis* (Stannius), *Allohercostomus rotundatus*, *Poecilobothrus aberrans*, and outside the Dolichopodinae in *Colobocerus alchymicus*.

Material Examined.

Gymnopternus aerosus (Fallén), [PA, OR]: 5 ♂♂, 4 ♀♀ (CNC); 5 ♂♂, 3 ♀♀ (LEM)

Gymnopternus annulatus Van Duzee, [NE]: 2 ♂♂ (CNC)

Gymnopternus barbatulus Loew, [NE]: 8 ♂♂, 4 ♀♀ (CNC)

Gymnopternus brevicornis (Staeger), [PA]: 3 ♂♂, 3 ♀♀ (LEM); 3 ♂♂, 1 ♀ (CNC)

Gymnopternus celer (Meigen), [PA]: 3 ♂♂, 3 ♀ (LEM); 2 ♂♂ (CNC)

Gymnopternus congruens (Becker), [OR]: 6 ♂♂, 4 ♀♀ (CNC); 2 ♂♂, 1 ♀ (LEM)

Gymnopternus crassicauda Loew, [NE]: 3 ♂♂, 2 ♀♀ (CNC)

Gymnopternus cupreus (Fallén), [PA]: 1 ♂ (CNC); 4 ♂♂, 1 ♀ (LEM)

Gymnopternus debilis Loew, [NE]: 3 ♂♂, 2 ♀♀ (CNC)

Gymnopternus exilis Loew, [NE]: 9 ♂♂, 2 ♀♀ (CNC)

Gymnopternus flavus Loew, [NE]: 5 ♂♂, 3 ♀♀ (CNC)

- Gymnopternus frequens* Loew, [NE]: 11 ♂♂, 5 ♀♀ (CNC)
- Gymnopternus humilus* Loew, [NE]: 12 ♂♂, 3 ♀♀ (CNC)
- Gymnopternus lividifrons* Van Duzee, [NE]: 2 ♂♂, 1 ♀ (CNC)
- Gymnopternus nigribarbis* Loew, [NE]: 8 ♂♂, 3 ♀♀ (CNC)
- Gymnopternus ohioensis* Robinson, [NE]: 2 ♂♂ (CAS)
- Gymnopternus opacus* Loew, [NE]: 6 ♂♂, 3 ♀♀ (CNC)
- Gymnopternus petilus* Yang and Saigusa, [PA]: 1 ♂ paratype, 1 ♀ paratype (ISNB)
- Gymnopternus propriofores* Robinson, [NE]: 5 ♂♂ (CAS)
- Gymnopternus scotias* Loew, [NE]: 1 ♂, 1 ♀ (CNC)
- Gymnopternus silvestris* Pollet, [PA]: 2 ♂♂, 2 ♀♀ (LEM)
- Gymnopternus spectabilis* Loew, [NE]: 7 ♂♂, 7 ♀♀ (CNC)
- Gymnopternus subdilatatus* Loew, [NE]: 6 ♂♂, 3 ♀♀ (CNC)
- Gymnopternus subulatus* Loew, [NE]: 7 ♂♂, 6 ♀♀ (CNC)
- Gymnopternus vockerothi* Robinson, [NE]: 6 ♂♂, 4 ♀♀ (CNC)
- Gymnopternus weemsi* Robinson, [NE]: 2 ♂♂ (CAS)

GENUS *HERCOSTOMUS* LOEW

(Figs. 14A-E, 15A-F, 16A-E)

Hercostomus Loew, 1857: 9. Type species: *Sybistroma longiventris* Loew [Palearctic], by original designation.

Phalacrosona Becker 1922b: 44. Type species: *Phalacrosona amoenum* Becker, designation by Dyte, 1975: 242. **syn. nov.**

Microhercostomus Stackelberg, 1949: 687 (as subgenus). Type species: *Hercostomus* (*Microhercostomus*) *dilatitarsis* Stackelberg, by original designation. Synonymized by Grichanov (1997) (see “Remarks”).

Steleopyga Grootaert and Meuffels, 2001: 208. Type species: *Steleopyga dactylocera* Grootaert and Meuffels, by original designation. **syn nov.**

Ahercostomus Yang and Saigusa, 2001c: 239 (as subgenus). Type species: *Hercostomus* (*Ahercostomus*) *jiangchenganus* Yang and Saigusa, by original designation (see “Remarks”).

New Combinations. The following new combinations are hereby established:

Hercostomus amoenus (Becker, 1922b) **comb. nov.** (*Phalacrosona*); *Hercostomus argyreus* (Wei and Lui, 1996) **comb. nov.** (*Phalacrosona*); *Hercostomus briarea* (Wei and Lui, 1996) **comb. nov.** (*Phalacrosona*); *Hercostomus dactylocera* (Grootaert and Meuffels, 2001) **comb. nov.** (*Steleopyga*); *Hercostomus fulgidipes* (Becker, 1922b) **comb. nov.** (*Phalacrosona*); *Hercostomus hubeiensis* (Yang, 1998a) **comb. nov.** (*Phalacrosona*); *Hercostomus imperfectus* (Becker, 1922b) **comb. nov.** (*Phalacrosona*); *Hercostomus postiseta* (Yang and Saigusa, 2001b) **comb. nov.** (*Phalacrosona*); *Hercostomus zygolipes* (Grootaert and Meuffels, 2001) **comb. nov.** (*Steleopyga*).

Recognition. *Hercostomus* sensu lato, as traditionally defined, is a polyphyletic assemblage of species with wing vein M straight or weakly bent anteriorly beyond crossvein dm-cu, R₄₊₅ and M parallel or convergent and lacking the defining features of the other dolichopodine genera. *Hercostomus* sensu lato can be recognized by the following combination of characters: vertical setae stronger than postverticals; clypeus of male not strongly bulging, lower margin usually straight and not reaching lower eye margin; scape and pedicel normally developed; arista simple with short to moderately developed pubescence, rarely with apical lamella; eyes separated at lower margin; proboscis and palps usually short, sometimes slightly elongated; thorax lacking distinct dark spot above notopleuron; usually with 6 dorsocentral setae; sutural and presutural setae present; pleural surface in front of posterior spiracle bare; fore tarsus usually simple, mid and hind femur usually with 1 preapical seta; hind basitarsus usually without dorsal setae; wing vein M beyond crossvein dm-cu with weak sinuous anterior bend or straight; R₄₊₅ and M convergent or parallel; male genitalia with sperm pump rounded or

cylindrical, not folded back on itself, postgonite usually lacking medioventral projection, apicoventral epandrial lobe not greatly elongate and setose; female terminalia with T6, T7, S6, S7 undivided, T8 and S8 separate anterolaterally. *Hercostomus* in its strictest sense (i.e. the lineage including the type species *H. longiventris*) can be recognized by the following combination of characters: vein M beyond crossvein dm-cu with weak sinuous anterior bend, fore tarsus of male simple or modified, mid femur with 1 strong posterior preapical about even with anterior preapical, hypopygium with basiventral epandrial lobes and hypandrium forming a complex of entangled asymmetrical lobes.

Description (based on *H. longiventris* lineage). Head: Vertex not excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2.0-4.2x wider than high, sides convergent anteriorly. Face narrow to broad in male, sides converging below, usually broader in female with sides weakly converging; clypeus flat to weakly produced in male, usually more strongly produced in female, lower margin usually straight and ending above lower eye margin, rarely strongly produced and beak-like in lateral view with lower margin angled outward and rounded below, projecting to or beyond lower eye margin (e.g., *H. amoenus*). Palp usually small, ovoid, with fine setae on outer surface, 1 distinct to strong apical seta. Proboscis occasionally enlarged (e.g., *H. amoenus*). Antenna: Scape short to slightly elongated, subconical, with weak to well-developed acute medioventral process; pedicel short, occasionally with medial margin strongly projecting into first flagellomere (e.g., *H. dactylocera*); first flagellomere variable, subtriangular to subrectangular or ovoid, often shorter in female; arista dorsal, 2-segmented, distal segment with short pubescence, arista rarely arising from preapical dorsal projection of first flagellomere (e.g., *H. dactylocera*). Postvertical setae usually stronger than uppermost pair of postoculars, occasionally reduced in male and subequal to postverticals (e.g., *H. amoenus*).

Thorax: Setae usually well-developed, occasionally reduced in male (e.g., *H. amoenus*). Acrostichals biserial; 6 dorsocentrals, fifth pair aligned or weakly offset medially; 1 strong outer posthumeral, 1 weak inner posthumeral, sometimes indistinct; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with fine, often sparse hairs; lower part propleuron with 1 strong prothoracic

seta; pleural surface in front of posterior spiracle bare; metepisternum bare or with 1 or more fine hairs. Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin, sometimes with a few marginal hairs.

Legs: Pulvilli developed normally on all legs. Foreleg: Tibia occasionally with anterodorsal comb-like row of setae (e.g., *H. fulvicaudis*, *H. tibialis*); femur sometimes with distinct posterior preapical; tarsus of male unmodified or modified with tarsomeres 1 and 2 slender, sometimes laterally flattened (e.g., *H. chetifer*), tarsomere 2 occasionally with curved medial setae (e.g., *H. enghoffi* Grichanov), tarsomeres 3-5 usually with a crest of dorsal setae, tarsomere 3 usually flattened and broad, tarsomeres 4 and 5 flattened and broad or slender, tarsomere 4 occasionally with dorsal projection (e.g., *H. patellitarsis* (Parent)), tarsomere 5 occasionally elongate (e.g., *H. enghoffi*). Midleg: Femur with 1 anterior or anterodorsal preapical seta, occasionally lost in male (e.g., *H. amoenus*), 1 posterior preapical, about even with anterior preapical, in addition to terminal posteroventral preapical seta which is sometimes developed, occasionally with long setae ventrally (e.g., *H. fulvicaudis*, *H. imperfectus*); tibia of male sometimes with specialized hairs or spines (e.g., *H. amoenus*); tarsus of male occasionally modified, with long fine hairs (e.g., *H. amoenus*). Hindleg: Coxa with strong lateral seta near or slightly above middle; femur usually with 1 strong anterodorsal preapical seta, occasionally with a preapical anteroventral row of 4 weaker setae (e.g., *H. dactylocera*, *H. zygolipes*); tibia occasionally with dorsal comb-like row of setae (e.g., *H. fulvicaudis*, *H. tibialis*), male with distinct posteroapical projection, occasionally large (e.g., *H. enghoffi*, *H. fulvicaudis*, *H. tibialis*); basitarsus shorter than second tarsomere, usually with 3-4 ventral setae, occasionally with distinct basiventral seta (e.g., *H. krivosheinae* Grichanov, *H. dactylocera*), or tuft of short, flattened setae (e.g., male *H. amoenus*), male with pointed or ridge-like process posterobasally, occasionally bifurcate (e.g., *H. enghoffi*).

Wing: Greyish to brownish, sometimes with brown infuscation anteriorly in males (e.g., *H. amoenus*). Costa occasionally thickened in male (e.g., *H. amoenus*); R_{2+3} relatively straight, sometimes with weak anterior bend near apex; R_{4+5} straight or with weak to distinct posterior curve in apical portion; distal section of M beyond crossvein dm-cu with weak sinuous anterior bend before middle, ending slightly before wing apex, bend occasionally stronger in male (e.g., *H. amoenus*); R_{4+5} and M weakly to distinctly

convergent distally, sometimes widely spaced in male (e.g., *H. amoenus*); crossvein dm-cu distinctly longer to distinctly shorter than distal section of CuA₁, rarely absent (e.g., *H. zygolipes*).

Abdomen: Usually subconical, cylindrical in males of some species (e.g., *H. longiventris*, *H. amoenus*). Male: T6 bare; S2 unmodified to weakly sclerotized; S3 weakly sclerotized, often emarginate and membranous posteriorly; S4 usually weakly sclerotized, emarginate and membranous posteriorly or divided and membranous medially; S5 mainly membranous, sometimes with medial Y-shaped sclerite, occasionally with a pair of internal glandular structures (e.g., *H. longiventris*); S6 mainly membranous, sclerotized along anterior margin and sometimes along lateral margin; segment 7 forming well-developed peduncle, often elongate; S8 usually ovoid to teardrop or heart-shaped, setose, occasionally pedunculate with a cluster of thick spines near base of left margin (e.g., *H. dactylocera*, *H. zygolipes*, Fig. 16D). Hypopygium (Figs. 14A-C, 15A-D, 16A-C,E): Usually asymmetrical, occasionally somewhat twisted dextrally on longitudinal axis (e.g., *H. dactylocera*). Epandrium about 1.4-2.3x longer than high; foramen usually mid-lateral to anterolateral, usually well-separated from base of cerci, sometimes dorsolateral and close to base of cerci (e.g., *H. longiventris*, Fig. 14A); basiventral epandrial lobes shifted ventrally and lying beside hypandrium, right and left lobes asymmetrical, apex of one or both lobes often with contrasting, pointed or knob-like tip (modified basiventral epandrial seta) (Figs. 14A-C, 15A,C,D), sometimes absent or indistinct, left basiventral epandrial lobe sometimes bifurcate; apicoventral epandrial lobe variable, elongate to weakly developed, usually with 3 setae, sometimes dorsoventrally flattened (e.g., *H. longiventris*, Fig. 14B,C), epandrium occasionally with textured, sac-like accessory lobe near base of apicoventral lobe and ventral surstylar lobe (e.g., *H. chetifer*, *H. amoenus* Fig. 15A,D). Surstylus 2-lobed. Ventral lobe variable in shape, often digitiform, usually with thickened or flattened mediodorsal seta, lobe occasionally bifurcate with flattened seta arising apically on dorsal fork (e.g., *H. longiventris*, Fig. 14B). Dorsal lobe variable in shape, with strong dorsal to dorsoapical seta, which is occasionally flattened. Postgonite with anteroventral portion weakly to moderately sclerotized, occasionally somewhat flattened laterally (e.g., *H. longiventris*), sometimes absent; posterodorsal portion well-developed, often strongly upturned (e.g., *H. longiventris*, Fig. 14B),

sometimes with well-sclerotized medioventral projection, projection often textured, occasionally bifurcate (e.g., *H. amoenus*, Fig. 15B). Proctiger brushes absent. Cerci usually arising near apex of epandrium, sometimes arising preapically (e.g., *H. longiventris*, Fig. 14A), variable in shape, often with well-developed basolateral lobe, occasionally with thick setae on apical margin (Figs. 14A, 16A,B). Hypandrium variable in shape, often asymmetrical, laterally flanked by basiventral epandrial lobes and usually fused with lobes basally, forming an asymmetrical complex (Figs. 14C, 15B,D, 16A,B,E); hypandrial apodeme present or absent, sometimes well-developed (e.g., *H. longiventris*, Fig. 14B); hypandrial arms usually connected to hypandrium, sometimes reduced to narrow bands, occasionally absent (e.g., *H. chetifer*, *H. dactylocera*, Fig. 16C). Sperm pump spherical, usually small; ejaculatory apodeme usually short and rod-like, sometimes flattened laterally (e.g., *H. longiventris*), occasionally very reduced (e.g., *H. dactylocera*, Fig. 16C); basal sclerite of sperm pump usually weakly developed, straight or V-shaped in dorsal view, occasionally forming elongate rod (e.g., *H. dactylocera*, Fig. 16C). Phallus usually long and slender (Figs. 14B, 15B), occasionally thick with broad flattened apex (e.g., *H. dactylocera*, Fig. 16C), sometimes with weak preapical dentiform projections (e.g., *H. krivosheinae*). Female (Figs. 14D,E, 15E,F): T6, T7, S6 and S7 undivided; T8 divided medially, S8 undivided, sometimes very weakly sclerotized, tergite and sternite not fused anterolaterally; T10 divided medially into hemitergites each bearing 4-5 acanthoporous spines, apex of spines pointed. Upper lobe of cercus with short apical seta.

Geographical Distribution. *Hercostomus* sensu lato is known from the Holarctic, Afrotropical, Oriental, Australasian (New Zealand) and Neotropical regions. Robinson (1970b) considered that the Neotropical species likely belong to other genera. Most *Hercostomus* species are known from the Palaearctic. *Hercostomus* sensu stricto (the *H. longiventris* lineage) occurs in the Holarctic, Afrotropical and Oriental regions.

Phylogenetic Relationships. As demonstrated in the cladistic analysis (Figs. 1, 4) *Hercostomus* sensu lato is polyphyletic with species related to *Dolichopus*,

Parahercostomus and *Poecilobothrus*. The *Hercostomus longiventris* lineage is most closely related to *Sybistroma*.

Remarks. In addition to Grichanov's (1999a) Afrotropical species group 2, *H. chetifer*, *H. fulvicaudis*, *H. tibialis*, and species formerly in *Steleopyga* and *Phalacrosoma* (except "*Phalacrosoma*" *zhejiangense* Yang and "*Phalacrosoma*" *sichuanense* Yang and Saigusa, see below), the following species also appear to be part of the *Hercostomus longiventris* lineage based on the examination of genitalic figures and descriptions from the literature: *H. absimilis* Yang and Grootaert, *H. acutangulatus* Yang and Saigusa, *H. acutatus* Yang and Yang, *H. apicilaris* Yang and Grootaert, *H. apiciniger* Yang and Grootaert, *H. basiflavus* Yang, *H. beijingensis* Yang, *H. bigeminatus* Yang and Grootaert, *H. bispinifer* Yang and Saigusa, *H. calcaratus* Stackelberg, *H. concavus* Yang and Saigusa, *H. crassiseta* Yang and Saigusa, *H. curvispinosus* Yang and Saigusa, *H. curvispinus* Yang and Saigusa, *H. cuspidiger* Yang and Saigusa, *H. dissectus* Yang and Saigusa, *H. dissimilis* Yang and Saigusa, *H. emeiensis* Yang, *H. erectus* Yang and Grootaert, *H. exacutus* Wei, *H. flavicans* Grootaert and Meuffels, *H. flaviscapus* Yang and Saigusa, *H. flaviscutellum* Yang, *H. guizhouensis* Wei, *H. henanus* Yang, *H. jindinganus* Yang and Saigusa, *H. longifolius* Yang and Saigusa, *H. longisetus* Yang and Grootaert, *H. loushanguanensis* Yang and Saigusa, *H. luoshanensis* Yang and Grootaert, *H. proctus* Wei, *H. projectus* Yang and Saigusa, *H. prolongatus* Yang, *H. proxilus* Wei, *H. quadratus* Yang and Grootaert, *H. serrulatus* Yang and Grootaert, *H. sichuanensis* Yang, *H. spiniger* Yang, *H. spinitarsis* Yang and Saigusa, *H. subnovus* Yang and Yang, *H. wudangshanensis* Yang, *H. xanthodes* Yang and Grootaert, *H. xishuangbannensis* Yang and Grootaert, *H. yadonganensis* Yang, *H. zunyianus* Yang and Saigusa.

Phalacrosoma was erected for a group of three autapomorphic species with silvery colour, reduced setation, broad face and clypeus with the lower margin rounded and extending beyond the lower eye margin, and a modified fore tarsus in males. Becker (1922b) apparently did not notice the setae on the dorsal surface of the scape and placed the genus in the Hydrophorinae. Following an examination of the types, Negrobov (1980) placed the genus in Dolichopodinae and this classification has been followed by subsequent authors (e.g., Ulrich, 1981; Yang et al. 2001). The male genitalia of the type

species of *Phalacrosoma* are remarkably similar to that of *H. chetifer* and this genus is part of a species group within the *H. longiventris* lineage that does not warrant generic status. Two of the species recently described in *Phalacrosoma*, i.e. “*Phalacrosoma*” *zhejiangense* and “*Phalacrosoma*” *sichuanense*, do not appear to belong to the *H. longiventris* lineage. “*Phalacrosoma*” *zhejiangense* appears to be part of the *Poecilobothrus* + *Parahercostomus* + “*Hercostomus*” *straeleni* clade based on the genitalic figure in Yang (1997b). The placement of “*Phalacrosoma*” *sichuanense* is currently unclear. Rather than transferring these two species to *Hercostomus*, I have left them as unplaced until further phylogenetic studies can ascertain their position.

Steleopyga was established for two Southeast Asian species known only from males. Although Grootaert and Meuffels (2001) described *Steleopyga* as a separate genus they indicated that it was part of the “*Hercostomus* complex”. The genus was based primarily on the possession of a cluster of spines on sternite 8 and a preapical anteroventral row of 4 setae on the hind femur. Like *Phalacrosoma*, *Steleopyga* is an autapomorphic species group within the *H. longiventris* lineage. The hypopygium of *Hercostomus dactylocera* represents the most complex and extreme case of male genitalic asymmetry encountered in this study. This asymmetry is further complicated by the complete loss of the hypandrial arms which often serve as important landmark structures in homologizing the hypandrium. These two factors resulted in some uncertainty regarding the limits of the hypandrium and basiventral epandrial lobes (i.e. characters 63 and 65). Despite these uncertainties, it is apparent that these elements form a complex of entangled asymmetrical lobes (character 64: 1, Figs. 16A,B,E), which I interpret to be homologous with the condition observed in the other members of the *Hercostomus longiventris* lineage.

The recently erected subgenus *Ahercostomus* (Yang and Saigusa, 2001c) and the recently synonymized subgenus *Microhercostomus* (Grichanov, 1997) are provisionally listed as synonyms of *Hercostomus* until a more extensive analysis can determine their phylogenetic position.

Dasyarthrus was synonymized with *Hercostomus* by Becker (1917-1918); however, the type species, *Gymnopternus inornatus* Loew, and the closely related species *Hercostomus lorifer* Mik, are clearly congeneric with *Sybistroma* based on the

symmetrical, digitiform basiventral epandrial lobes and the elongate and setose apicoventral epandrial lobes. Accordingly, these species have been transferred to *Sybistroma* and *Dasyarthrus* is listed as a junior synonym of *Sybistroma*. *Hercostomus caudatus* (Loew) also appears to be referable to *Sybistroma* based on figures in Becker (1917-1918) and Parent (1938); however, I have not examined specimens of this species and cannot confirm this generic assignment at present.

Although this study has confirmed that *Hercostomus* is a polyphyletic assemblage and has provided a phylogenetic framework for future studies, the analysis itself is not extensive enough to resolve all of the associated problems with this group. As such, *Hercostomus* will have to continue to serve as holding genus for many of the species listed below until more detailed phylogenetic work is done.

In addition to the species included in Grichanov's Afrotropical *Hercostomus* group 1, the following examined species appear to be referable to the *Poecilobothrus* + *Parahercostomus* + "*Hercostomus*" *straeleni* clade: *H. fuscipennis* (Meigen), *H. germanus* (Wiedemann), *H. nigripennis* (Fallén), *H. gracilis* (Stannius), *H. nigriplantis*, *H. sahlbergi* (Zetterstedt) and *H. vockerothi* Assis Fonseca. The following species (not examined) appear to belong to this lineage based on genitalic figures in Parent (1938): *Hercostomus argentifrons* Oldenberg, *Hercostomus conformis* Loew, *Hercostomus flavipes* von Roder, *Hercostomus laufferi* Strobl, *Hercostomus lichtwardti* Villeneuve, *Hercostomus pandellei* Parent, *Hercostomus rostellatus* (Loew). As noted above, "*Phalacrosona*" *zhejiangense* also appears to be referable to this clade.

The following examined species may be more closely related to *Sybistroma*: *H. cachae* Harmston and Knowlton, *H. nanus* (Macquart), *H. orbicularis* Harmston, *H. parvilamellatus* (Macquart) and *H. truncatus* Harmston and Knowlton. *Hercostomus nanus* and *H. parvilamellatus* seem close to *Sybistroma nodicornis* in the structure of the phallus and sperm pump, but the basiventral epandrial lobe-hypandrium complex is more extensively fused and not symmetrical. Several additional species currently placed in *Hercostomus* (not examined) also seem to be referable to *Sybistroma* based on genitalic figures in the literature (i.e. all apparently have elongate, symmetrical basiventral epandrial lobes): *H. curvatus* Yang and Saigusa, *H. curvatus* Yang and Saigusa, *Hercostomus digitatus* Yang, *H. flavimarginatus* Yang, *H. incisus* Yang and Saigusa, *H.*

longus Yang and Saigusa, *H. nudiusculus* Yang, *H. polleti* Yang and Saigusa, *H. shennongjiensis* Yang and *H. sublongus* Yang and Saigusa. Many of the remaining examined species do not show obvious affinities to any of the clades in the analysis.

Material Examined.

- Hercostomus additus* Parent, [PA]: 2♂♂ syntypes, 6♀♀ syntypes (MNHN)
- Hercostomus amoenus* Becker, [OR]: 2♂♂, 2♀♀ (LEM)
- Hercostomus argentifacies* Parent, [AU]: 2♂♂, 1♀ (CNC); 1♂, 1♀ (BMNH)
- Hercostomus argyropus par* Parent, [AF]: 3♂♂, 1♀♀ (ISNB)
- Hercostomus aurifacies* Parent, [AU]: 1♂, 1♀ (BMNH)
- Hercostomus aurifer* (Thompson), [NE]: 3♂♂, 2♀♀ (CAS)
- Hercostomus blagoderovi* Grichanov, [AF]: 1♂ (CNC)
- Hercostomus cachae* Harmston and Knowlton, [NE]: 1♂ (CAS)
- Hercostomus chetifer* (Walker), [OR]: 5♂♂, 1♀ (CNC); 4♂♂ paratypes, 1♀ paratype of *Hercostomus ornatus* (Van Duzee) (CAS);
- Hercostomus congoensis* (Curran), [AF]: 3♂♂, 1♀ (ISNB); 1♂ (CNC)
- Hercostomus curvativus* Yang and Saigusa, [PA]: 2♂♂ paratypes (ISNB)
- Hercostomus dactylocera* (Grootaert and Meuffels), [OR]: 1♂ paratype (ISNB)
- Hercostomus dissectus* Yang and Saigusa, [PA]: 1♂ paratype (ISNB)
- Hercostomus enghoffi* Grichanov, [AF]: 1♂ paratype (ISNB)
- Hercostomus eronis* Curran, [AF]: 1♂ (ISNB)
- Hercostomus fugax* (Loew), [PA]: 7♂♂, 4♀♀ (CNC); 2♂♂ (LEM)
- Hercostomus fulvicaudis* (Haliday), [PA]: 1♂ (LEM)
- Hercostomus fuscipennis* (Meigen), [PA]: 1♂, 1♀ (CAS)
- Hercostomus germanus* (Wiedemann), [PA]: 4♂♂, 2♀♀ (CNC); 1♂, 1♀ (LEM)
- Hercostomus gracilus* (Stannius), [PA]: 3♂♂, 3♀♀ (CNC)
- Hercostomus krivosheinae* Grichanov, [AF]: 2♂♂ paratypes (BMNH)
- Hercostomus longiventris* (Loew), [PA]: 2♂♂, 2♀♀ (CNC)
- Hercostomus nanus* (Macquart), [PA]: 3♂♂, 3♀♀ (LEM)
- Hercostomus nigripennis* (Fallén), [PA]: 1♂, 1♀ (CNC); 1♂, 1♀ (LEM)

- Hercostomus nigriplantis* (Stannius), [PA]: 2♂♂, 2♀♀ (CNC); 1♂, 1♀ (LEM)
- Hercostomus occidentalis* Cole, [NE]: 3♂♂, 2♀♀ (CAS)
- Hercostomus orbicularis* Harmston, [NE]: 2♂♂ (CAS)
- Hercostomus ovchinnikovae* Grichanov, [AF]: 4♂♂ (MRAC)
- Hercostomus parvilamellatus* (Macquart), [PA]: 7♂♂ (LEM)
- Hercostomus regularis* Becker, [OR]: 1♂, 1♀ (DEI)
- Hercostomus sahlbergi* (Zetterstedt), [PA]: 4♂♂, 2♀♀ (CNC)
- Hercostomus straeleni* Vanschuytbroeck, [AF]: 2♂♂ paratypes, 2♀♀ (ISNB); 1♂ (BMNH)
- Hercostomus strictilamellatus* Parent, [AF]: 3♂♂ paratypes, 2♀♀ paratypes (ISNB)
- Hercostomus syncolus* Steyskal, [NE]: 4♂♂, 2♀♀ (CNC)
- Hercostomus tibialis* (Van Duzee), [NE]: 8♂♂, 10♀♀ (CAS)
- Hercostomus tobiassi* Grichanov, [AF]: 2♂♂ paratypes, 1♀ paratype (BMNH)
- Hercostomus truncatus* Harmston and Knowlton, [NE]: 4♂♂, 2♀♀ (CAS)
- Hercostomus ultimus* Parent, [AF]: 1♂, 1♀ (ISNB); 1♂, 1♀ (MRAC)
- Hercostomus unicolor* Loew, [NE]: 9♂♂, 9♀♀ (CNC)
- Hercostomus utahensis* Harmston and Knowlton, [NE]: 1♂ (CAS)
- Hercostomus vivax* (Loew), [PA]: 6♂♂, 3♀♀ (CNC)
- Hercostomus vockerothi* Assis Fonseca, [PA]: 4♂♂, 3♀♀ (CNC)
- Hercostomus wasatchensis* Harmston and Knowlton, [NE]: 1♂ (CAS)
- Hercostomus wittei* Grichanov, [AF]: 2♂♂ paratypes (ISNB)

GENUS *METAPARACLIUS* BECKER

(Fig. 17A-F)

Metaparaclius Becker, 1922b: 33. Type species: *Metaparaclius subapicalis* Becker [Australasian], by monotypy.

Recognition. *Metaparaclius* can be distinguished by the distal part of M which is strongly bent anteriorly, convex and strongly convergent with R_{4+5} , scape of male enlarged and thickened, pedicel reduced, arista subapical, bare and elongate with an apical lamella. Male and female *M. australiensis* are further distinguished by a dark black spot above the notopleuron and 2 strong setae on the proepisternum in front of the anterior spiracle.

Description. Head: Vertex not excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2x wider than high, concave near base of antennae especially in male, sides subparallel. Face and clypeus very narrow in male, broad in female; clypeus flat, triangular in male, strongly and evenly produced in female, lower margin straight, not reaching lower eye margin. Palp and proboscis smaller in male; palp ovoid with subtriangular apex, with fine setae on apical third and 1 stronger apical seta. Antenna: Male scape greatly enlarged, elongate and thick, with weak medioventral process, *M. australiensis* with 6-8 stronger setae on apicodorsal margin in addition to usual dorsal setae; pedicel reduced and funnel-shaped; first flagellomere conical or subtriangular, 2-2.5x as long as wide, pointed apically, with weak dorsal seta in *M. australiensis*; arista subapical, 1 or 2 segmented, basal segment very short when present, distal segment elongate, bare, with apical lamella. Female scape short, subconical, setose dorsally, with well-developed acute medioventral process; pedicel short; first flagellomere rounded; arista dorsal. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 5-6 dorsocentrals, aligned; 1 strong outer posthumeral, 1 weaker inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. *Metaparaclius australiensis* with distinct dark metallic spot above notopleuron. Upper part of propleuron of *M. australiensis* with 2 strong black setae and several fine hairs; lower part of propleuron with 1 strong prothoracic seta and fine hairs; pleural surface in front of posterior spiracle bare; metepisternum with fine hairs. Scutellum with 1 strong inner seta and a weak outer seta on lateral margin.

Legs: Pulvilli developed normally on all legs. Midleg: Femur with 1 anterodorsal preapical seta. Hindleg: Coxa with strong lateral seta near middle; femur with 1 anterodorsal preapical seta; tibia of male *M. australiensis* with weak ridge-like process

posteroapically; basitarsus shorter than second tarsomere, with 1-2 short anterior setae, 4-5 short ventral setae, male *M. australiensis* with bulging dentiform projection posterobasally.

Wing: R₂₊₃ nearly straight; R₄₊₅ straight with posterior bend apically; distal section of M beyond crossvein dm-cu with obtuse to 90° anterior bend, arcuate and strongly convergent with R₄₊₅, ending well before wing apex; crossvein dm-cu equal to or slightly longer than distal portion of CuA₁.

Abdomen: Subconical. Male: T6 bare; S2 unmodified; S3 weakly emarginate posteriorly; S4-S6 mainly membranous, S4 and S6 weakly sclerotized along lateral and anterior margins; segment 7 forming elongate peduncle, about as long as segments 5 and 6 combined; S8 heart-shaped, narrowed proximally, setose. Hypopygium (Fig. 17A-D): Epandrium subrectangular in lateral view, about 1.7x as long as high; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe not developed, basiventral epandrial seta near apex of ventral margin, slightly anterior to apicoventral epandrial lobe; apicoventral epandrial lobe well-developed with subquadrate ventral portion bearing 2 strong setae, dorsal portion rounded, keel-like, with seta on ventral surface. Surstylus 2-lobed, both lobes about equal in length, long, thin. Ventral lobe digitiform with 1 short, weak dorsal seta near middle and several setae near apex. Dorsal lobe with apex enlarged and laterally flattened, dorsal surface emarginate preapically with keel-like projection. Postgonite with anteroventral portion well-sclerotized, laterally flattened (Fig. 17B), with anterodorsal and ventral margin flared laterally; posterodorsal portion well-developed, widened and tripartate apically (Fig. 17D). Proctiger brushes absent. Cercus large, oval to subquadrate, *M. australiensis* with fine branched setae on apical margin (Fig. 17A). Hypandrium elongate, thin, free laterally, connected to epandrium basiventrally; hypandrial arm not connected to hypandrium, fused to ventral margin of epandrium (Fig. 17B); hypandrial apodeme well-developed, hypandrial arms fused with apicoventral epandrial margin. Sperm pump small; ejaculatory apodeme well-developed, laterally flattened, basal sclerite of sperm pump U-shaped in dorsal view, with long, thin lateral arms. Phallus thin, apical portion with 2 weak dentiform processes. Female (Fig. 17E,F): T6, S6, T7 and S7 undivided, T8 and S8

divided medially, tergite and sternite not fused anterolaterally. Furca present, narrow and triangular. T10 divided medially into hemitergites each bearing 4 acanthoporous spines.

Geographical Distribution. *Metaparaclius* includes two Australasian species, *M. subapicalis* from Papua New Guinea and *M. australiensis* from Queensland, Australia.

Phylogenetic Relationships. Until additional specimens of the type species, *M. subapicalis*, are identified (see “Remarks”), the systematic position and monophyly of this genus will remain ambiguous. Based on the cladistic analysis, *Metaparaclius australiensis* is related to a lineage of Oriental species including “*Polymedon*” *inopinatus*, *Paraclius abbreviatus*, *P. pilosellus* and related species (see “*Tachytrechus* genus group” section above). *Metaparaclius australiensis* also appears to be closely related to the Australasian species *Paraclius neglectus*, which has a similarly modified postgonite, similar overall genitalic structure and several strong setae on the upper part of the propleuron.

Remarks. Becker deposited the unique male holotype of *Metaparaclius subapicalis* in the Hungarian Museum, which was destroyed during the Hungarian Revolution of 1956 (M. Foldvari, pers. comm.). No other specimens are known.

Material Examined.

Metaparaclius australiensis Parent, [AU]: ♂ holotype (BMNH); 5 ♂♂, 4 ♀♀ (CNC);
3 ♂♂, 3 ♀♀ (LEM)

GENUS *MUSCIDIDEICUS* BECKER

(Fig. 18A-E)

Muscidideicus Becker, 1917: 268. Type species *Dolichopus praetextatus* Haliday [Palearctic], by original designation.

Muscideicus Parent, 1938: 265. Type species *Dolichopus praetextatus* Haliday, automatic. Unjustified emendation.

Recognition. This genus can be distinguished by the following combination of characters: abdomen dorsoventrally flattened, 7 dorsocentral setae, setation of mid and hind hind femora well-developed, nearly as strong as preapicals, R_{4+5} and M parallel and sinuous, upper and lower part of propleuron with long dense hair, prothoracic seta pale or brown.

Description. Head: Distinctly wider than high in frontal view. Vertex not excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2x wider than high, sides converging anteriorly. Face and clypeus narrow in male, broad in female. Face concave in both sexes, concavity more pronounced in female; narrowest near middle in male, parallel sided in female. Clypeus weakly produced, lower margin straight, not reaching lower eye margin. Palp small, subtriangular, with weak setae on outer surface. Antenna: Scape short, subconical, with distinct acute medioventral process; pedicel short, with apical ring of fine setae; first flagellomere ovoid with subtriangular apex; arista short, dorsal, 2-segmented; distal segment bare. Lower postocular setae finer and slightly longer, postgenal area behind lower postoculars sometimes with dense setae. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Broad; acrostichals biserial; 7 dorsocentrals, sixth strongly offset medially; 1 strong outer posthumeral, 1 slightly weaker inner posthumeral, with adjacent row of 2-4 weaker setae; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalar; 1 postalar. Upper and lower part of propleuron with a cluster of long dense hairs; lower part of propleuron with 1 strong, pale to brown prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum with 1-2 hairs. Scutellum with 1 strong inner seta and 1 weaker outer seta on lateral margin.

Legs: Pulvilli well-developed on all legs. Femora with well-developed clothing setae, nearly as long as preapicals. Foreleg: Tarsus short, tarsomeres 2-5 subequal in length, male with dense pile ventrally. Midleg: Femur with 1-2 anterodorsal preapical setae; 1 distinct posterior preapical seta in addition to weak terminal posteroventral seta,

sometimes weak. Hindleg: Coxa with strong lateral seta near middle; femur with strong setae dorsally, 1 anterodorsal preapical seta slightly stronger than surrounding setae; tibia of male with dentiform process posteroapically; basitarsus slightly shorter than second tarsomere, with a few weak to indistinct ventral setae, male with dentiform process posterobasally.

Wing: Hyaline, male with brown infuscation apically, venation somewhat pale. R_{2+3} nearly straight; distal portion of R_{4+5} and M of male subparallel with pronounced convex curve; R_{4+5} of female nearly straight with posterior bend in distal section; distal section of M beyond crossvein dm-cu of female with weak sinuous bend near middle, weakly convex beyond bend, weakly convergent with R_{4+5} ; M ending slightly before wing apex in both sexes; crossvein dm-cu distinctly shorter than distal section of CuA_1 .

Abdomen dorsoventrally flattened. Male: T6 bare; S2-3 unmodified; S4 widely emarginate posteriorly; S5 mostly membranous, weakly sclerotized laterally, with narrow sclerite posteromedially; S6 mostly membranous, weakly sclerotized at anterior margin; segment 7 forming well-developed peduncle; S8 subtriangular, setose. Hypopygium (Fig. 18A-C) large. Epandrium longer than high, with strong dorsolateral bulge in apical half; foramen positioned laterally just before middle, well-separated from base of cerci; basiventral epandrial lobe weakly developed, with weak basiventral epandrial seta; apicoventral epandrial lobe well-developed, elongate, projecting laterally and bent dorsally, with 3 setae on apical half. Surstylus 2-lobed. Ventral lobe large and bulbous, with thick, digitiform process apically and a pair of rounded projections dorsally. Dorsal lobe longer than ventral lobe; wide, laterally flattened, with dorsal projection bearing a pair of thick curved setae. Postgonite with weakly sclerotized anteroventral portion; posterodorsal portion not developed (Fig. 18B). Proctiger brushes absent. Cercus subquadrate. Hypandrium more or less symmetrical in ventral view, apex pointed, base broad with narrow medial sclerite, free, not fused to epandrium laterally or basally; hypandrial apodeme present, well-developed; hypandrial arms connected to hypandrium. Sperm pump cylindrical; ejaculatory apodeme rod-like; basal sclerite of sperm pump heavily sclerotized, broadly V-shaped in dorsal view. Phallus slender with dentiform process at distal third. Female (Fig. 18D,E): T6, T7, S6 and S7 undivided; T8 and S8 divided medially, tergite and sternite fused anterolaterally forming a narrow sclerite (Fig.

18E). Furca present. T10 divided medially into hemitergites each bearing 5-7 acanthoporous spines, medial spines flattened and rounded apically. Upper lobe of cercus lacking strong apical seta.

Geographical Distribution. This monotypic genus is restricted to the western Palearctic region (Negrobov, 1991).

Phylogenetic Relationships. *Muscidideicus* is the basal genus of the *Ortochile* genus group and forms the sister taxon to the large clade including *Sybistroma*, *Hercostomus*, *Ortochile*, *Poecilobothrus* and *Parahercostomus*. Autapomorphies of *Muscidideicus* include the possession of seven pairs of dorsocentral setae and a dorsoventrally flattened abdomen.

Remarks. Although Becker (1917) referred to *Muscidideicus* as a genus on pages 124, 125 and 224, he clearly indicated on pages 268-269 that he regarded it as a subgenus of *Hercostomus*, and this classification was subsequently followed by Dyte (1969, 1976) and Assis Fonseca (1978). In contrast, Stackelberg (1930) and Negrobov (1980, 1991) treated *Muscidideicus* as a genus. The latter classification is supported by the cladistic analysis.

Material Examined.

Muscidideicus praetextatus (Haliday), [PA]: 2 ♂♂, 2 ♀♀ (MNHN); 2 ♂♂ (LEM).

GENUS *ORTOCHILE* LATREILLE

(Figs. 19A-E)

Ortochile Latreille, 1809: 289. Type species *Ortochile nigrocoerulea* Latreille [Palearctic], by monotypy.

Orthochile incorrect subsequent spelling by Latreille, 1825: 489, followed by Berthold, 1827: 497, 587. Erroneously listed as an emendation by Neave, 1940: 469.

Recognition. Species of *Ortochile* can be recognized by their greatly elongated mouthparts which are longer than the height of the head.

Description. Head: Vertex not distinctly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2.3x wider than high, sides weakly convergent anteriorly. Face slightly broader in female, sides distinctly convergent below, lower portion of face produced at boundary with clypeus. Clypeus produced along upper margin, weakly rounded below, not reaching lower eye margin. Palp and proboscis greatly elongated. Palp shorter than labium, rounded apically with weak setae on outer surface, lacking distinct apical seta. Labrum-epipharynx, epipharyngeal armature and hypopharynx narrow and elongate, hypopharynx tapering to a fine point apically. Labium about 1.2-1.6x as long as head is high, labellum divided medially into narrow, subtriangular lobes. Antenna: Scape subconical, with distinct acute medioventral process; pedicel short; first flagellomere ovoid to subtriangular; arista dorsal to subapical, 2-segmented, distal segment with very short pubescence. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Acrostichals weakly developed, biserial anteriorly, irregular or absent posteriorly; 6 dorsocentrals, fifth offset medially; 1 strong outer posthumeral, 1 weaker inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalar; 1 postalar. Upper part of propleuron with a cluster of fine hairs; lower part of propleuron with 1 strong prothoracic seta and a few fine hairs; pleural surface in front of posterior spiracle bare; metepisternum bare. Scutellum with 1 strong inner seta and 1 weak outer seta on lateral margin.

Legs: Pulvilli developed normally on all legs. Foreleg: Basitarsus usually with 3-4 distinct ventral setae. Midleg: Femur with 1 anterior preapical seta, with or without distinct posterior preapical seta in addition to terminal posteroventral preapical; fifth tarsomere sometimes dorsoventrally flattened (e.g., *O. soccata* Loew). Hindleg: Coxa with strong lateral seta near middle; femur with 1 anterodorsal preapical seta, sometimes with distinct anteroventral preapical seta; basitarsus subequal to slightly shorter than

second tarsomere, with or without distinct basiventral seta, male with small dentiform process posterobasally.

Wing: Grey to brownish, usually darker anteriorly. R_{2+3} nearly straight; R_{4+5} curved posteriorly in distal section; distal section of M beyond crossvein dm-cu with weak anterior bend before middle, convergent with R_{4+5} , ending well before wing apex, close to apex of R_{4+5} (very close in *O. soccata*); crossvein dm-cu distinctly shorter than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare, well-developed; S2 and S3 unmodified, S4 emarginate posteriorly, S5 mainly membranous, with a pair of weakly sclerotized longitudinal bands; S6 Y-shaped, fused to T6 posterolaterally, with narrow base extending anteromedially to middle of S5; segment 7 forming well-developed peduncle; S8 teardrop-shaped, setose. Hypopygium (Fig. 19A-C): Epandrium longer than wide, ovoid with rounded anterior margin in lateral view, symmetrical, laterally compressed, especially in anterior half; foramen positioned laterally, slightly before middle, well-separated from base of cerci; basiventral lobe weakly developed, with small dentiform process immediately anterior to weak basiventral epandrial seta; apicoventral epandrial lobe well-developed, subrectangular in lateral view with expanded apex, with 1-2 lateral and 2 apical setae, medial surface with well-developed mediodorsal ridge. Surstylus 2-lobed. Ventral lobe laterally flattened, subquadrate, narrowed apicoventrally, with strong seta on inner surface and stout apical seta. Dorsal lobe digitiform, slightly longer than ventral lobe. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion well-developed, simple, tapered distally and curved ventrally. Proctiger brushes absent. Cercus subtriangular with long marginal and apical setae. Hypandrium simple, trough-like, as long as apicoventral epandrial lobe, fused to epandrium laterally near basiventral epandrial lobe/seta; hypandrial apodeme present, well-developed; hypandrial arms connected to hypandrium. Sperm pump small, spherical; ejaculatory apodeme well-developed, weakly flattened laterally; basal sclerite of sperm pump heavily sclerotized, V-shaped in dorsal view. Phallus long and slender with preapical fin-like projection. Female (Fig. 19D, E): Terminalia elongate, longer than abdomen. T6, T7, S6 and S7 undivided; T8 and S8 divided medially, tergite and sternite not fused anterolaterally. Furca present, elongate and narrow. T10 not divided, each side with 3 long apically

flattened and rounded acanthophorous spines and a small inner medial spine or seta (Fig. 19E). Upper lobe of cercus with 1 long ventral preapical seta and 1 long apical seta.

Geographical Distribution. *Ortochile* is known from the western Palaearctic region, including Europe, Turkey, Israel and North Africa (Negrobov, 1991; Parvu, 1997).

Phylogenetic Relationships. This genus is most closely related to the clade including *Poecilobothrus*, *Parahercostomus* and Grichanov's (1999a) Afrotropical *Hercostomus* species group 1 based on characters of the male and female genitalia.

Remarks. Unlike most dolichopodine genera, adults of *Ortochile* are associated with flowers (in particular those of the family Asteraceae) and two species are known to feed on nectar (Dyte, unpublished manuscript). During genitalic dissections, I found pollen grains in the rectum of both *O. nigrocoerulea* and *O. soccata*, further supporting the hypothesis of flower feeding habits of this genus.

Nectar-feeding is also known in some species of *Hercostomus*, including *H. germanus* and *H. nigripennis* (Dyte, unpublished manuscript), the latter of which possesses elongated mouthparts, which are similar to, but distinctly shorter than those of *Ortochile*. As noted by Dyte, these species have very similar male genitalia and appear to be closely related to each other. My studies of the male genitalia indicate that these species are part of the sister group to *Ortochile* based on the possession of preapical lateroventral lobes on the postgonite (character 59:1). As noted by Dyte, *Hercostomus conformis*, *H. morenae* (Strobl), *H. pandellei* and *H. rostellatus* also appear to be closely related to *H. germanus* and *H. nigripennis* based on the genitalic illustrations and descriptions in Parent (1938).

Material Examined.

Ortochile nigrocoerulea Latreille, [PA]: 2♂♂, 6♀♀ (CNC)

Ortochile soccata Loew, [PA]: 2♂♂, 2♀♀ (LEM).

Ortochile unicolor Loew, [PA]: 5♂♂, 5♀♀ (USNM)

GENUS *PARACLIUS* LOEW

(Fig. 20A-E)

Paraclius Loew, 1864: 97. Type species: *Pelastoneurus arcuatus* Loew [Neotropical], designation by Coquillett, 1910: 583. Erroneously treated as an emendation of *Paracleius* Bigot in Foote et al. (1965) and elsewhere (see Brooks et al. (2002) and Cumming and Vockeroth (2003)).

Leptocorypha Aldrich, 1896: 315. Type species: *Leptocorypha pavo* Aldrich, by monotypy. Synonymized by Robinson (1970b).

Leptorhethum, Parent, 1934a, not Aldrich, 1893, misid. listed by Bickel and Dyte (1989).

Recognition. *Paraclius*, as currently recognized, is a polyphyletic assemblage of species which can be recognized by the following combination of characters: arista bare to strongly pubescent, not plumose (i.e. with dorsal and ventral hairs longer than lateral hairs), rarely with apical lamella in male; clypeus flat or weakly produced, distinctly shorter than face in male, lower margin usually straight and ending above lower eye margin, rarely rounded below and extending beyond lower eye margin; wing vein M beyond crossvein dm-cu with strong anterior bend near or beyond middle, strongly convergent with R_{4+5} and usually arcuate; hind coxa with strong lateral seta usually near apex; mid and hind femur usually with 1 anterior to anterodorsal preapical seta; hind basitarsis without dorsal setae. *Paraclius* sensu stricto (the *P. arcuatus* lineage), can be distinguished by the following combination of characters: face of male very narrow and strongly converging below; distal section of M beyond crossvein dm-cu with strong, arcuate anterior bend beyond middle; hind femur wide and flat with anterior preapical near apex, hypopygium with elongate anterior apicoventral epandrial seta and distinctive elongate ventral surstylus, cercus lacking basolateral tail.

Description (based on *P. arcuatus* lineage). Head: Vertex flat to weakly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2.7-2.9x wider than high, sides weakly to distinctly convergent below. Face and clypeus very narrow in male, broad in female. Face with sides strongly convergent below in male, sides subparallel or convergent below in female. Clypeus flat and often slightly recessed to weakly produced, occasionally strongly bulging in female, lower margin straight, ending above lower eye margin. Palp small in male slightly larger in female, ovoid, with weak hairs on outer surface, distinct apical seta present. Antenna: Scape short, subconical, with well-developed acute medioventral process and weaker acute process ventrally; pedicel short; first flagellomere ovoid to subtriangular, shorter in female; arista dorsal, near base, 2-segmented, distal segment strongly pubescent. Lower postocular setae flattened, lowermost seta usually stronger. Postvertical setae slightly to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 5 dorsocentrals, fourth pair aligned or slightly offset medially; 1 strong outer posthumeral, 1 weak to indistinct inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with sparse fine hairs, upper part of propleuron with 1-3 somewhat stronger setae immediately in front of anterior spiracle; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum with several fine hairs. Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin, posterior margin sometimes with a pair of weak setae (e.g., *P. arcuatus*).

Legs: Pulvilli developed normally on all legs. Foreleg: Femur often with 1-2 distinct preapicals anteroventrally and posteroventrally. Midleg: Femur somewhat laterally flattened and wide, with 1 anterior preapical seta, sometimes with 1 weak anteroventral preapical seta or a series of progressively longer setae towards apex, terminal posteroventral seta often well-developed. Hindleg: Coxa with strong lateral seta near apex; femur laterally flattened and wide, 1 anterior preapical seta relatively close to apex, 1 well-developed to indistinct anteroventral preapical seta and/or series of progressively longer setae towards apex; tibia of male with thickened spinules on ctenidia; basitarsus shorter than second tarsomere, with 2-3 ventral setae; male with small dentiform posterobasal process.

Wing: Brownish or greyish. R_{2+3} straight; R_{4+5} straight or with weak posterior curve in apical part; distal section of M beyond crossvein dm-cu with strong anterior bend beyond middle, arcuate, ending well before wing apex, strongly convergent with R_{4+5} ; crossvein dm-cu shorter than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare (e.g., *P. arcuatus*), or with a few setae along lateral margin (e.g., *P. pumilio* Loew, *Paraclius* sp. 1); S2 weakly sclerotized, sometimes divided medially; S3 emarginate and membranous posteromedially or divided; S4 mainly membranous, sclerotized anterior and laterally; S5 mainly membranous anteriorly, weakly sclerotized posteriorly and continuous with S6 forming a plate-like sclerite; segment 7 forming well-developed peduncle; S8 subovoid, setose on posterior half. Hypopygium (Fig. 20A-C) somewhat slender, in lateral view, subequal in height to segment 7. Epandrium ovoid in lateral view, about 2.3-2.7x longer than high, with lateral ridge on apical half forming an acute apical projection directly above apicoventral epandrial setae; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe not developed, small basiventral epandrial seta present along ventral epandrial margin; apicoventral epandrial lobe not developed, 2 apicoventral epandrial setae present, anterior seta elongate, posterior seta elongate or relatively short. Surstylus 2-lobed. Ventral lobe elongate slender and digitiform with stout modified apical seta. Dorsal lobe broad basally, with 2 thick dorsal setae, apex blunt or acute. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion well-developed, simple, digitiform. Undivided proctiger brush sometimes present (e.g., *P. arcuatus* Fig. 20B). Cercus ovoid to subtriangular and weakly pointed apically, sometimes with elongate lateral setae. Hypandrium elongate, trough-shaped, with weak connection to epandrium basiventrally, free laterally, apex bifurcate, lateral margin with 1-2 dentiform or knob-like preapical projections, base of hypandrium projecting up inside epandrial capsule, cradling phallus (Fig. 20B); hypandrial apodeme absent or not distinctly separated from basal sclerite of sperm pump; hypandrial arms connected to base of hypandrium. Sperm pump relatively large; ejaculatory apodeme elongate, laterally flattened, sometimes weakly sclerotized; basal sclerite of sperm pump well-developed, V-shaped to broadly U-shaped in dorsal view. Phallus long, slender, with small bumps or spinules, apical part with dentiform or rounded projections. Female (Fig. 20D,E): T6, S6

and S7 undivided, T7 undivided, or weakly divided medially; T8 and S8 divided medially, tergite and sternite fused anterolaterally forming a narrow sclerite (Fig. 20E). T10 divided medially into hemitergites each bearing 5 acanthoporous spines, innermost pair sometimes slightly offset, spines rounded and somewhat flattened apically.

Geographical Distribution. *Paraclius* occurs in all zoogeographical regions, but is most diverse in the Neotropics. The *Paraclius arcuatus* lineage is known from the New World.

Phylogenetic Relationships. As indicated by the cladistic analysis, *Paraclius* is a polyphyletic group within the clade including *Cheiromyia*, *Stenopygium*, *Pelastoneurus*, *Platyopsis*, *Tachytrechus* and *Metaparaclius*. Much additional work is needed to resolve the phylogenetic relationships of *Paraclius* on a worldwide basis. At present the only phylogenetically meaningful generic concept includes the lineage closely related to the generic type, *P. arcuatus* (e.g., *P. pumilio*, *Paraclius* sp. 1), as diagnosed and described above. Based on the material examined in this study there appear to be several recognizable species groups within *Paraclius* sensu lato and it is likely that additional genera will have to be established to accommodate these lineages; however, this is beyond the scope of my study. Until all the species of this genus can be studied in more detail, *Paraclius* will serve as a holding genus, like *Hercostomus*.

In addition to the *P. arcuatus* lineage, I have seen two additional New World species groups of *Paraclius*. The first group is primarily characterized by the possession of a basolateral tail on the male cercus and was recently discussed by Bickel and Sinclair (1997). This group includes *P. alternans*, *P. claviculatus* Loew, *P. desenderi* Bickel & Sinclair, *P. difficilis* Becker, *P. discifer* Aldrich, *P. hebes* Van Duzee and *P. filifer* Aldrich, which were examined in this study, as well as *P. affinis* Robinson, *P. propinquus* Wheeler, *P. maritimus* Van Duzee, *P. flagellatus* (Harmston) for which specimens were not examined. This group is further characterized by a greatly enlarged and somewhat spherical sperm pump and a pair of proctiger brushes similar to those observed in *Pelastoneurus* (absent in *Paraclius filifer*). *Paraclius hybridus* Melander and *P. quadrinotatus* Aldrich apparently belong to this group, but lack the tail on the cercus. *Paraclius sarcionoides* Robinson may also be related to this group but lacks an enlarged

sperm pump. This species is also unusual in that it has a spiny, divided phallus and a very well-developed hypandrial apodeme. *Paraclius arcuatus* possesses an undivided, haired proctiger lobe similar to the proctiger brushes of this species group, but this lobe is absent in the other examined members of the *P. arcuatus* lineage.

The other New World species group includes *P. brevicornis* Van Duzee, *P. dominicus* Robinson, *P. flavicauda* Van Duzee, *P. floridensis* Robinson, *P. longicornis* Van Duzee, *P. ovatus* Van Duzee and *P. venustus*. This group is characterized by the possession of a ring-shaped sclerite surrounding the base of the phallus. This sclerite appears to be an extension of the postgonite, as illustrated by *P. flavicauda*, where the anteroventral portion of the postgonite and ring-shaped sclerite are fused. This connection is absent in the other species. *Paraclius megalocerus* seems to be close to this group, but lacks the characteristic basal phallic ring. Most of the species in this group also possess a greatly enlarged sperm pump, similar to the *P. alternans* group discussed above (sperm pump not enlarged in *P. ovatus*), but lack proctiger brushes. The male genitalia of species in this group show an overall similarity to that of *Cheiromyia*; however, at present I have not found a synapomorphy to support this relationship.

All of the Oriental species examined (i.e. *P. abbreviatus*, *P. emeiensis*, *P. pilosellus* and *P. luculentus*) share a patch of setae on the posterolateral margin of the metepimeron (character 16:1). The latter three species, plus "*Polymedon*" *inopinatus*, form a distinctive species group characterized by the possession of finely branched setae on the apicoventral epandrial lobe, large, dark cerci, and a complex, eversible, apicodorsal epandrial sac. The following species (not examined) also seem referable to this group: *P. acutatus* Yang and Li, *P. curvispinus* Yang and Saigusa, *P. longicornutus* Yang and Saigusa, *P. menglunensis* Yang and Grootaert, *P. xanthocerus* Yang and Grootaert, *P. yunnanus* Yang. This Oriental species group appears to be related to a species group including *Metaparaclius australiensis* and *Paraclius neglectus* (see "Phylogenetic relationships" under the generic treatment of *Metaparaclius*).

Remarks. Aldrich (1902) recorded a "light variety" of *P. arcuatus* from Grenada in which the hind legs are mainly yellow. I have examined a male and several females from this series and compared them with the female holotype of *P. arcuatus* as well as other

identified specimens of *P. arcuatus* showing the typical leg colour, i.e. with the hind femur dark on distal half and hind tibia dark brown. The pale-legged specimens from Grenada belong to a separate, apparently undescribed species (*Paraclius* sp. 1). Genitalic differences are seen in the structure of the hypandrium, apex of the phallus and shape of the dorsal surstylar lobe. Like *P. pumilio*, the male of *Paraclius* sp. 1 lacks the hairy undivided apical proctiger lobe, present in *P. arcuatus* (Fig. 20B). These two species also possess lateroventral setae on abdominal T6, which represents a rare exception to the dolichopodine groundplan in which T6 is bare.

The cradle-like extension of the hypandrium (Fig. 20B) noted in the description of the *P. arcuatus* lineage is potentially an informative character that requires further study. This feature is also shared by the *P. alternans* species group; but had to be excluded from the analysis due to problems with apparent intermediates and cases of uncertain homology encountered while attempting to code and score this character across the range of exemplars.

Material Examined.

Paraclius arcuatus (Loew), [NT]: ♀ holotype (MCZ); 1 ♂, 7 ♀ ♀ (USNM); 2 ♂ ♂ (CAS)

Paraclius abbreviatus Becker, [OR]: 1 ♂, 1 ♀ (BMNH)

Paraclius alternans (Loew), [NE]: 2 ♂ ♂, 1 ♀ (CAS), 2 ♂ ♂, 1 ♀ (CNC)

Paraclius brevicornis Van Duzee, [NT]: 2 ♂ ♂ paratypes, 1 ♀ paratype (CAS)

Paraclius claviculatus (Van Duzee), [NE, ?NT]: 1 ♂ (CAS)

Paraclius desenderi Bickel and Sinclair, [NT]: 1 ♂ paratype, 1 ♀ paratype (CAS)

Paraclius discifer Aldrich, [NT]: 2 ♂ ♂, 2 ♀ ♀ (USNM)

Paraclius difficilis Becker, [NT]: 1 ♂ (USNM)

Paraclius dominicus Robinson, [NT]: 3 ♂ ♂ paratypes, 2 ♀ ♀ paratypes (USNM)

Paraclius emeiensis Yang and Saigusa, [OR]: 1 ♂ paratype, 1 ♀ paratype (ISNB)

Paraclius filifer Aldrich, [NE, NT]: 5 ♂ ♂, 2 ♀ ♀ (CAS)

Paraclius flavicauda Van Duzee, [NT]: 1 ♂ (CAS)

Paraclius floridensis Robinson, [NE]: 1 ♂ (CAS)

Paraclius hebes Van Duzee, [NT]: 1 ♂ paratype, 1 ♂, 1 ♀ (CAS)

- Paraclius hybridus* Melander, [NE]: 3 ♂♂, 1 ♀ (CAS)
- Paraclius longicornis* Van Duzee, [NT]: 2 ♂♂ paratypes, 1 ♀ paratype (CAS)
- Paraclius luculentus* Parent, [OR]: 1 ♂, 1 ♀ (BMNH)
- Paraclius megalocerus* Robinson, [NT]: 2 ♂♂ paratypes, 2 ♀♀ paratypes (USNM)
- Paraclius microproctus* Parent, [AF]: ♂ holotype (MRAC)
- Paraclius neglectus* Becker, [AU]: 4 ♂♂, 2 ♀♀ (CNC)
- Paraclius ovatus* Van Duzee, [NE, ?NT]: 4 ♂♂ (CAS)
- Paraclius pilosellus* Becker, [OR]: 1 ♂ syntype, 2 ♀♀ syntypes (DEI)
- Paraclius pumilio* Loew, [NE, NT]: 3 ♂♂, 2 ♀♀ (CAS)
- Paraclius quadrinotatus* Aldrich, [NE]: 3 ♂♂, 1 ♀ (CAS)
- Paraclius sarcionoides* Robinson, [NT]: 2 ♂♂ paratypes, 2 ♀♀ paratypes (USNM)
- Paraclius solivagus* Lamb, [AF]: 2 ♂♂, 1 ♀ (LEM)
- Paraclius venustus* Aldrich, [NT]: 1 ♂, 1 ♀ (CAS)
- Paraclius* sp. 1, [NT, Grenada]: 1 ♂, 1 ♀ (BMNH); 2 ♀♀ (USNM); 1 ♀ (CAS)
- “*Polymedon*” *inopinatus* Parent, [OR]: 2 ♂, 2 ♀ (ISNB)

GENUS *PARAHERCOSTOMUS* YANG, SAIGUSA AND MASUNAGA

(Fig. 21A-E)

Parahercostomus Yang, Saigusa and Masunaga, 2001: 176. Type species: *Hercostomus zhongdianus* Yang [Oriental], by original designation.

Recognition. This genus can be recognized by the following combination of characters: sutural, presutural and acrostichal setae absent; vertical setae weaker than postverticals, hind basitarsus with 1-3 dorsal setae, male with R_{2+3} and R_{4+5} thickened in basal part.

Description. Head: Vertex slightly excavated, 1 pair of weak vertical setae, about equal to postverticals. Frons about 1.3x wider than high in male, about 1.7x wider than high in female, sides nearly parallel. Face and clypeus narrow in male, broad in female, lower

margin straight, not reaching lower eye margin. Palp smaller in male, rounded below, with setae on outer surface and a weak apical seta. Antenna: Scape subrectangular, somewhat elongated in male, medioventral process very weakly developed in female, absent in male; pedicel short; first flagellomere oval, apex rounded to subtriangular; arista dorsal, 2-segmented, basal segment somewhat elongated, distal segment weakly pubescent. Lower postocular setae fine. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Acrostichals absent; 6 dorsocentrals, aligned; 1 outer posthumeral, 1 inner posthumeral weakly developed or absent; 2 notopleurals; presutural and sutural absent; 2 supraalars; 1 postalar. Upper part of propleuron with cluster of fine hairs, lower part of propleuron with 1 strong prothoracic seta and fine hairs; pleural surface in front of posterior spiracle and metepisternum bare. Scutellum with 1 strong inner seta and a minute outer hair on lateral margin, posterior margin with or without (e.g., *P. trisetata* Yang, Saigusa and Masunaga) fine hairs.

Legs: Pulvilli developed normally on all legs. Foreleg: Apex of basitarsus and distal tarsomeres of male piliferous ventrally. Midleg: Femur with 1 anterior preapical seta. Hindleg: Coxa with strong lateral seta slightly below middle; femur with 1 anterodorsal preapical seta; tibia of male with posterodorsal ridge apically; basitarsus distinctly longer than second tarsomere with 1-3 anterodorsal setae, 1 strong basiventral seta, longer than width of basitarsus, 2-4 weaker ventral setae, male with dentiform process posterobasally.

Wing: Brownish to mainly hyaline. Costa thickened beyond R_1 in male; R_{2+3} nearly straight; R_{4+5} curved posteriorly in distal section; R_{2+3} and R_{4+5} of male thickened in basal half to three-quarters; distal section of M beyond crossvein dm-cu nearly straight or with weak sinuous anterior bend before middle and posterior curve in distal section, ending near or slightly before wing apex, subparallel or convergent with R_{4+5} ; crossvein dm-cu subequal to distinctly shorter than distal section of CuA_1 .

Abdomen: Subconical, longer and more strongly tapering in male. Male: T6 bare, well-developed; S2 and S3 unmodified; S4 unmodified or weakly sclerotized posteriorly; S5 mostly membranous, divided medially into weakly sclerotized longitudinal bands fusing with S6 posteriorly; S6 sclerotized along anterior margin, Y-shaped, fused to T6

posterolaterally, with base extending anteromedially into S5; segment 7 forming well-developed peduncle; S8 teardrop-shaped, setose. Hypopygium (Fig. 21A-C) large. Epandrium subrectangular to ovoid, longer than high; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe weakly developed, with weak basiventral epandrial seta; apicoventral epandrial lobe elongate with rounded or subtriangular apex bearing three setae. Surstylus 2-lobed. Ventral lobe subquadrate with 1 dorsobasal seta, 1 mid-ventral seta, 1 thickened medial seta, and subtriangular apicoventral extension bearing thick apical seta. Dorsal lobe slightly longer than ventral lobe, broad with acute apex, 1 strong dorsal seta. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion well-developed, with preapical lateroventral lobes (Fig. 21B). Proctiger brushes absent. Cercus subtriangular with strong marginal setae. Hypandrium narrow, tapered distally, as long as or slightly longer than apicoventral epandrial lobe, fused to epandrium laterally near basiventral epandrial lobe (Fig. 21A,C); hypandrial apodeme present, well-developed, hypandrial arms connected to hypandrium. Sperm pump cylindrical; ejaculatory apodeme well-developed, elongate and laterally flattened; basal sclerite of sperm pump heavily sclerotized, V-shaped in dorsal view. Phallus long and slender with dentiform process in apical portion (present in *P. zhongdianus* and *P. orientalis* Yang, Saigusa and Masunaga). Female (Fig. 21D,E): T6, T7, S6 and S7 undivided; T8 and S8 divided medially; tergite and sternite weakly fused anterolaterally. T10 divided medially into hemitergites each bearing 4 acanthoporous spines along outer margin and a single inner medial spine, spines rounded and flattened apically. Upper lobe of cercus with long apical seta.

Geographical Distribution. This genus includes three species, all of which are known only from Oriental China (Yunnan) (Yang, 1998a; Yang et al., 2001).

Phylogenetic Relationships. *Parahercostomus* appears to be closely related to Grichanov's (1999a) Afrotropical *Hercostomus* species group 1.

Remarks. Although not mentioned by Yang et al. (2001), the loss of the presutural seta is an autapomorphy of *Parahercostomus*. Yang (pers. comm.) has confirmed that this seta is absent in *P. trisetata*.

Material Examined.

Parahercostomus zhongdianus (Yang), [OR]: 2 ♂ paratypes, 2 ♀ paratypes (SKU);
1 ♂ paratype, 1 ♀ paratype (LEM).

Parahercostomus orientalis Yang, Saigusa and Masunaga, [OR]: 2 ♂ paratypes, 1 ♀
paratype (SKU); 1 ♂ paratype, 1 ♀ paratype (LEM).

GENUS PELASTONEURUS LOEW

(Figs. 22A-E, 23A-F, 24A-E)

Paracleius Bigot, 1859: 215, 227. Type species: *Dolichopus heteronevrus* Macquart, by monotypy. See comments under *Paraclius* Loew. Application to the I.C.Z.N. for the suppression of *Paracleius* Bigot (Brooks et al., 2002) has been approved (I.C.Z.N., pers. comm.).

Pelastoneurus Loew, 1861b: 36. Type species: *Pelastoneurus vagans* Loew [Nearctic], designation by Coquillett, 1910: 586.

Metapelastoneurus Aldrich, 1894: 152. Type species: *Metapelastoneurus kansensis* Aldrich, by monotypy.

Sarcionus Aldrich, 1901: 341. Type species. *Pelastoneurus lineatus* Aldrich, by original designation. **syn. nov.**

Phylarchus Aldrich, 1901: 342. Type species: *Phylarchus tripartitus* Aldrich, by monotypy. Preoccupied by *Phylarchus* Simon, 1888. **syn. nov.**

Paraclius Kertész, 1909: 230. Type species: *Dolichopus heteronevrus* Macquart, automatic. Unjustified emendation of *Paracleius* Bigot, 1859.

Proarchus Aldrich, 1910: 100. Type species: *Phylarchus tripartitus* Aldrich, automatic. N. name for *Phylarchus* Aldrich, 1901. **syn. nov.**

Palastoneurus, subsequent misspelling by Parent (1933a: 249).

Pelastroneurus, subsequent misspelling by Robinson (1964: 177).

New Combinations and Transfers. The following new combinations are hereby established: *Pelastoneurus acutispina* (Van Duzee, 1931) **comb. nov.** (*Sarcionus*); *Pelastoneurus currani* (Van Duzee, 1931) **comb. nov.** (*Sarcionus*); *Pelastoneurus obtusus* (Van Duzee, 1933) **comb. nov.** (*Sarcionus*); *Pelastoneurus pectinicauda* (Van Duzee, 1934) **comb. nov.** (*Sarcionus*); *Pelastoneurus pusillus* (Macquart, 1846) **comb. nov.** (*Dolichopus*); *Pelastoneurus rotundicornis* (Van Duzee, 1931) **comb. nov.** (*Sarcionus*); *Pelastoneurus tripartitus* (Aldrich, 1901) **comb. nov.** (*Phylarchus*). The following species is reassigned to *Pelastoneurus*: *Pelastoneurus lineatus* Aldrich, 1896. The re-establishment of this combination renders *Pelastoneurus lineatus* de Meijere, 1916 a junior secondary homonym for which the replacement name *Pelastoneurus neolineatus* **nom. nov.** is hereby proposed.

Recognition. Most species currently assigned to *Pelastoneurus* on a global scale may be distinguished by the possession of a strong anterior bend in wing vein M and plumose arista; however, many Old World species do not appear to be congeneric with those of the New World. The lineage of *Pelastoneurus* including the type species *P. vagans* appears to be restricted to the New World and can be recognized by the following combination of characters: clypeus usually strongly bulging and subequal in height to face (often taller than face in females), proboscis large, arista plumose, 5 dorsocentral setae, wing vein M beyond crossvein dm-cu usually with strong anterior bend and distinctly convergent with

R₄₊₅, hind coxa usually with lateral seta near apex. *Pelastoneurus* is close to *Stenopygium* and *Platyopsis* with which it shares a similarly modified clypeus.

Description (based on *P. vagans* lineage). Head: Usually thick in lateral view. Vertex usually flat to weakly excavated, sometimes strongly excavated (e.g., *P. currani*), 1 pair of strong vertical setae, stronger than postverticals. Frons about 2-3x wider than high, sides weakly to distinctly convergent anteriorly. Face and clypeus usually broad, occasionally narrow (e.g., male *P. lineatus*), broader in female; face usually concave with sides subparallel to convergent below; clypeus usually strongly bulging and subequal in height to face in both sexes (often taller than face in female), occasionally distinctly shorter than face and weakly bulging in male (e.g., *P. lineatus*), widening below, lower margin straight to rounded or subtriangular, ending above or extending slightly beyond lower eye margin. Palp usually large and subtriangular with weak hairs on outer surface, usually with a weakly differentiated to distinct apical seta. Proboscis usually large and thick, occasionally relatively small (e.g., *P. lineatus*). Antenna: Scape short, subconical, with well-developed acute medioventral process and weaker acute process ventrally; pedicel short; first flagellomere rounded or ovoid to subquadrate, occasionally pointed apically, shorter in female; arista dorsal, usually near base, 2-segmented, basal segment occasionally elongate in male (e.g., *P. neglectus* Wheeler), distal segment plumose, dorsal and ventral hairs longer than lateral hairs and usually widely spaced. Lower postocular setae sometimes flattened (e.g., *P. vagans*), lowermost seta usually stronger. Postvertical setae slightly to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 5 dorsocentrals, aligned or with fourth pair weakly offset medially; 1 outer posthumeral, 1 weaker inner posthumeral, sometimes indistinct; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Scutum occasionally with black spot or region above notopleuron, sometimes also with similar spot beside postpronotum and at wing base (e.g., *P. tripartatus*). Upper and lower part of propleuron with fine to coarse hairs; upper part of propleuron sometimes with several stronger setae amongst hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum with a cluster or row of fine hairs. Scutellum with 1 strong inner seta and 1-2 small outer seta on lateral margin, often with 1

fine ventral seta (occasionally 2-3 setae) even with or slightly medial to strong inner seta (e.g., *P. vagans*), occasionally with several weak marginal hairs.

Legs: Pulvilli usually developed normally on all legs, occasionally enlarged on foreleg of male (e.g., *P. umbripictus*). Foreleg: Femur usually with well-developed posterior preapical seta, or a series of progressively longer setae; tarsus of male often with dense pile ventrally, basitarsus occasionally with distinct basiventral seta (e.g., *P. umbripictus*), inner claw enlarged in males of some species (e.g., *P. unguiculatus* (Aldrich)). Midleg: Femur with 1 anterior or anterodorsal preapical seta, males occasionally with long anteroventral hairs or setae (e.g., *P. nititus* Van Duzee, *P. tripartitus*) or basiventral piliferous patch (e.g., *P. unguiculatus*). Hindleg: Coxa with strong lateral seta usually near apex, sometimes slightly below middle (e.g., *P. tripartitus*); femur with 1 anterodorsal preapical seta and usually 1 distinct anteroventral preapical seta, occasionally with 1 weak anterior seta near apex (e.g., *P. aldrichi* Van Duzee), males of some species with long basiventral hairs (e.g., *P. nitidus*), or 2-3 strong setae along middle third (e.g., *P. tripartitus*); tibia of male with ctenidia usually enlarged with thickened or modified spinules (e.g., *P. vagans*), occasionally with distinct hook-like posteroapical process (e.g., *P. umbripictus*); basitarsus slightly to distinctly shorter than second tarsomere, usually with 2-3 ventral setae, basiventral seta sometimes distinct, male usually lacking a distinct posterobasal process.

Wing: Greyish to brownish, occasionally infuscated near veins, or with dark spots or bands (e.g., *P. umbripictus*, *P. turbidus*). Costa occasionally swollen basally before R_1 (e.g., *P. unguiculatus*); R_{2+3} often weakly sinuous basally, relatively straight in distal section; R_{4+5} relatively straight, usually with distinct posterior curve in distal section; distal section of M beyond crossvein dm-cu usually with strong anterior bend, ending well before wing apex, occasionally with weak bend (e.g., *P. unguiculatus*), rarely straight and ending at apex (e.g., *P. tripartitus*); R_{4+5} and M usually strongly convergent, rarely subparallel (e.g., *P. tripartitus*); crossvein dm-cu subequal to distinctly shorter than distal section of CuA_1 .

Abdomen: Subconical, occasionally short and contracted in male (e.g., *P. brevis* Robinson). Male: T6 bare; S2 and S3 unmodified to weakly sclerotized, often emarginate and membranous posteromedially; S4 emarginate and membranous posteromedially; S5

usually membranous medially; S6 mainly membranous, sclerotized along anterior margin and often fused to T6 laterally; segment 7 forming well-developed peduncle; S8 usually subquadrate to rounded, setose. Hypopygium (Figs. 22A-C, 23A-D, 24A-C) large, usually about as long as abdomen, often held in ventral pocket of abdomen. Epandrium variable in shape, ovoid to subrectangular or subtriangular in lateral view, about 1.5-3x longer than high, occasionally with keel-like process above apicoventral epandrial lobe/setae (e.g., *P. lineatus*, *P. umbripictus*, Fig. 23A); foramen positioned anterolaterally, usually well-separated from base of cerci, rarely close to base of cerci (e.g., *P. kansensis*); basiventral epandrial lobe usually absent (Figs. 22A, 24A), occasionally weakly developed (e.g., *P. lineatus* Fig. 23A), small to minute basiventral epandrial seta usually present along infolded ventral epandrial margin, seta positioned near middle (Figs. 23A,D, 24A,C) or close to base of apicoventral epandrial lobe where the hypandrial arm connects to the epandrium (Fig. 22A,C), occasionally absent; apicoventral epandrial lobe absent or weakly developed as an elevated ridge (e.g., *P. tripartitus*, Fig. 24A) to well-developed (e.g., *P. vagans*, Fig. 22A), with 2-8 setae, often with one or more branched setae, setae occasionally scimitar-shaped (e.g., *P. lineatus*, Fig. 23A). Surstylus 2-lobed. Ventral and dorsal lobe variable, broad to slender and digitiform; ventral lobe often with bulbous basal projection (e.g., *P. laetus*). Postgonite: anteroventral portion usually well-sclerotized with well-defined margin, usually dorsoventrally flattened, narrow to broad in ventral view, sometimes with bulbous base positioned below sperm pump (e.g., *P. tripartitus* Fig. 24B); posterodorsal portion well-developed, with single lobe (e.g., *P. lineatus*, *P. tripartitus* Figs. 23B, 24B), or with dorsal and ventral lobe (e.g., *P. vagans* Fig. 22B), dorsal lobe occasionally strongly upturned. Proctiger brushes usually present (Figs. 22B, 23B,C), rarely absent (e.g., *P. tripartitus*, Fig. 24B). Cercus variable in shape and size. Hypandrium long, variable in shape, more or less trough-like, usually asymmetrical, often complex with multiple lobes or projections, with narrow sclerotized or membranous connection to epandrium basiventrally, free laterally; hypandrial apodeme usually absent or indistinct, sometimes present and well-developed; hypandrial arms not connected to hypandrium, usually weakly connected to epandrium near basiventral epandrial seta and/or base of apicoventral epandrial lobe (Figs. 22B, 23B, 24B). Sperm pump usually small and round; ejaculatory apodeme elongate, laterally flattened, apex

sometimes split medially; basal sclerite of sperm pump usually elongate and tubular (Figs. 22B, 23B), occasionally relatively short (Fig. 24B) and V-shaped in dorsal view (e.g., *P. tripartitus*, *P. umbripictus*). Phallus slender in basal part, apical half highly variable in structure, often serrate (e.g., *P. vagans* Fig. 22B), and/or with well-developed projections (e.g., *P. lineatus* Fig. 23B), sometimes complex, multilobate and intertwined with hypandrium (e.g., *P. brasiliensis* Van Duzee). Female (Figs. 22D,E, 23E,F, 24D,E): T6 and T7 divided medially, S6 and S7 usually undivided, occasionally divided (e.g., *P. brasiliensis*); T8 and S8 divided medially, tergite and sternite fused anterolaterally forming a narrow sclerite (Figs. 22E, 23E, 24E). Furca usually present, shape variable, often weakly sclerotized. T10 divided medially into hemitergites each bearing 4-7 acanthoporous spines, spines pointed or rounded apically.

Geographical Distribution. Species of *Pelastoneurus* have been described or recorded from the Nearctic, Neotropical, Afrotropical and Oriental regions as well the Hawaiian islands. However, many species from outside of the New World appear to be questionably placed in this genus.

Phylogenetic Relationships. *Pelastoneurus* (in the sense of the *P. vagans* lineage) seems to be most closely related to *Stenopygium* based on the possession of a pair of proctiger brushes and a well-sclerotized anteroventral portion of the postgonite; however this relationship is not supported in all of the equally parsimonious trees.

Based on the examination of several Afrotropical and Oriental *Pelastoneurus*, and a survey of descriptions in the literature, it appears that many of these Old World species are not congeneric with the concept of *Pelastoneurus* adopted here (i.e. the lineage including the type species *P. vagans*) and probably require the establishment of additional genera. For the present, these species are left in *Pelastoneurus* until a more detailed phylogenetic study of the world species of this genus is completed.

Remarks. Despite the recent application by Brooks et al. (2002) to suppress *Paracleius* Bigot in favour of the junior synonym *Pelastoneurus* Loew, Grichanov (2004) used *Paracleius* Bigot as the valid name for this genus in his monograph of the Afrotropical

Dolichopodinae. Grichanov (2004) also considered *Paraclius* Loew to be a synonym of *Paracleius* Bigot and transferred all Afrotropical species of *Paraclius* Loew to *Paracleius* Bigot. The Commission has since ruled to suppress *Paracleius* Bigot and the Opinion will be published in the June, 2004 issue, i.e. volume 62(1), of the Bulletin of Zoological Nomenclature (I.C.Z.N., pers. comm.). As a result of this ruling, all species names newly proposed by Grichanov (2004) must be combined with *Pelastoneurus*. Similarly, all previously proposed species names combined with *Paracleius* by Grichanov (2004) must be recombined with their former generic name.

Both syntypes of *Pelastoneurus tripartitus* (formerly in *Proarchus*) are in poor condition. One specimen is missing its head, left wing, right tibia and has damage to the dorsum of the thorax. The other specimen is in slightly better shape, but has damage to both wings and is missing the tibiae and tarsi from the hind legs. Recently, I found a male in the miscellaneous holdings of the USNM from the western tip of Jamaica, near Negril.

Material Examined.

Pelastoneurus abbreviatus Loew, [NE]: 9♂♂, 6♀♀ (CNC)

Pelastoneurus acutispina (Van Duzee), [NT]: 1♀ paratype (AMNH), 1♀ paratype (CAS)

Pelastoneurus aldrichi Van Duzee, [NE]: 1♂ paratype, 2♂♂, 2♀♀ (CAS)

Pelastoneurus argentifer Aldrich, [NT]: 2♂♂, 2♀♀ (USNM); 1♂, 1♀ (CAS)

Pelastoneurus barri Harmston, [NE]: 2♂♂ paratypes, 2♀♀ paratypes (CAS)

Pelastoneurus bigeminatus Aldrich, [NT]: 1♂, 1♀ (USNM)

Pelastoneurus brasiliensis Van Duzee, [NT]: 1♂ paratype, 1♀ paratype (CAS)

Pelastoneurus brevis Robinson, [NE]: 3♂♂, 2♀♀ (CAS)

Pelastoneurus caeruleus Van Duzee, [NT]: 1♂ paratype (CAS); 1♂, 1♀ (USNM)

Pelastoneurus confusibilis Parent, [AF]: 1♂ paratype, 2♀♀ paratypes, 1♂ (ISNB)

Pelastoneurus congoensis Parent, [AF]: 4♂♂, 2♀♀ (MRAC)

Pelastoneurus costalis Van Duzee, [NT]: 1♂, 1♀ (USNM)

Pelastoneurus currani Van Duzee, [NT]: 4♂♂ paratypes (AMNH); 1♂ paratype (CAS)

Pelastoneurus cyaneus Wheeler, [NE]: 4♂♂, 2♀♀ (CAS); 2♂♂ (CNC)

Pelastoneurus dissimilipes Wheeler, [NE]: 3♂♂, 2♀♀ (CAS)

- Pelastoneurus diversifemur* Parent, [AF]: 3 ♂♂, 2 ♀♀ (ISNB)
- Pelastoneurus dorsalis* Van Duzee, [NE, NT]: 1 ♂ (CAS)
- Pelastoneurus emasculatus* Parent, [AF]: 2 ♂♂ paratypes, 2 ♀♀ paratypes (ISNB)
- Pelastoneurus floridanus* Wheeler, [NE]: 3 ♂♂, 2 ♀♀ (CAS)
- Pelastoneurus intactus* Becker, [OR]: 2 ♂♂ (BMNH)
- Pelastoneurus kansensis* (Aldrich), [NE]: 3 ♂♂, 2 ♀♀ (USNM); 1 ♂ (CAS); 1 ♂ (LEM)
- Pelastoneurus laetus* Loew, [NE]: 4 ♂♂, 3 ♀♀ (CNC)
- Pelastoneurus lamellatus* Loew, [NE]: 4 ♂♂ (CAS); 2 ♂♂ (CNC)
- Pelastoneurus lineatus* Aldrich, [NT]: 3 ♂♂ syntypes, 1 ♀ syntype, 5 ♂♂, 7 ♀♀ (USNM)
- Pelastoneurus longicauda* Loew, [NE]: 1 ♂, 1 ♀ (USNM)
- Pelastoneurus lugubris* Loew, [NE, NT, AU]: 2 ♂♂ (CAS); 1 ♂ (CNC)
- Pelastoneurus micrurus* Parent, [AF]: 3 ♂♂ (MRAC)
- Pelastoneurus neglectus* Wheeler, [NE]: 3 ♂♂, 2 ♀♀ (USNM); 2 ♂♂ (CAS)
- Pelastoneurus nigricornis* Van Duzee, [NE]: 1 ♂ (USNM)
- Pelastoneurus nigrifacies* Van Duzee, [NT]: 1 ♂ (CAS); 1 ♂ (USNM)
- Pelastoneurus nitidus* Van Duzee, [NT]: 2 ♂♂ paratypes, 1 ♀ paratype
- Pelastoneurus pectinatus* Van Duzee, [NT]: 2 ♂♂ paratypes, 1 ♀ paratype (USNM); 1 ♂ paratype (CAS)
- Pelastoneurus pectinicauda* (Van Duzee), [NT]: 1 ♂, 1 ♀ (AMNH)
- Pelastoneurus pedunculatus* Parent, [AF]: 6 ♂♂ (MRAC)
- Pelastoneurus rotundicornis* (Van Duzee), [NT]: ♂ holotype (AMNH); 4 ♂♂ paratypes, 1 ♀ paratype (AMNH); 1 ♂ paratype, 1 ♀ paratype (CAS)
- Pelastoneurus taeniatus* Becker, [NE, NT]: 2 ♂♂, 2 ♀♀ (USNM)
- Pelastoneurus tibialis* Van Duzee, [NE]: 4 ♂♂, 4 ♀♀ (CNC)
- Pelastoneurus tripartitus* (Aldrich), [NT]: 2 ♀♀ syntypes (BMNH); 1 ♂ (USNM)
- Pelastoneurus turbidus* Becker, [NT]: 1 ♂ (USNM)
- Pelastoneurus umbricola* (Parent), [AF]: 2 ♀♀ (ISNB)
- Pelastoneurus umbripictus* Becker, [NE, NT]: 2 ♂♂, 2 ♀♀ (USNM)
- Pelastoneurus unguiculatus* (Aldrich), [NT]: 3 ♂♂, 2 ♀♀ (CNC)

Pelastoneurus vagans Loew, [NE, NT]: 12 ♂♂, 6 ♀♀ (CNC) 2 ♂♂, 2 ♀♀ (LEM)

Pelastoneurus varius (Walker), [NE]: 4 ♂♂, 1 ♀ (CAS); 2 ♂♂ (CAS)

Pelastoneurus wheeleri Melander, [NE]: 3 ♂♂, 2 ♀♀ (CAS)

“*Sarcionus*” *flavicoxa* (Aldrich), [NT]: 1 ♂ syntype, 1 ♀ syntype (BMNH)

“*Sarcionus*” *intermedius* (Van Duzee), [NT]: 1 ♂ paratype (AMNH)

“*Sarcionus*” *maculatus* (Van Duzee), [NT]: ♂ holotype, 1 ♀ paratype (USNM)

GENUS *PLATYOPSIS* PARENT

(Fig. 25A-E)

Platyopsis Parent, 1929b: 12. Type species: *Hercostomus (Platyopsis) maroccanus* Parent [Palearctic], by monotypy.

Recognition. *Platyopsis* is distinguished by the following combination of characters: face broad, clypeus strongly bulging and subequal in height to face, mid femur with 2-4 anterior and 2 posteroventral preapical setae, hind femur with 2 anterodorsal preapical setae, hind basitarsus with 1 strong basiventral seta, distal section of M beyond crossvein dm-cu with weak anterior bend before middle.

Description. Head: Vertex not excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2.5-3.0x wider than high, raised medially, sides weakly converging anteriorly, with violet metallic reflections. Face broad, concave, sides slightly convergent below; clypeus strongly bulging and subequal in height to face, not reaching lower eye margin. Palp large, subtriangular, with weak hairs on outer surface and a distinct apical seta. Proboscis large and thick. Antenna: Scape short, subconical, with well-developed acute medioventral process; pedicel short; first flagellomere triangular; arista dorsal, 2-segmented, second segment pubescent. Lowermost postocular seta stronger. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Scutum dull green medially with shining violet longitudinal lateral stripe along each row of dorsocentrals. Acrostichals biserial; 6 dorsocentrals, aligned; 1 strong

outer posthumeral, 1 weak inner posthumeral, sometimes indistinct; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalar; 1 postalar. Upper and lower part of propleuron with cluster of fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum bare or with a few fine hairs. Scutellum with 1 strong inner seta and 1 weaker outer seta on lateral margin.

Legs: Pulvilli developed normally on all legs. Foreleg: Femur with 2-3 weak posteroventral preapical setae; apex of basitarsus and tarsomeres 2-5 piliferous ventrally in male. Midleg: Femur with 2-4 anterior preapical setae, 2 strong posteroventral preapical setae in addition to terminal posteroventral preapical seta which is weakly developed. Hindleg: Coxa with strong lateral seta near middle; femur with 2 anterodorsal preapical setae; basitarsus shorter than second tarsomere, with a well-differentiated, strong basiventral seta, longer than width of basitarsus, male with darkened ridge and dentiform process posterobasally.

Wing: Hyaline with weak brown infuscation along crossvein dm-cu and at bend in M. R_{2+3} nearly straight with anterior apical bend; R_{4+5} curved posteriorly in distal portion; distal section of M beyond crossvein dm-cu with weak anterior bend before middle, ending before wing apex, convergent with R_{4+5} ; crossvein dm-cu equal to or slightly longer than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare; S2 and S3 unmodified; S4 strongly emarginate posteriorly, nearly divided; S5 entirely membranous; S6 Y-shaped, weakly fused with T6 posterolaterally, with narrow, rod-like base extending anteromedially to middle of S5; segment 7 forming short peduncle; S8 heart-shaped, narrowed proximally, setose. Hypopygium (Fig. 25A-C) large. Epandrium longer than high, foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe moderately developed, with preapical basiventral epandrial seta; apicoventral epandrial lobe narrow, digitiform with 3 apical setae. Surstylus 2-lobed. Ventral lobe digitiform with rounded apex, with a weak ventral and medial seta near basal third. Dorsal lobe as long as ventral lobe, apex with curved projection. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion simple, short, not extending beyond edge of epandrium. Proctiger brushes absent. Cercus broad, ovoid, with long, fine marginal setae. Hypandrium long, serrate laterally, free laterally, membranously connected to epandrium

basiventrally, hypandrial arms weakly connected to hypandrium, hypandrial apodeme absent. Sperm pump cylindrical, weakly sclerotized; ejaculatory apodeme weakly sclerotized, rod-like; basal sclerite of sperm pump well-developed, straight in dorsal view, with lateral subtriangular projections. Phallus heavily sclerotized in basal half with fin-like process near middle. Female (Fig. 25D,E): T6, S6 and S7 undivided, T7 weakly divided medially; T8 and S8 divided medially, tergite and sternite fused anterolaterally forming a narrow sclerite. T10 divided medially into hemitergites each bearing 6-7 acanthoporous spines and a single inner medial spine (Fig. 25D), spines pointed apically. Upper lobe of cercus with minute apical seta.

Geographical Distribution. This monotypic Palaearctic genus is known from North Africa, including Morocco and Algeria.

Phylogenetic Relationships. Based on the cladistic analysis, *Platyopsis* appears to be closely related to *Stenopygium* and *Pelastoneurus*; however, the male genitalia seem closer to *Tachytrechus* in overall structure, but without the distinctive upturned and flared postgonite (Fig. 33D,E). *Platyopsis maroccanus* also possesses a strong basiventral seta on the hind basitarsus like *Tachytrechus*, but this feature is homoplasious and could not be coded into discrete states due to intermediates among the exemplars examined in this study.

Remarks. Parent (1929b) indicated that the type of *P. maroccanus* was deposited in the Madrid Museum, but I found the male holotype and a female paratype in the MNHN along with a male and female from Arris, Algeria.

Material Examined.

Platyopsis maroccanus (Parent), [PA]: 1 ♂ holotype, 1 ♀ paratype, 1 ♂, 1 ♀ (MNHN)

GENUS POECILOBOTHRUS MIK

(Figs. 26A-E, 27A-C)

Achanthipodus Rondani, 1856: 201. Type species: *Dolichopus regalis* Meigen [Palearctic], by original designation. *Nomen oblitum*. [I treat this name as a *nomen oblitum* because it has not been used as a valid taxon since 1899 (I.C.Z.N Code (1999), Article 23.9.1] (see “Remarks”).

Achantipodus Rondani 1856: 144. Incorrect original spelling by revision of Negrobov (1991: 82).

Poecilobothrus Mik, 1878: 3. Type species: *Dolichopus regalis* Meigen, by original designation. *Nomen protectum*. [I treat this name as a *nomen protectum* because it has been used as a valid name in more than 25 works by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years (I.C.Z.N Code (1999), Article 23.9.2] (see “Remarks”).

Pterostylus Mik, 1878: 4. Type species: *Gymnopternus aberrans* Loew, by original designation. **syn. nov.**

Chaetosphyria Enderlein, 1936: 109. Type species: *Dolichopus regalis* Meigen, by monotypy (see “Remarks”).

Acanthipodus, subsequent misspelling by Stackelberg (1941: 183).

New Combinations and Transfers. The following new combinations are hereby established: *Poecilobothrus aberrans* (Loew, 1871) **comb. nov.** (*Pterostylus*); *Poecilobothrus chrysozygos* (Wiedemann, 1817) **comb. nov.** (*Hercostomus*). The following species is reassigned to *Poecilobothrus*: *Poecilobothrus bigoti* Mik, 1883.

Recognition. *Poecilobothrus* can be distinguished by the possession of a distinct dark metallic spot above the notopleuron, and 1 strong posterior to posteroventral preapical seta on the mid femur. Males are further distinguished by their distinctive postgonite and

short, conical hypandrium which is fused to the epandrium laterally. Females are further distinguished by the possession of an inner, medial pair of acanthoporous spines on T10. Some species (e.g., *P. regalis*, *P. aberrans*) have 1 dorsal seta on hind basitarsus.

Description. Head: Vertex not distinctly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons 1.8-2.6x wider than high, sides weakly convergent anteriorly. Face moderately narrow in male, sides converging below, narrowest just above clypeus, broad in female, nearly parallel-sided. Clypeus often produced, stronger in female, lower margin straight, not reaching lower eye margin. Palp ovoid, smaller in male, with weak setae on apical half of outer surface and a distinct apical seta. Antenna: Scape short, subconical, with distinct, acute medioventral process; pedicel short; first flagellomere subtriangular; arista dorsal, 2-segmented, second segment pubescent to plumose. Lowermost postocular seta usually longer. Postvertical setae stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 6 dorsocentrals, aligned or with fifth pair very weakly offset medially; postpronotum with 1 strong medioclinate seta; 1 strong outer posthumeral, 1 weaker inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalar; 1 postalar. Distinct dark metallic spot above notopleuron. Upper and lower part of propleuron with cluster of fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum with distinct cluster or vertical row of fine hairs. Scutellum with 1 strong inner seta and 1 weak outer seta on lateral margin, dorsal surface usually with sparse fine hairs.

Legs: Pulvilli developed normally on all legs. Midleg: Femur with 1 anterior preapical seta, 1 strong posterior to posteroventral preapical seta about even with anterior preapical in addition to terminal posteroventral preapical which is also sometimes developed; basitarsus sometimes with 1 strong dorsal seta present (e.g., *P. aberrans*). Hindleg: Coxa with strong lateral seta near middle; femur with 1 anterodorsal preapical seta; basitarsus subequal to slightly shorter than second tarsomere, 3-6 ventral seta, basiventral seta subequal or slightly longer than distal ventral setae, male with weak dentiform process posterobasally, sometimes with 1 strong dorsal seta (e.g., *P. aberrans*, *P. regalis*).

Wing: Greyish to brownish, sometimes strongly infuscated in males (e.g., *P. nobilitatus*). R_{2+3} nearly straight; R_{4+5} curved posteriorly in distal section, R_{2+3} and R_{4+5} weakly undulating in male *P. nobilitatus*; distal section of M beyond crossvein dm-cu with weak to distinct sinuous anterior bend before middle, nearly straight to weakly curved posteriorly beyond bend, ending slightly to distinctly before wing apex; R_{4+5} and M weakly to distinctly convergent; crossvein dm-cu distinctly shorter to distinctly longer than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare; S2-4 unmodified; S5 entirely membranous or with weakly sclerotized medial and lateral bands fusing with proximal margin of S6, sometimes with eversible, glandular projections (e.g. *P. ducalis* (Loew), *P. nobilitatus*); S6 sclerotized along lateral and anterior margin, moderately sclerotized to membranous posterolaterally; segment 7 forming well-developed peduncle; S8 teardrop-shaped to subtriangular, setose. Hypopygium (Figs. 26A-C, 27A-C) large. Epandrium about 1.5x longer than high, subrectangular to subrhomboid in lateral view, with rounded, sometimes strongly projecting anteroventral margin (Fig. 26A); foramen positioned anterolaterally on dorsal half, well-separated from base of cerci; basiventral epandrial lobe weakly developed, rounded to subquadrate, basiventral epandrial seta present on lobe; apicoventral epandrial lobe well-developed, subquadrate to subtriangular with 1 basiventral, 1 apical and usually 1 dorsal seta (absent in *P. chrysozygos*). Surstylus 2-lobed. Ventral lobe subrectangular to subtriangular, narrowed apicoventrally with 1 dorsobasal seta, 1 midventral seta, and 1 medial seta which is enlarged and modified in some species (e.g., *P. aberrans*), 1-3 stout apical setae. Dorsal lobe subtriangular, elongate, slightly longer than ventral lobe, laterally flattened and tapered to an acute upcurved point apically. Postgonite with anteroventral portion weakly sclerotized; posterodorsal portion well-developed, with acute ventrally curved medial lobe and 1-2 preapical lateroventral lobes (Figs. 26B, 27B). Proctiger brushes absent. Cercus triangular to subquadrate with long, curved marginal setae, sometimes with apical and lateral margin jagged, with elongate digitiform projections (e.g., *P. regalis*, Fig. 26A). Hypandrium short, conical, slightly dorsoventrally flattened, fused to epandrium laterally near basiventral epandrial lobe (Figs. 26C, 27C); hypandrial apodeme present, well-developed; hypandrial arms connected to hypandrium. Sperm pump more or less

cylindrical; ejaculatory apodeme well-developed, elongate and laterally flattened; basal sclerite of sperm pump heavily sclerotized, V-shaped in dorsal view. Phallus long and slender with preapical projection. Female (Fig. 26D,E): Terminalia about as long as abdomen. T6, T7, S6 and S7 undivided (weakly sclerotized in *P. regalis*); T8 and S8 divided medially, tergite and sternite not fused anterolaterally. T10 divided medially into hemitergites each bearing 3-4 acanthoporous spines along outer margin and a single, smaller, inner medial spine (Fig. 26D), spines rounded and flattened apically. Upper lobe of cercus with long apical seta.

Geographical Distribution. *Poecilobothrus* is known from the western Palaearctic ranging from western Europe to West Siberia, south to North Africa (Algeria) and the Middle East (Iran).

Phylogenetic Relationships. *Poecilobothrus* is most closely related to *Parahercostomus* and Grichanov's (1999a) Afrotropical *Hercostomus* group 1 based on the distinctive postgonite. As noted above (under "*Ortochile* genus group"), *Poecilobothrus* should be regarded as a genus and not placed in *Hercostomus* as a subgenus.

Remarks. The name *Poecilobothrus* Mik, 1878 has been threatened by the senior objective synonym *Achanthipodus* Rondani, 1856 which is not in use. *Achanthipodus* Rondani, 1856 has not, to my knowledge, been used as the valid name of this taxon since Rondani (1861: 6). Dyte (in litt.) has pointed out that *Achanthipodus* apparently did not come into use because of an erroneously presumed homonymy with *Acanthopodus* Lacépède in Pisces (Loew, 1857: 10; Bigot, 1859: 219). Furthermore, *Poecilobothrus* has been used as the presumed valid name for this taxon in over 25 works, published by over 10 authors in the last 50 years and spanning more than 34 years (e.g., Dyte, 1969; Couturier, 1974; Dyte, 1976; Negrobov and Marina, 1976; Assis Fonseca, 1978; Negrobov, 1979; Negrobov, 1980; Olejníček, 1980; Ulrich, 1981; Negrobov, 1986; Pollet and Grootaert, 1987; Pollet et al., 1988; Meyer and Heydemann, 1990; Negrobov, 1991; Pollet and Grootaert, 1991; Sato, 1991; Lunau, 1992; Pollet et al., 1992; Evenhuis, 1994; Pollet and Grootaert, 1994; Pollet and Grootaert, 1996; Grichanov, 1997; Maes and

Pollet, 1997; Chandler, 1998; Naglis, 1999; Tulowitzki et al., 1999; Pollet, 2000; Ulrich and Schmelz, 2001. In accordance with Articles 23.9.1.1 and 23.9.1.2 of the International Code of Zoological Nomenclature (1999), the precedence of *Achanthipodus* Rondani, 1856 is reversed and *Poecilobothrus* Mik, 1878 is the valid name of this taxon.

Negrobov (1991) listed *Chaetosphyria* Enderlein as a doubtful taxon because no type species was designated. However, Dyte (unpublished manuscript) points out that Enderlein (1936: 109) clearly indicated *Dolichopus regalis* Meigen as the only included species of *Chaetosphyria*, which is therefore the type species by monotypy. Stackelberg (1941) correctly listed *Chaetosphyria* as synonym of *Poecilobothrus*.

Parent's (1938) diagnosis of *Poecilobothrus* included the possession of cerci with a jagged lateral margin; however, this feature seems to only define a subgroup of species within a larger clade that also includes the newly transferred species *Poecilobothrus aberrans*, *P. chrysozygos* and *P. bigoti* Mik.

Material Examined.

Poecilobothrus aberrans (Loew), [PA]: 1 ♂ (BMNH); 1 ♂, 1 ♀ (HNHM)

Poecilobothrus bigoti Mik, [PA]: 1 ♂, 1 ♀ (MNHN)

Poecilobothrus chrysozygos (Wiedemann), [PA]: 6 ♂ ♂, 3 ♀ ♀ (LEM); 1 ♂ (CNC)

Poecilobothrus ducalis (Loew), [PA]: 1 ♂, 1 ♀ (LEM)

Poecilobothrus fumipennis (Stannius), [PA]: 2 ♂ ♂, 2 ♀ ♀ (LEM)

Poecilobothrus nobilitatus (Linnaeus), [PA]: 5 ♂ ♂, 4 ♀ ♀ (CNC); 4 ♂ ♂, 4 ♀ ♀ (LEM)

Poecilobothrus regalis (Meigen), [PA]: 1 ♂, 1 ♀ (BMNH)

GENUS *PROHERCOSTOMUS* GRICHANOV

Prohercostomus Grichanov, 1997: 83. Type species: *Dolichopus noxialis* Meunier [from Baltic amber], by original designation.

New Combinations. Grichanov (2000a) elevated *Prohercostomus* to full generic status but did not make the corresponding new combinations for the included species and their

synonyms. Accordingly, the following new combinations are hereby proposed:

Prohercostomus bickeli (Evenhuis, 1994) **comb. nov.** (*Dolichopus*); *Prohercostomus vulgaris* (Meunier, 1907) **comb. nov.** (*Dolichopus*); *Prohercostomus interceptus* (Meunier, 1907) **comb. nov.** (*Gymnopternus*); *Prohercostomus intremulus* (Meunier, 1907) **comb. nov.** (*Gymnopternus*); *Prohercostomus meunierianus* (Evenhuis, 1994) **comb. nov.** (*Dolichopus*); *Prohercostomus notabilis* (Meunier, 1907) **comb. nov.** (*Dolichopus*); *Prohercostomus monotonus* (Meunier, 1907) **comb. nov.** (*Dolichopus*); *Prohercostomus negotiosus* (Meunier, 1907) **comb. nov.** (*Dolichopus*); *Prohercostomus noxialis* (Meunier, 1907) **comb. nov.** (*Dolichopus*).

Diagnosis (based on Grichanov 1997, 2000a). Head: Face evenly narrowed toward clypeus, relatively narrow in male; clypeus not convex. Palp small. Antenna with first flagellomere subtriangular, asymmetrical; arista practically bare. Postocular setae black, numerous.

Thorax: Acrostichals biserial, reaching fifth pair of dorsocentrals; 6 dorsocentrals; 1 stout postpronotal with several short setae; notopleural pit without purple spot; posterior part of mesoscutum without dark hairs. Propleuron with 1 stout seta. Scutellum with 1 stout inner seta and 1 outer hair on lateral margin.

Legs simple. Fore and mid coxae with small hairs and setae on distal half, hind coxa with 1 strong lateral seta. Mid and hind femur with 1 stout but short anterior preapical seta. Tibial setae poorly developed, scarcely as long as diameter of tibia, ventral bristles underdeveloped, dorsal setae on fore and hind tibiae arranged in a single series along entire length. Hind basitarsus without setae above, without stout ventral seta.

Wing elliptical, about twice as long as wide; R_1 reaching wing at midlength; R_{4+5} and M parallel in distal half of wing; M reaching costa near wing apex; anal lobe broad, alula not developed.

Abdomen and sternite 8 setose: Hypopygium not large, without stalk; cercus simple; male surstylus and epandrial lobe massive, simple.

Phylogenetic Relationships. The systematic position of *Prohercostomus* within the Dolichopodinae is currently unknown.

Remarks. Grichanov (1997) originally described *Prohercostomus* as a subgenus of *Hercostomus* based on Baltic amber fossils, but did not provide any synapomorphy-based evidence to support his subgeneric classification. Recently, Grichanov (2000a) elevated *Prohercostomus* to generic status, but did not discuss the reason for this action. Ulrich (2003) considered it inappropriate to treat *Prohercostomus* as a subgenus of *Hercostomus* because *Hercostomus* is a polyphyletic assemblage of species and *Hercostomus*, in the sense of the type species *H. longiventris*, has not been found in amber.

GENUS *STENOPYGIUM* BECKER

(Figs. 28A-C, 29A-E)

Stenopygium Becker, 1922a: 75. Type species: *Stenopygium nubeculum* Becker [Neotropical], by monotypy.

New Combination. The following new combination is proposed: *Stenopygium punctipennis* (Say, 1829) **comb. nov.** (*Pelastoneurus*).

Recognition. *Stenopygium* can be recognized by the following combination of characters: clypeus bulging and subequal in height to face, arista usually pubescent (occasionally plumose in females), 6 dorsocentrals, wing with brownish spots or bands, vein M beyond crossvein dm-cu with weak anterior bend before middle, hypopygium distinctive, subtriangular, phallus strongly wrinkled. *Stenopygium* is similar to *Pelastoneurus* and *Platyopsis* and can be distinguished from these genera by the characters given above and in the key.

Description. Head: Vertex more or less flat to weakly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 3-4x wider than high, sides slightly convergent anteriorly. Face and clypeus broad, broader in female; face with sides subparallel to weakly converging below; clypeus strongly bulging and subequal in height

to face, widening below, lower margin straight, not reaching lower eye margin. Palp large, subtriangular with weak setae on outer surface and a weakly differentiated to distinct apical seta. Proboscis large and thick. Antenna: Scape short, subconical, with well-developed acute medioventral process; pedicel short; first flagellomere subrectangular to subtriangular, weakly to strongly pointed dorsoapically, longer than high in male, about as long as high in female; arista dorsal, close to base in male, 2-segmented, distal segment strongly pubescent, occasionally plumose in females (e.g. *S. punctipennis*). Postvertical setae slightly to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 6 dorsocentrals, aligned or with fifth pair weakly offset medially; 1 strong medioclinate postpronotal; 1 outer posthumeral, 1 weaker inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with weak hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum with a row of fine hairs. Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin.

Legs: Pulvilli developed normally on all legs. Foreleg: Basitarsus with distinct basiventral seta. Midleg: Femur with 1 anterior preapical seta, *S. nubeculum* with a series of long, fine hairs basiventrally; basitarsus with weak to distinct basiventral seta. Hindleg: Coxa with strong lateral seta slightly to distinctly below middle; femur with 1 anterior to anterodorsal preapical seta, sometimes with 1 weak anteroventral preapical seta; tibia of male without posteroapical process; basitarsus distinctly shorter than second tarsomere, usually with distinct basiventral seta and 1-2 weaker ventral setae, male with well-developed, dentiform to hook-like process posterobasally.

Wing: Greyish with several distinct to weakly defined dark spots or bands. R_{2+3} relatively straight to weakly curved; R_{4+5} curved posteriorly in distal section; distal section of M beyond crossvein dm-cu with weak anterior bend before middle, convergent with R_{4+5} , ending before wing apex; crossvein dm-cu subequal to or longer than distal section of CuA_1 .

Abdomen: Subconical. Male: T6 bare; S2-S3 unmodified; S4 emarginate and membranous posteromedially; S5 sclerotized along anterolateral margin, mainly

membranous posteromedially; S6 mainly membranous, weakly sclerotized along anterior margin; segment 7 forming well-developed peduncle; S8 subrectangular, narrowed basally, setose. Hypopygium (Figs. 28A-C, 29A-C): Epandrium subtriangular in lateral view, about 2.0-2.4x longer than high; foramen positioned anterolaterally, well-separated from base of cerci; basiventral epandrial lobe not developed, basiventral seta positioned before middle of ventral epandrial margin; apicoventral epandrial lobe weakly developed, ridge-like, bearing 2 setae. Surstylus 2-lobed. Ventral lobe digitiform to subtriangular with broadened base, 1 lateral seta, 1-2 strong apical setae. Dorsal lobe digitiform with 2 strong apical setae. Postgonite with anteroventral portion well-sclerotized, with trough-like base positioned below sperm pump; posterodorsal portion well-developed, digitiform. Proctiger brushes present. Cercus subtriangular, narrow and elongate in *S. nubeculum* (Fig. 28A). Hypandrium long, symmetrical, membranously connected to epandrium basiventrally, free laterally, with rounded preapical lobes laterally, apex weakly emarginate (Fig. 28C) or bifurcate (Fig. 29C); hypandrial apodeme absent; hypandrial arms connected to hypandrium. Sperm pump subcylindrical; ejaculatory apodeme variable, rod-like to distinctly flattened laterally, apex sometimes medially split; basal sclerite of sperm pump V-shaped to nearly straight in dorsal view. Phallus long and slender, elbowed at base, middle section strongly wrinkled (Figs. 28B, 29A,B). Female (Fig. 29D,E): T6, S6 and S7 undivided, T7 weakly divided medially; T8 and S8 divided medially, tergite and sternite fused anterolaterally forming a narrow sclerite (Fig. 29E). T10 divided medially into hemitergites each bearing 5 acanthoporous spines.

Geographical Distribution. *Stenopygium* is known from Mexico, Costa Rica and Bolivia.

Phylogenetic Relationships. This genus appears to be closely related to *Pelastoneurus*; however, the precise relationships between *Stenopygium*, *Pelastoneurus* and *Platyopsis* is currently unclear.

Remarks. Becker (1992a) originally erected this genus based on the possession of a ventral indentation on the first flagellomere of males and an elongate male cercus.

However, both of these features are autapomorphies of *S. nubeculum*, and the former character is not always as distinct as indicated in Becker's figure.

Material Examined.

Stenopygium nubeculum Becker, [NT]: 3 ♂ ♂ syntypes (SMTD)

Stenopygium punctipennis (Say), [NT]: 7 ♂ ♂, 4 ♀ ♀ (USNM); 1 ♂ (CAS); 1 ♂ (CNC)

GENUS SYBISTROMA MEIGEN

(Figs. 30A-E, 31A-E, 32A-E)

Sybistroma Meigen, 1824: 71. Type species: *Dolichopus discipes* Germar (as "Ahrens") [Palearctic], designation by Westwood 1838-1840: 135 (see "Remarks").

Hypophyllus Haliday, 1832: 359. Type species *Dolichopus obscurellus* Fallén, by monotypy (see "Remarks").

Ludovicius Rondani, 1843: 43. Type species: *Ludovicius impar* Rondani, by monotypy. **syn. nov.**

Nodicornis Rondani, 1843: 46. Type species: *Nodicornis wiedemanni* Rondani, by monotypy [= *Sybistroma nodicornis* Meigen, 1824: 72]. **syn. nov.**

Haltericerus Rondani, 1856: 143. Type species: *Ludovicius impar* Rondani, by original designation. **syn. nov.**

Nemospathus Bigot, 1859: 215. Type species: *Sybistroma dufouri* Macquart, by original designation. **syn. nov.**

Osodostylus Bigot, 1859: 215. Type species: *Sybistroma nodicornis* Meigen (as "Macq."), by original designation. **syn. nov.**

Dasyarthrus Mik, 1878: 5. Type species: *Gymnopternus inornatus* Loew, by original designation. **syn. nov.**

Spathitarsis Bigot, 1888a: xxiv. Type species: *Dolichopus discipes* Germar (as “Ahrens”), by original designation.

Hyppophyllus, incorrect subsequent spelling by Bigot, 1890: 276.

Hyphyllus, incorrect subsequent spelling by Becker, 1917: 255

New Combinations and Transfers: The following new combinations are hereby established: *Sybistroma acutatus* (Yang, 1996b) **comb. nov.** (*Ludovicius*); *Sybistroma apicicrassus* (Yang and Saigusa, 2001a) **comb. nov.** (*Ludovicius*); *Sybistroma apicilarius* (Yang, 1999a) **comb. nov.** (*Ludovicius*); *Sybistroma biaristatus* (Yang, 1999a) **comb. nov.** (*Ludovicius*); *Sybistroma biniger* (Yang and Saigusa, 1999) **comb. nov.** (*Ludovicius*); *Sybistroma bogoria* (Grichanov, 2004) **comb. nov.** (*Ludovicius*); *Sybistroma brevidigitatus* (Yang and Saigusa, 2001a) **comb. nov.** (*Ludovicius*); *Sybistroma crinicauda* (Zetterstedt, 1849) **comb. nov.** (*Dolichopus*); *Sybistroma curvatus* (Yang, 1998c) **comb. nov.** (*Ludovicius*); *Sybistroma digitiformis* (Yang, Yang and Li, 1998) **comb. nov.** (*Ludovicius*); *Sybistroma dorsalis* (Yang, 1996a) **comb. nov.** (*Ludovicius*); *Sybistroma emeishanus* (Yang, 1998a) **comb. nov.** (*Ludovicius*); *Sybistroma eucerus* (Loew, 1861a) **comb. nov.** (*Haltericerus*); *Sybistroma fanjingshanus* (Yang, Grootaert and Song, 2002) **comb. nov.** (*Ludovicius*); *Sybistroma flavus* (Yang, 1996b) **comb. nov.** (*Ludovicius*); *Sybistroma golanicus* (Grichanov, 2000b) **comb. nov.** (*Ludovicius*); *Sybistroma henanus* (Yang, 1996b) **comb. nov.** (*Ludovicius*); *Sybistroma impar* (Rondani, 1843) **comb. nov.** (*Ludovicius*); *Sybistroma incisus* (Yang, 1999b) **comb. nov.** (*Ludovicius*); *Sybistroma inornatus* (Loew, 1857) **comb. nov.** (*Gymnopternus*); *Sybistroma israelensis* (Grichanov, 2000b) **comb. nov.** (*Ludovicius*); *Sybistroma longiaristatus* (Yang and Saigusa, 1999) **comb. nov.** (*Ludovicius*); *Sybistroma longidigitatus* (Yang and Saigusa, 2001a) **comb. nov.** (*Ludovicius*);

Sybistroma lorifer (Mik, 1878) **comb. nov.** (*Hercostomus*); *Sybistroma luteicornis* (Parent, 1944) **comb. nov.** (*Hypophyllus*); *Sybistroma miricornis* (Parent, 1926) **comb. nov.** (*Ludovicius*); *Sybistroma neixianganus* (Yang, 1999a) **comb. nov.** (*Ludovicius*); *Sybistroma qinlingensis* (Yang and Saigusa, 2001a) **comb. nov.** (*Ludovicius*); *Sybistroma sciophyllus* (Loew, 1869) **comb. nov.** (*Hypophyllus*); *Sybistroma sheni* (Yang and Saigusa, 2000b) **comb. nov.** (*Ludovicius*); *Sybistroma sichuanensis* (Yang, 1998b) **comb. nov.** (*Ludovicius*); *Sybistroma sinaiensis* (Grichanov, 2000b) **comb. nov.** (*Ludovicius*); *Sybistroma spectabilis* (Parent, 1928) **comb. nov.** (*Ludovicius*); *Sybistroma sphenopterus* (Loew, 1859) **comb. nov.** (*Hypophyllus*); *Sybistroma transcaucasius* (Stackelberg, 1941) **comb. nov.** (*Ludovicius*); *Sybistroma yunnanensis* (Yang, 1998a) **comb. nov.** (*Ludovicius*). The following species are reassigned to *Sybistroma*: *Sybistroma dufouri* Macquart, 1838; *Sybistroma nodicornis* Meigen, 1824.

Recognition. Most males of *Sybistroma* can be distinguished by the following combination of characters: antenna usually modified, with enlarged scape, reduced pedicel, arista 1-segmented and usually with one or more lamellae; wing with weak sinuous anterior bend before middle; hypopygium usually with basiventral epandrial lobes elongate and digitiform with pointed or frayed knob-like tip, shifted ventrally and lying beside hypandrium. Males lacking modified antennae can be distinguished by the possession of greatly elongated and setose apicoventral epandrial lobes. Females cannot readily be distinguished from some species currently placed in *Hercostomus*.

Description. Head: Sometimes distinctly broader than high in male (e.g., *S. dufouri*). Vertex more or less flat to weakly excavated, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2-3x wider than high, sides weakly convergent anteriorly, male occasionally with dense tuft of velvety hairs between antennal socket and eye margin near frons-face boundary (e.g., *S. nodicornis*). Face very narrow to broad in male, with sides converging below, broad in female, sides subparallel to weakly converging below; clypeus relatively narrow and flat to weakly produced in male, broad and often strongly produced in female, lower margin straight to weakly emarginate, not reaching lower eye margin. Palp usually small, ovoid, occasionally enlarged and flattened (e.g., *S. dorsalis*)

with fine setae on outer surface, distinct apical seta present or absent. Antenna often modified in male, occasionally inserted just slightly above middle of head in male; scape of male usually slightly to greatly swollen and semi-globular (e.g., *S. impar*), sometimes unmodified and subconical (e.g., *S. obscurellum*), medioventral process usually absent or indistinct, sometimes weakly developed; scape of female short, subconical, with well-developed to indistinct medioventral process; pedicel short, often strongly reduced in male (e.g., *S. impar*); first flagellomere of male variable in size and shape, short and rounded apically (e.g., *S. spectabilis*) to greatly elongated and acute apically (e.g., *S. nodicornis*); first flagellomere of female short, usually about as long as wide, rounded or pointed apically; arista of male dorsobasal to apical, 1 or 2-segmented, short to greatly elongated, often with apical lamella, occasionally also with 1-2 medial lamellae, basal segment occasionally elongate (e.g., *S. discipes*), distal segment weakly pubescent to glabrous; arista of female dorsal to subapical, 2-segmented, distal segment weakly pubescent. Lower postocular setae sometimes weaker. Postvertical setae subequal to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals usually biserial, occasionally extending to base of scutellum (e.g., *S. nodicornis*), sometimes uniserial (e.g., *S. biniger*), reduced or absent (e.g., *S. flavus*); 6 dorsocentrals, fifth pair slightly to strongly offset medially; 1 strong mediocline postpronotal; 1 strong outer posthumeral, 1 weak to indistinct inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle bare; metepisternum usually with 1 or more fine hairs in a cluster or row, occasionally absent (e.g., *S. inornatus*); katepisternum sometimes with sparse fine hairs (e.g., *S. impar*, *S. eucerus*, *S. dufouri*). Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin, dorsum and posterior margin often with fine setae, sometimes dense (e.g., *S. nodicornis*).

Legs: Pulvilli usually developed normally on all legs, occasionally somewhat reduced on foreleg of males with enlarged fifth tarsomere (e.g., *S. discipes*). Foreleg: Femur usually with distinct posteroventral preapical seta; tibia occasionally with distinct anterodorsal comb-like row of strong setae (e.g., *S. flavus*); tarsus of male sometimes modified (e.g., *S. crinipes* Staeger, *S. discipes*, *S. eucerus*). Midleg: Coxa of male

occasionally with elongate, curved marginal setae (e.g., *S. eucerus*); femur with 1 anterior preapical seta, occasionally with weakly differentiated to distinct posterior preapical in addition to terminal posteroventral preapical seta which is usually present (e.g., *S. lorifer*, some specimens of *S. impar*), male sometimes with 2-3 long basiventral setae (e.g., *S. flavus*), or with row of elongate ventral setae (e.g., *S. eucerus*); tarsus of male occasionally modified, with distal segments flattened (e.g., *S. nodicornis*). Hindleg: Coxa with strong lateral seta near or slightly above middle; femur with 1 anterodorsal preapical seta, male occasionally with 1 or more long ventral setae in basal part (e.g., *S. miricornis*), male sometimes with well-developed setae dorsobasally (e.g., *S. nodicornis*); tibia of male with or without weak dentiform posteroapical process; basitarsus usually shorter than second tarsomere, occasionally subequal, often with a few ventral setae, male with or without weak dentiform or hook-like process posterobasally.

Wing: Brownish to greyish. R_{2+3} relatively straight; R_{4+5} with distinct posterior curve in distal section; distal section of M beyond crossvein dm-cu with weak sinuous anterior bend before middle, ending near to distinctly before wing apex; R_{4+5} and M weakly to distinctly convergent, occasionally subparallel; crossvein dm-cu distinctly shorter than distal section of CuA_1 .

Abdomen: Subconical, sometimes elongate and slender in male, with tergites long. Male: T5 sometimes with elongate setae on posterior margin; T6 bare; S2 and S3 unmodified to weakly sclerotized and partially membranous; S4 emarginate posteromedially to mainly membranous; S5 mainly membranous, often with weakly sclerotized longitudinal bands; S6 mainly membranous, weakly sclerotized along anterior margin; segment 7 forming well-developed peduncle; S8 subtriangular or heart-shaped to subquadrate, setose. Hypopygium (Figs. 30A-C, 31A-C, 32A-C) large. Epandrium variable in shape, about 1.5-3x longer than high, often deeply cleft dorsally with cerci arising preapically (Figs. 30A, 31A); foramen slightly to distinctly dorsolateral, close to base of cerci (e.g., *S. obscurellum*, Fig. 30A) or well-separated from base of cerci (e.g., *S. nodicornis*, Fig. 32A); basiventral epandrial lobes shifted ventrally and lying beside hypandrium, right and left lobes usually elongate, digitiform and symmetrical, occasionally asymmetrical, basiventral epandrial seta apical usually thickened, knob-like with pointed or frayed tip (Figs. 31A, 32A), occasionally unmodified (Fig. 30B);

apicoventral epandrial lobe variable, weakly to strongly developed, with or without setae, lobe sometimes greatly elongated, with elongate and/or modified setae (e.g., *S. obscurellum*, *S. impar* Figs. 30A,C, 31A,C). Surstylus 2-lobed. Ventral and dorsal lobe more or less digitiform and similar in size, sometimes extremely elongate and slender (e.g., *S. obscurellum*, *S. impar*, Figs. 30B, 31B), dorsal lobe occasionally with frayed seta (e.g., *S. nodicornis*, Fig. 32B). Postgonite with anteroventral portion weakly to moderately sclerotized, sometimes distinctly flattened laterally; posterodorsal portion well-developed, slightly to strongly upturned, sometimes elongate (e.g., *S. obscurellum*, *S. impar*, Figs. 30B, 31B), usually with weak lateral projection in basal portion, projection occasionally well-developed and subapical (e.g., *S. nodicornis*), extreme base occasionally with weak, sometimes bifurcate, projection (e.g., *S. discipes*, *S. eucerus*). Proctiger brushes absent. Cercus variable in shape, subrectangular to subtriangular or ovoid, sometimes with distinct notch along apical margin, often with 1 or more thick, modified setae (e.g., *S. obscurellum*, *S. impar* Figs. 30A, 31A). Hypandrium variable, trough-like (e.g., *S. obscurellum*, Fig. 30C), to asymmetrical, sometimes partially membranous and/or with dorsal projections (e.g., *S. nodicornis*, Fig. 32B,C), hypandrium laterally flanked by basiventral epandrial lobes and fused with lobes basally; hypandrial apodeme present, well-developed; hypandrial arms connected to hypandrium. Sperm pump small, rounded to subconical; ejaculatory apodeme usually short and rod-like, often upturned, apex occasionally weakly flattened laterally; basal sclerite of sperm pump weakly developed, widening apically, subtriangular to V-shaped in dorsal view. Phallus long, slender and curved (e.g., *S. obscurellum*, Fig. 30B) to relatively short and straight, with distinct articulation basally with sperm pump (e.g., *S. nodicornis*, *S. impar*, Figs. 31B, 32B). Female (Figs. 30D,E, 31D,E, 32D,E): T6, T7, S6 and S7 undivided; T8 divided medially, S8 divided medially or undivided, tergite and sternite not fused anterolaterally; T10 divided medially into hemitergites each bearing 3-5 acanthoporous spines, apex of spines rounded and flattened. Upper lobe of cercus usually with long apical seta.

Geographical Distribution. *Sybistroma*, as newly defined above (i.e. including species of *Ludovicus* and *Nodicornis*), occurs in the Palaearctic (Europe and North Africa to China), Oriental China (Yunnan) and in the Afrotropical realm.

Phylogenetic Relationships. *Sybistroma* is most closely related to the *Hercostomus longiventris* lineage based primarily on the position of the basiventral epandrial lobes which are shifted ventrally and laterally flanking the hypandrium (character 63:1).

Remarks. As noted by Chandler (1998: Note 3), *Hypophyllus* Haliday, 1932 is a junior synonym of *Sybistroma* Meigen, 1824 because of the designation of *Dolichopus discipes* Germar, 1821 as the type species of *Sybistroma* by Westwood (1838-1840: 135). *Dolichopus discipes* Germar, 1822 is considered to be congeneric with *Dolichopus obscurellus* Fallén, 1823, the type species of *Hypophyllus*.

Yang (1996c) described *Hypophyllus sinensis* Yang from Palaearctic China; however, this species is not congeneric with *Sybistroma* and clearly belongs to the clade including *Poecilobothrus*, *Parahercostomus* and Grichanov's (1999a) Afrotropical *Hercostomus* species group 1, based on the possession of preapical dorsolateral lobes on the postgonite. In particular, this species appears to be closely related to Grichanov's (1999a) Afrotropical *Hercostomus* species group 1 based on the modified hind tarsus of males; however, until a more extensive phylogenetic analysis of this lineage is completed this species will remain unplaced. For the present I have listed it below as "*Hypophyllus*" *sinensis* indicating the problematic generic assignment.

Parent (1938) noted that the arista of males of *S. miricornis* is 2-segmented; however, a more detailed examination (including a slide mount of the arista under a compound microscope at high power) indicates that the arista is actually 1-segmented.

Material Examined.

Sybistroma binodicornis Stackelberg, [PA]: 1 ♂ (USNM)

Sybistroma crinipes (Staeger), [PA]: 3 ♂ ♂, 5 ♀ ♀ (LEM)

Sybistroma discipes (Germar), [PA]: 2 ♂ ♂ (CNC); 1 ♂, 1 ♀ (BMNH)

Sybistroma dufouri Macquart, [PA]: 2 ♂ ♂, 1 ♀ (CNC)

- Sybistroma eucerus* (Loew), [PA]: 2♂♂ (DEI)
- Sybistroma flavus* (Yang), [PA]: 1♂ (LEM)
- Sybistroma impar* (Rondani), [PA]: 1♂, 2♀♀ (DEI); 1♂ (BMNH)
- Sybistroma inornatus* (Loew), [PA]: 2♂♂, 2♀♀ (USNM); 1♂, 1♀ (USNM)
- Sybistroma lorifer* (Mik), [PA]: 1♂, 1♀ (ISNB)
- Sybistroma maerens* Loew, [PA]: 2♂♂, 2♀♀ (DEI)
- Sybistroma miricornis* (Parent), [PA]: 2♂♂ syntypes, 2♀♀ syntypes (DEI); 2♂♂ syntypes, 2♀♀ syntypes (MNHN)
- Sybistroma nodicornis* Meigen, [PA]: 2♂♂, 2♀♀ (LEM); 1♂ (BMNH); 1♂ (CNC)
- Sybistroma obscurellum* (Fallén), [PA]: 13♂♂, 4♀♀ (LEM); 4♂♂, 2♀♀ (CNC)
- Sybistroma setosa* Schiner, [PA]: 2♂♂, 1♀ (DEI)
- Sybistroma spectabilis* (Parent), [PA]: 1♂ (MNHN)
- Sybistroma sphenopterum* (Loew), [PA]: 1♂ (LEM)
- “*Hypophyllus*” *sinensis* Yang, [PA]: 1♂ paratype, 1♀ paratype (LEM)

GENUS *TACHYTRECHUS* STANNIUS

(Figs. 33A-G, 34A-E, 35A-E, 36A-E)

Ammobates Stannius, 1831: 33. Incorrect original spelling by revision of Haliday (1851: 173).

Tachytrechus Stannius, 1831: 261. Erroneously treated as a nomen nudum by Foote et al. (1965), Robinson (1970b), Dyte (1975), Dyte and Smith (1980), Bickel and Dyte (1989), Negrobov (1991) and Sabrosky (1999), Type species: *Ammobates notatus* Stannius [Palearctic], designation by Rondani, 1856: 143 from species first included by Stannius (1831: 268-270).

Hammobates, subsequent misspelling by Rondani, 1856: 143.

Stannia Rondani, 1857: 14. Type species: *Ammobates notatus* Stannius, automatic.
Unnecessary n. name for *Ammobates* Stannius, 1831.

Gongophora Philippi, 1875: 86. Type species: *Gongophora medinae* Philippi, by monotypy. Synonymized by Robinson (1970b).

Congophora Philippi, 1875: 86. Incorrect original spelling by revision of Pollet et al. (2004).

Polymedon Osten Sacken, 1877: 317. Type species: *Polymedon flabellifer* Osten Sacken, by monotypy. Synonymized by Robinson (1970b).

Macellocerus Mik, 1878: 5. Type species: *Tachytrechus moechus* Loew, by original designation.

Psilischium Becker, 1922a: 93. Type species: *Psilischium laevigatum* Becker, by monotypy. Synonymized by Robinson (1970b).

Gonioneurum Becker 1922a: 98. Type species: *Gonioneurum varum* Becker, by monotypy. **syn. nov.**

Syntomoneurum Becker, 1922a: 123. Type-species *Syntomoneurum alatum* Becker, 1922a: 124, by monotypy. **syn. nov.**

Tetrectus, error by Van Duzee (1924: 43).

Gongrophora, subsequent misspelling by Porter (1929: 230), repeated by Robinson (1970b: 53).

Syntormoneurum, subsequent misspelling by Parent, (1931: 17; 1934c: 273; 1954: 226).

Tachytrechus, subsequent misspelling by Dyte (1975: 238).

New Combinations. The following new combinations are hereby established:

Tachytrechus alatus (Becker, 1922a) **comb. nov.** (*Syntomoneurum*); *Tachytrechus analis* (Parent, 1954) **comb. nov.** (*Syntomoneurum*); *Tachytrechus beckeri* (Parent, 1931) **comb. nov.** (*Syntomoneurum*); *Tachytrechus giganteus* (Brooks in Brooks and Wheeler, 2002) **comb. nov.** (*Syntomoneurum*); *Tachytrechus varus* (Becker, 1922a) **comb. nov.** (*Gonioneurum*).

Recognition. Most species of *Tachytrechus* can be recognized by the clypeus which usually extends to or beyond the lower eye margin and/or is rounded below. Other species can be recognized by the face narrowed below the antennae and widening below, 1 very strong basiventral seta on the hind basitarsus, usually 2 or more anterodorsal preapical setae on the hind femur, and by the distinctive upturned and flared postgonite of the male genitalia.

Description. Head: Usually unmodified, occasionally anteroposteriorly flattened (e.g., *T. laevigatus*) or dorsoventrally elongated (e.g., male *T. auratus* (Aldrich), *T. moechus*). Dorsal part of occiput occasionally slightly concave (e.g., *T. aldrichi*). Vertex usually distinctly excavated, sometimes weakly or strongly, 1 pair of vertical setae, usually stronger than postverticals, occasionally reduced (*T. seriatus* Robinson, males of *T. laevigatus*, *T. flabellifer*, *T. transversus* (Van Duzee)). Frons about 2-5x wider than high, sides weakly to strongly convergent anteriorly, some males (e.g., *T. greeni* Foote, Coulson and Robinson, *T. moechus* and related species) with dense tuft of velvety hairs between antennal socket and eye margin near frons-face boundary. Face very narrow to broad, usually narrowest below antennae or near middle and widening below, sometimes parallel-sided, often broader in female, boundary with clypeus indistinct in some species; clypeus usually extending to or beyond lower margin of eyes, sometimes far beyond margin in males (e.g., *T. flabellifer*), occasionally not reaching lower margin of eyes (e.g., *T. costalis* (Becker), male *T. olympiae* (Aldrich), females of some species), usually broad (at least as broad as face), usually not produced, occasionally weakly produced in females

of some species, usually rounded or subtriangular below, occasionally subquadrate. Palp usually small, occasionally large (e.g., *T. castus*, *T. transversus*), ovoid, apex rounded to subtriangular, with fine setae on outer surface, distinct apical seta present or absent, occasionally very strong (e.g., *T. transversus*). Proboscis sometimes enlarged and projecting (e.g. *T. giganteus*). Antennae sometimes inserted very high on head (e.g., male *T. moechus*); scape usually subconical, short to elongate and somewhat flattened laterally, acute medioventral process usually well-developed, sometimes indistinct, males of some species (e.g., *T. moechus*) with scape elongate, thickened and densely setose dorsally; pedicel usually short, apical margin often with 1 strong dorsal seta and/or 1-2 strong ventral setae, pedicel sometimes greatly reduced and funnel-shaped with apical ring of setae reduced or absent in male (e.g., *T. moechus*, *T. laevigatus*); first flagellomere round or ovoid to subtriangular; arista dorsal to subapical, usually 2-segmented, occasionally 1-segmented in male (e.g., *T. binodatus* Loew), distal segment glabrous, bare or shortly pubescent, sometimes elongated with apical lamella in male (e.g., *T. moechus*), rarely with second lamella near middle (e.g., *T. binodatus*). Postocular setae well-developed, occasionally finer in male, lowermost seta/setae often stronger, postgenal area behind lower postoculars occasionally with dense setae. Postvertical setae usually stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial, occasionally absent in male (e.g., *T. flabellifer*); anterior part of notum sometimes with clothing setae extending to level of transverse suture, with anterior pair of dorsocentrals arising near level of transverse suture (e.g., *T. albonotatus* (Loew)); 5-6 dorsocentrals, penultimate pair in line or offset medially; posterior mesonotum in front of scutellum usually bare, rarely with fine setae (e.g., *T. aldrichi*); 1 strong medioclinate postpronotal; 1 strong outer posthumeral, 1 weaker to sometimes indistinct inner posthumeral; usually 2 notopleurals, posterior notopleural sometimes strongly reduced (e.g., *T. aldrichi*, *T. flabellifer*), occasionally absent (e.g., *T. alatus*), rarely with 1-2 fine setae between anterior and posterior notopleural (e.g., *T. nigripes* (Aldrich), *T. parvicauda* (Van Duzee)); 1 presutural, occasionally indistinct (e.g., *T. calyptopygeus* Robinson); 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with very fine to relatively coarse hairs, sometimes dense and/or long, upper part of propleuron occasionally with 2-3 strong setae amongst hairs (e.g., *T. tessellatus*

(Macquart)), lower part of propleuron usually with 1 strong prothoracic seta, occasionally reduced (e.g., *T. utahensis* Harmston and Knowlton); pleural surface in front of posterior spiracle usually bare, occasionally with a cluster of fine hairs (e.g., *T. aldrichi*, *T. angustipennis* Loew, *T. granditarsis* Greene, *T. utahensis*, *T. seriatus*); metepisternum usually with a cluster of several fine hairs, sometimes bare or with 1-2 hairs. Scutellum with 1 strong inner seta and 1 small to moderately-sized outer seta (up to about 0.5x inner seta) on lateral margin, outer seta occasionally absent (e.g., *T. flabellifer*), dorsum and/or posterior margin occasionally with fine setae (e.g., *T. aldrichi*, *T. parvicauda*).

Legs: Pulvilli usually present on all legs, occasionally absent on mid- and hindleg (e.g., *T. alatus* group). Foreleg: Femur occasionally with 1 strong basiventral seta close to joint with trochanter (e.g., *T. alatus* group), sometimes with strong anterior preapical seta (e.g. *T. castus*); tarsus often laterally flattened in both sexes. Foreleg often modified in male: femur and tibia with variably modified setae and hairs; femur sometimes swollen basally, occasionally with bare patch on medial surface (e.g., *T. binodatus*, *T. utahensis*) and/or opaque, velvety, dark spot basally (e.g., *T. olympiae*); tibia occasionally thickened or strongly flattened dorsoventrally (e.g., *T. aldrichi*, *T. laevigatus*, *T. fusiformis* (Becker)) or laterally (e.g., *T. laticrus* Van Duzee); tarsus occasionally laterally flattened with modified dorsal setae (e.g., *T. ammobates* (Haliday)), males of some species with pile ventrally (e.g., *T. planifacies* Robinson, *T. seriatus*), occasionally with whitish or silver pollinosity in male; pulvilli sometimes larger in male (e.g., *T. calyptopygeus*), outer pulvillus occasionally larger than inner pad (e.g., male *T. binodatus*, *T. olympiae*). Midleg: Coxa of male occasionally with cluster of 2-3 strong setae anteriorly (e.g., *T. alatus* group). Femur with 1-5 anterior preapical setae, sometimes with weak anteroventral and posteroventral setae, chaetotaxy variable, occasionally with long setae ventrally (e.g., *T. laevigatus*, *T. ammobates*, *T. ripicola* Loew, male *T. auratus*), males of some species (e.g., *T. notatus*) with ventral tubercle; tibial chaetotaxy occasionally modified in male (e.g., *T. binodatus*); tarsus usually unmodified, occasionally tarsomeres enlarged and flattened in male (e.g., *T. granditarsis*). Hindleg: Coxa with strong lateral seta positioned slightly above to slightly below middle, seta occasionally reduced (e.g., *T. laevigatus*); femur with 1-6 strong anterodorsal preapical setae, distal seta sometimes shifted anteriorly, occasionally with a cluster of up to 10 preapical setae (e.g., *T.*

ammobates), preapical seta sometimes shifted proximally (e.g., *T. vanduzeei* Robinson), femur sometimes laterally flattened and wide, occasionally with ventral setae (e.g., *T. novus* Parent); tibia usually unmodified, occasionally with modified setae in male (e.g., *T. angustipennis*), male with variably developed posteroapical process, usually dentiform or claw-like, occasionally flat and subquadrate (e.g., *T. flabellifer*); basitarsus slightly longer to slightly shorter than second tarsomere, with a well-differentiated, strong, thick basiventral seta, longer than width of basitarsus, often at extreme base of tarsomere, male with variably developed dentiform to hook-like posterobasal process.

Wing: Hyaline to brownish or greyish, occasionally with infuscated regions near bend in M and at dm-cu (e.g., *T. intermedius* Becker, *T. notatus*), or with apical spot usually only in male (e.g., *T. floridensis* Aldrich, *T. simulatus* Greene, *T. vorax* Loew). Costa of male often with swelling or pterostigma proximal to insertion of R₁, occasionally large, flap-like, covering middle part of R₁ (e.g., *T. flabellifer*, *T. dilaticosta* (Van Duzee), *T. nigrifemoratus* (Van Duzee), *T. nimus* (Aldrich)), and/or with ventral invagination (e.g., *T. canacolli* Brooks), pterostigma weakly developed in some females, costa occasionally swollen beyond R₁ (e.g., *T. costalis*); R₂₊₃ straight to weakly sinuous, occasionally with posterior bend in distal section; R₄₊₅ with slight to strong posterior curve in distal section; distal section of M beyond crossvein dm-cu with strong to weak obtuse anterior bend before or near middle, occasionally distinctly S-shaped, M nearly straight to strongly arcuate beyond bend, sometimes bent anteriorly at apex (e.g., *T. utahensis*), usually ending distinctly before wing apex close to R₄₊₅, occasionally ending at or near wing apex (e.g., *T. laevigatus*, *T. castus*); R₄₊₅ and M weakly to strongly convergent, occasionally subparallel (e.g., *T. laevigatus*, *T. castus*); crossvein dm-cu distinctly shorter to distinctly longer than distal section of CuA₁, usually about equal, sometimes bent or sinuous, distal section of CuA₁ straight or curved toward wing margin; wing apex rather pointed in males of a few species (e.g., *T. vorax*, *T. floridensis*); calypter of male sometimes with dense cluster of elongate setae (e.g., *T. dilaticosta*, *T. flabellifer*, *T. nimus*).

Abdomen: Subconical, weakly to strongly tapering distally. Male: T5 occasionally with large posterior membranous region (e.g., *T. alatus*), T6 bare, occasionally membranous posteriorly; S2 unmodified or weakly emarginate and membranous

anteriorly and/or posteriorly; S3 unmodified or weakly to strongly emarginate and membranous posteriorly; S4 unmodified to strongly emarginate and membranous posteriorly; S5 weakly sclerotized to entirely membranous, sometimes with narrow medial sclerotization often fusing with S6 posteriorly, occasionally with an eversible glandular structure (e.g., *T. indianus* (Harmston and Knowlton), *T. longiciliatus* (Van Duzee), *T. transversus*); S6 entirely membranous to weakly sclerotized, usually more strongly sclerotized along anterior margin, sometimes fused with T6 laterally; segment 7 forming well-developed peduncle, occasionally elongate (e.g., *T. olympiae*); S8 heart-shaped to subtriangular, sometimes elongate-subtriangular, rarely ovoid, occasionally with short pedunculate base, almost entirely setose to sparsely setose laterally.

Hypopygium (Figs. 33A-E, 34A-C, 35A-C, 36A-C) large. Epandrium 1-1.8x as long as high, usually longer than high, shape variable, sometimes flattened dorsally (e.g., *T. olympiae*); foramen usually positioned anterolaterally, occasionally closer to middle, well-separated from base of cerci; basiventral epandrial lobe highly variable, weak to extremely well-developed, sometimes complex with multiple projections (e.g., *T. moechus*, Fig. 34A,C), right and left lobes symmetrical or asymmetrical, sometimes in close association with hypandrium, usually 1 basiventral epandrial seta present, sometimes absent (e.g., *T. notatus*, Fig. 33A,C), occasionally with 2 setae; flap-like epandrial projection between basiventral and apicoventral lobes sometimes developed (e.g., *T. mchughi* Harmston, *T. tenuiseta* Greene); apicoventral epandrial lobe variable, weak to well-developed, with 2 setae, upper/medial seta often thickened and frayed apically (Fig. 36A), sometimes with membranous sac arising medially to dorsally near base of apicoventral lobe (e.g., *T. notatus*, *T. moechus*, Figs. 33C, 34C), occasionally with acute process above apicoventral epandrial lobe (e.g., *T. laevigatus*, Fig. 35A,C).

Surstylus 2-lobed. Ventral lobe variable, more or less digitiform, often ridged ventrally, occasionally dorsoventrally flattened, usually with 1 distinct, dark mediodorsal seta, 1 stout or flattened apical seta, occasionally with strong ventral preapical seta. Dorsal lobe variable, digitiform to club-shaped and usually enlarged apically, sometimes slightly flattened dorsoventrally, often with patch of setae near apex, occasionally with 1-2 plumose setae (e.g., *T. laevigatus*, Fig. 35B). Postgonite with anteroventral portion weakly to moderately sclerotized, bifurcate anteriorly; posterodorsal portion well-

developed with apex distinctly upturned and flared laterally (Fig. 33D,E), rarely absent (e.g., *T. nigrifemoratus*). Proctiger brushes absent. Cercus large to rather small, shape and setation variable. Hypandrium variable, usually well-developed, occasionally reduced or weakly sclerotized (e.g., *T. auratus*, *T. olympiae*), symmetrical or asymmetrical, free laterally with sclerotized or membranous connection to epandrium basally, occasionally closely associated with basiventral epandrial lobes but not distinctly fused to lobes laterally (e.g., *T. vorax*); hypandrial apodeme absent; hypandrial arms connected to hypandrium, sometimes weakly. Sperm pump spherical to cylindrical, sometimes narrowed basally (e.g., *T. nimus*); ejaculatory apodeme rod-like, apex flared and more or less T-shaped in dorsal view, sometimes with elongated, flexed basal projections (e.g., *T. beckeri*, Fig. 36B); basal sclerite of sperm pump variably sclerotized, with lateral subtriangular projections, often V-shaped in dorsal view. Phallus elongate and slender to relatively short and thick, sometimes heavily sclerotized, simple or with variably developed projections, occasionally serrate, some species with modified apex. Female (Figs. 33F,G, 34D,E, 35D,E, 36D,E): Terminalia usually short and broad (e.g., *T. notatus*), sometimes more elongate (e.g., *T. indianus*). T6 and T7 divided medially; S6 usually complete, often emarginate anteriorly, occasionally divided medially; S7 complete or divided medially; T8 divided medially; S8 usually divided medially, sometimes complete, occasionally forming a well-sclerotized apicoventral plate-like process (e.g., *T. ammobates*); T8 and S8 separate, weakly connected or fused anterolaterally forming a short blunt projection or a broad, rounded process (process sometimes present in the absence of fusion of T8 and S8) (Figs. 33G, 34E). Furca present or absent, variable in structure, often well-developed. T10 divided medially into hemitergites each bearing 3-8 acanthoporous spines along outer margin, spines short or long, rounded or pointed apically, occasionally with a pair of inner medial spines (Figs. 34D, 36D). Upper lobe of cercus rounded or pointed apically, often with short to minute apical seta.

Geographical Distribution. *Tachytrechus* has a worldwide distribution, but is most diverse in the Neotropical region.

Phylogenetic Relationships. *Tachytrechus* is part of the clade that also includes *Cheiromyia*, *Paraclius*, *Stenopygium*, *Pelastoneurus* and *Platyopsis* based on the loss of the hypandrial apodeme (character 67:0, see discussion above under “*Tachytrechus* genus group”).

Remarks. The generic concept of *Tachytrechus* is expanded here to include the Neotropical genera *Syntomoneurum* and *Gonioneurum*. *Syntomoneurum* was originally placed in the Hydrophorinae by Becker (1922a); however, Ulrich (1981) considered it to be closely related to *Tachytrechus* and transferred it to the Dolichopodinae. Brooks and Wheeler (2002) confirmed Ulrich’s (1981) hypothesis of a close relationship between *Tachytrechus* and *Syntomoneurum* and further hypothesized that *Syntomoneurum* may represent a species group within *Tachytrechus*, making the latter paraphyletic. This hypothesis is supported by the results of the cladistic analysis and *Syntomoneurum* is considered to be congeneric with *Tachytrechus*.

Becker (1922a) erected the monotypic genus *Gonioneurum* from Colombia based on the unusual wing venation of *G. varum* (i.e. M and R₄₊₅ bent anteriorly beyond crossvein dm-cu and subparallel to each other). Becker deposited the two male syntypes in the Hungarian Museum. These specimens were subsequently destroyed during the Hungarian Revolution in 1956 (M. Foldvari, pers. comm.) and no other specimens are known. However, based on Becker’s description, *G. varum* possesses an elongate clypeus extending beyond the lower eye margin and a calypter with elongate, tightly crowded setae, which strongly suggests placement within *Tachytrechus*, near *T. flabellifer*, the type species of the junior synonym *Polymedon*. Becker also noted the similarity between *Gonioneurum* and *Polymedon*. I consider *Gonioneurum* to be congeneric with *Tachytrechus*.

Material Examined.

Tachytrechus alatus (Becker), [NT]: ♂ lectotype (ZMHB), 1 ♂ paralectotype (STMD),
2 ♀ ♀ paralectotypes (STMD), 1 ♀ paralectotype (ZMHB)
Tachytrechus albonotatus (Loew), [NE, NT]: 4 ♂ ♂, 2 ♀ ♀ (CAS)

- Tachytrechus aldrichi* (Van Duzee), [NT]: 1 ♂ paratype, 1 ♀ paratype (USNM); 1 ♂ paratype, 1 ♀ paratype (CAS)
- Tachytrechus alternatus* (Curran), [AF]: 3 ♂ ♂, 2 ♀ ♀ (BMNH); 1 ♂ (ISNB)
- Tachytrechus ammobates* (Haliday), [PA]: 1 ♂, 1 ♀ (CNC); 1 ♂, 1 ♀ (ISNB)
- Tachytrechus analis* (Parent), [NT]: ♂ holotype (MNHN)
- Tachytrechus angulatus* (Van Duzee), [NE]: 3 ♂ ♂, 1 ♀ (USNM)
- Tachytrechus angustipennis* Loew, [NE, NT, AU]: 9 ♂ ♂, 5 ♀ ♀ (CNC)
- Tachytrechus argentipes* Van Duzee, [NT]: 1 ♂ paratype (CAS)
- Tachytrechus auratus* (Aldrich), [NE]: 3 ♂ ♂, 2 ♀ ♀ (CAS)
- Tachytrechus beckeri* (Parent), [NT]: ♀ holotype (SMTD); 1 ♂, 1 ♀ (MNHN)
- Tachytrechus binodatus* Loew, [NE]: 4 ♂ ♂, 4 ♀ ♀ (CNC)
- Tachytrechus bracteatus* (Wiedemann), [AF]: 2 ♂ ♂, 1 ♀ (BMNH); 1 ♂, 1 ♀ (ISNB); 1 ♂, 1 ♀ (CAS)
- Tachytrechus californicus* (Harmston and Knowlton), [NE]: 1 ♂, 1 ♀ (CAS)
- Tachytrechus calyptopygeus* Robinson, [NT]: 3 ♂ ♂ paratypes, 2 ♀ ♀ paratypes (USNM)
- Tachytrechus canacolli* Brooks, [NE]: 1 ♂ paratype, 1 ♀ paratype (CAS)
- Tachytrechus castus* (Wheeler), [NE]: 2 ♂ ♂, 1 ♀ (CNC)
- Tachytrechus costalis* (Becker), [NT]: 2 ♂ ♂, 1 ♀ (CAS)
- Tachytrechus dilaticosta* (Van Duzee), [NE]: 3 ♂ ♂, 1 ♀ (CAS)
- Tachytrechus flabellifer* (Osten Sacken), [NE]: 6 ♂ ♂, 3 ♀ ♀ (CAS); 1 ♂, 1 ♀ (CNC)
- Tachytrechus floridensis* Aldrich, [NE]: 2 ♂ ♂, 1 ♀ (CNC)
- Tachytrechus fusicornis* (Aldrich), [NT]: 1 ♂ syntype, 1 ♀ syntype (USNM)
- Tachytrechus fusiformis* (Becker), [NT]: 2 ♂ ♂, 2 ♀ ♀ (CAS)
- Tachytrechus giganteus* (Brooks), [NT]: ♂ holotype, 1 ♂ paratype, 2 ♀ ♀ paratypes (USNM)
- Tachytrechus granditarsis* Greene, [NE]: 2 ♂ ♂, 2 ♀ ♀ (CNC)
- Tachytrechus greeni* Foote, Coulson and Robinson, [NE]: 3 ♂ ♂, 1 ♀ (CAS); 1 ♂, 1 ♀ (CNC)
- Tachytrechus harmstoni* Meuffels and Grootaert, [NE]: 1 ♂, 1 ♀ (CAS)

- Tachytrechus indianus* (Harmston and Knowlton), [NE]: 7 ♂♂, 4 ♀♀ (CNC)
- Tachytrechus intermedius* Becker, [NT]: 2 ♂♂ (CAS); 1 ♂, 1 ♀ (USNM)
- Tachytrechus keiferi* (Van Duzee), [NE, NT]: 3 ♂♂, 2 ♀♀ (CAS)
- Tachytrechus laevigatus* (Becker), [NT]: 1 ♂ syntype, 1 ♀ syntype, 1 ♂ (SMTD); 1 ♂ syntype, 1 ♀ (MNHN)
- Tachytrechus laticrus* Van Duzee, [NE]: 2 ♂♂, 2 ♀♀ (USNM)
- Tachytrechus longiciliatus* (Van Duzee), [NT]: 2 ♂♂ paratypes (CAS)
- Tachytrechus luteicoxa* Parent, [AF]: 3 ♂♂, 3 ♀♀ (MRAC)
- Tachytrechus mchughi* Harmston, [NE]: 3 ♂♂, 1 ♀ (CAS)
- Tachytrechus moechus* Loew, [NE]: 2 ♂♂, 2 ♀♀ (CNC); 2 ♂♂, 2 ♀♀ (USNM)
- Tachytrechus nigrifemoratus* (Van Duzee), [NE]: 4 ♂♂, 2 ♀♀ (CAS)
- Tachytrechus nigripes* (Aldrich), [NT]: 1 ♂ syntype (USNM)
- Tachytrechus nigripes* (Aldrich), [NT]: 3 ♂♂, 3 ♀♀ (USNM)
- Tachytrechus nimus* (Aldrich), [NE, NT]: 5 ♂♂, 2 ♀♀ (CAS)
- Tachytrechus notatus* (Stannius), [PA]: 1 ♂, 1 ♀ (CNC); 1 ♂, 1 ♀ (BMNH); 1 ♂ (CAS)
- Tachytrechus olympiae* (Aldrich), [NE]: 2 ♂♂, 2 ♀♀ (CAS)
- Tachytrechus parvicauda* (Van Duzee), [NT]: 1 ♂ (CAS)
- Tachytrechus planifacies* Robinson, [NT]: 2 ♂♂ syntypes, 2 ♀♀ syntypes (USNM)
- Tachytrechus ripicola* Loew, [PA]: 2 ♂♂, 2 ♀♀ (USNM)
- Tachytrechus sanus* Osten Sacken, [NE]: 2 ♂♂, 1 ♀ (CNC)
- Tachytrechus seriatus* Robinson, [NT]: 2 ♂♂ paratypes, 2 ♀♀ paratypes (USNM)
- Tachytrechus simulatus* Greene, [NE]: 3 ♂♂, 1 ♀♀ (CAS)
- Tachytrechus subcostatus* (Van Duzee), [NT]: 1 ♂ paratype, 1 ♀ paratype (CAS)
- Tachytrechus tenuiseta* Greene, [NE]: 1 ♂, 1 ♀ (CNC)
- Tachytrechus tessellatus* (Macquart), [PA, AF, OR, AU]: 3 ♂♂, 3 ♀♀ (CNC); 1 ♂, 1 ♀ (LEM); 1 ♂, 1 ♀ (USNM); 1 ♂ (CAS)
- Tachytrechus transversus* (Van Duzee), [NT]: ♂ holotype; 3 ♀♀ paratypes (USNM)
- Tachytrechus utahensis* Harmston and Knowlton, [NE]: 1 ♂, 1 ♀ (CAS)
- Tachytrechus vanduzeei* Robinson, [NT]: 1 ♂ (USNM)

Tachytrechus vorax Loew, [NE]: 5♂♂, 5♀♀ (CNC)

GENERA REMOVED FROM DOLICHOPODINAE

Of the 33 genera included in Dolichopodinae sensu Ulrich (1981), four (i.e. *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg, *Vetimicrotes* Dyte) have been removed from this subfamily based on the results of the cladistic analysis (Figs. 1 and 2). Their placement within the Dolichopodidae is discussed below.

GENUS *COLOBOCERUS* PARENT

Colobocerus Parent, 1933b: 403. Type species: *Colobocerus alchymicus* Parent [Australasian], by monotypy.

Remarks. Parent (1933b) erected this monotypic Australasian genus within the Sympycninae on the basis of the modified first flagellomere of the male of *C. alchymicus*. Ulrich (1981) transferred *Colobocerus* to the Dolichopodinae based on an examination of the female paratype of *C. alchymicus* (MNHN). He did not, however, provide a convincing argument to support this transfer, citing only a similarity in habitus, size, and the possession of thick, pale, stubble-like postocular setae. Ulrich's placement of *Colobocerus* in the Dolichopodinae was not followed by Bickel and Dyte (1989) and more recently Bickel (1991) suggested that *Colobocerus* should probably be synonymized with *Sympycnus*.

The results of the cladistic analysis support the exclusion of *Colobocerus* from the Dolichopodinae. *Colobocerus* lacks several ground plan features of the Dolichopodinae including a dorsally setose scape (character 1), a distinct pedicel condyle (character 3) and a bare male abdominal T6 (character 36), and based on my examination of the male holotype, appears to be a typical sympycnine. In all of the equally parsimonious trees (Fig. 1), *C. alchymicus* is grouped with the two sympycnine outgroup taxa (i.e. *Syntormon*

pallipes and *Sympycnus annulipes*) based on the reduction of segment 7 (character 37:1) and the presence of the hypandrial apodeme (character 67:1), supporting the original placement of *Colobocerus* in the Sympycninae. However, because permission to dissect the genitalia of the male holotype of *C. alchymicus* was not granted, the condition of segment 7 (character 37) could not be assessed and was scored as “?” in the matrix (Appendix 1). *Syntormon pallipes* and *C. alchymicus* are further grouped together based on the possession of a distinct posterior preapical seta on the mid femur (Character 27:1).

Material Examined.

Colobocerus alchymicus Parent, [AU]: ♂ holotype (CMNZ), 1 ♀ paratype (MNHN)

GENUS *KATANGAIA* PARENT

(Fig. 37A-E)

Katangaia Parent, 1933c: 12. Type species: *Katangaia longifacies* Parent [Afrotropical], by monotypy

Remarks. *Katangaia* was erected by Parent for the single Afrotropical species, *K. longifacies*, known only from males. Parent (1933c) originally assigned the genus to the Rhaphiinae. Negrobov (1980) considered *Katangaia* to be a dolichopodine, and Ulrich (1981) formally transferred the genus to the Dolichopodinae. Recently, Grichanov (2004) synonymized *Katangaia* with *Polymedon*, and recognized the latter as a valid genus independent of *Tachytrechus*, but did not provide any phylogenetic evidence to support his classification. Grichanov (2004) also proposed the replacement name *Polymedon octavianus* Grichanov for *Katangaia longifacies* Parent 1933c because of the homonymy created by the transfer of the latter species into *Polymedon* with the older name *Polymedon longifacies* Becker, 1922a. The results of my cladistic analysis (Figs. 1 and 2) suggests that *Katangaia* should be excluded from the Dolichopodinae. As discussed above under “*Tachytrechus* genus group”, my analysis also supports Robinson’s (1970) synonymy of *Polymedon* with *Tachytrechus*. As such, I reject the classification proposed

by Grichanov (2004). The male genitalia of “*Polymedon*” *ethiopiensis* Grichanov and “*Polymedon*” *mulanjensis* Grichanov (cf. fig. 130 and 133) appear to be very close to that of *K. longifacies* (Fig. 37A-E). These species should probably be transferred to *Katangaia*.

Katangaia is an enigmatic genus that possesses typical dolichopodine characters, such as a dorsally setose scape (character 1:1), in combination with several non-dolichopodine characters. As noted by Ulrich (1981) and Parent (1933c) this genus shows a resemblance to *Tachytrechus*, particularly in the structure of the clypeus which is elongate and rounded below (characters 8:1 and 9:1). These characters, albeit synapomorphic for *Tachytrechus*, also occur in other dolichopodine genera (e.g., *Dolichopus*, *Hercostomus*) and outside the Dolichopodinae. *Tachytrechus* and *Katangaia* also share a strong basiventral seta on the hind basitarsus; however, this feature is homoplasious within the Dolichopodinae and attempts to score it across the range of taxa examined in this study failed due to the presence of numerous intermediates. Unlike *Tachytrechus*, in which the posterodorsal part of the postgonite is distinctively upturned and laterally flared (character 61:1, Fig. 33D,E), the postgonite of *Katangaia* is simple (Fig. 37E).

Unlike most dolichopodines *Katangaia* lacks a distinct pedicel condyle (character 3:0), has a partially setose male abdominal T6 (character 36: 0), and lacks anterior preapical setae on the mid and hind femora (characters 26:0 and 28:0). Probably the most striking autapomorphy of *Katangaia* is the large male cercus which has claw-like medial projections (Fig. 37B,C). Currently, the phylogenetic position of *Katangaia* is uncertain.

Material Examined.

Katangaia longifacies Parent, [AF]: ♂ syntype (MRAC)

GENUS *PSEUDOHERCOSTOMUS* STACKELBERG

(Fig. 38A-F)

Pseudohercostomus Stackelberg, 1931: 776. Type species: *Pseudohercostomus echinatus* Stackelberg [Oriental], by original designation.

Remarks. Stackelberg (1931) erected this genus for the Oriental species *P. echinatus*. Negrobov (1988) described a second species, *P. allini* Negrobov from Chile, and recently Yang and Grootaert (1999) described a third species, *P. sinensis* Yang and Grootaert, from Oriental China. Dyte and Smith (1980) also recorded the genus from the Afrotropical region. Stackelberg (1931) placed *Pseudohercostomus* in the Dolichopodinae even though it has a bare scape and an encapsulated, non-pedunculate hypopygium. This subfamily placement has been followed by subsequent authors including Parent (1934c), Negrobov (1980), Ulrich (1981), Yang and Grootaert (1999) and Yang et al. (2001).

The systematic position of *Pseudohercostomus* is currently unclear. Although *P. echinatus* was excluded from the Dolichopodinae in the analysis, this species shows a number of similarities to certain species of Oriental *Paraclius* (e.g., *P. abbreviatus*) and Afrotropical *Pelastoneurus* (e.g. *P. diversifemur*) including the possession of dense clothing setae on the anterior portion of the thorax, and the apical position of the lateral seta on the hind coxa. The latter two features; however, could not be coded into discrete states due to the presence of numerous intermediates encountered among the examined exemplars. Grichanov (2004) also recognized the similarity between *Pseudohercostomus echinatus* and certain Afrotropical species of *Pelastoneurus* and proceeded to synonymize *Pseudohercostomus* with *Pelastoneurus* Loew (= *Paracleius* Bigot). However, as a result of Grichanov's (2004) alternate interpretation of the nomenclature involving the names *Paracleius* Bigot, *Pelastoneurus* Loew and *Paraclius* Loew, and the recent suppression of *Paracleius* Bigot by the I.C.Z.N. (see "Remarks" under the generic treatment of *Pelastoneurus*), his synonymy of *Pseudohercostomus* with *Pelastoneurus* Loew (= *Paracleius* Bigot) must be rejected as *Pseudohercostomus echinatus* is clearly not congeneric *Pelastoneurus* in the sense of the type species *Pelastoneurus vagans*.

Bickel (pers. comm.) has also suggested a possible relationship between *Pseudohercostomus* and the enigmatic New World genus *Keirosoma* Van Duzee. I have examined specimens of *K. albicinctum* Van Duzee (CNC) and agree that these genera

may be related as they share several features including a bulky habitus, similar wing venation with R_{4+5} and M slightly divergent, apical position of the lateral seta on the hind coxa (but see comments above), segment 7 of the male genitalia entirely membranous, and somewhat similar male genitalia. At present the systematic position of *Keirosoma* is uncertain and it has been assigned to the Rhaphiinae (Foote et al., 1965), Diaphorinae (Robinson, 1970a,b) and Sympycninae (Ulrich, 1981).

Based on the cladistic analysis, I have excluded *Pseudohercostomus* from the Dolichopodinae; however, further analyses incorporating additional exemplars of Oriental *Paraclius* as well as *Keirosoma* are needed to elucidate the position of this genus.

Apparent autapomorphic features of *Pseudohercostomus* include the possession of a very wide metepimeron, the bilobate male sperm pump (Fig. 38C) and the distinctive female terminalia with T10 densely covered with acanthoporous spines (Fig. 38E,F). Stackelberg (1931) considered the 4 rows of acrostichals present in *P. echinatus* to be a generic character; however, I have examined a female of an apparently undescribed species from New Britain, Papua New Guinea (CNC) which clearly possesses biserial acrostichals. This female also represents the first record of *Pseudohercostomus* in the Australasian and Oceanian region

Material Examined.

Pseudohercostomus echinatus Stackelberg, [AF, OR]: 2 ♂♂, 1 ♀ (MNHN); 2 ♀♀ (ISNB)

Pseudohercostomus sp. 1, [AU]: 1 ♀ (CNC)

GENUS *VETIMICROTES* DYTE

(Fig. 39A-C)

Microtes Becker, 1918: 132. Type species: *Microtes mediterraneus* Becker [Palearctic], by monotypy. Preoccupied by *Microtes* Scudder, 1900.

Vetimicrotes Dyte, 1980: 223. Type species: *Microtes mediterraneus* Becker, automatic. N. name for *Microtes* Becker, 1918.

Remarks. *Vetimicrotes* includes two Palaearctic species, *V. mediterraneus* (Becker) and *V. nartshukae* Negrobov. Beschovski (1972) redescribed *V. mediterraneus* based on new material from the Bulgarian coast of the Black Sea. Becker (1918) included *Vetimicrotes* (as *Microtes*) in the Sympycninae and this placement was subsequently followed by Parent (1938). This genus has since been placed either in the Dolichopodinae (Ulrich, 1981) or Peloropeodinae (Negrobov, 1986, 1991). The cladistic analysis indicates that *Vetimicrotes* is not a dolichopodine (Figs. 1 and 2); however, further studies are required to ascertain its systematic position within the Dolichopodidae. The flattened posterior mesonotum, and setose abdominal T6 and segment 7 suggest a possible relationship with Medeterinae; however, *Vetimicrotes* possesses a distinct anterior preapical seta on the mid and hind femur, unlike medeterines. The male genitalia of *V. mediterraneus* are illustrated in Figs 39A-C.

Material Examined.

Vetimicrotes mediterraneus (Becker), [PA]: 4♂♂, 4♀♀ (ZISB); 1♂, 1♀ (BMNH)

ACKNOWLEDGEMENTS

Thanks to the following curators for loans of specimens: Venelin Beschovski (ZISB), John Chainey (BMNH), Ruth Contreras-Lichtenberg (NMW), Jeff Cumming (CNC), Roy Danielsson (MZLU), Christophe Daugeron (MNHN), E. De Coninck (MRAC), Mihaly Foldvari (HNHM), David Grimaldi and Tam Nguyen (AMNH), Patrick Grootaert (ISNB), Uwe Kallweit (SMTD), Philip D. Perkins (MCZ), Simon Pollard (CMNZ), Keve Ribardo (CAS), Lars Vilhelmsen (ZMUC), Hella Wendt (ZMHB), Norm Woodley (USNM), Joachim Ziegler (DEI), Cheryl Barr (EMEC). Additional specimens were provided as gifts from Marc Pollet (ISNB), Peter Dyte (Datchet, UK), Dan Bickel (Australian Museum), Arne Panesar (Freiburg, Germany), Toyohei Saigusa (Fukuoka, Japan) and are deposited in the LEM.

I would like to thank Terry Wheeler for his advice, support, supervision and critical review of this work, Jeff Cumming for his regular guidance, help and encouragement, as well as his review of this manuscript, Jade Savage for her continual help and advice throughout this project, Marc Pollet for sharing his knowledge of dolichopodids with me through countless discussions and emails, and allowing me access to his systematic database and unpublished key of Palaearctic dolichopodid genera, Jeff Skevington for his help with the cladistic analysis, and Brian Driscoll for the use of his laboratory computer facilities. I would also like to thank Dan Bickel, Peter Dyte, Neal Evenhuis, Patrick Grootaert, Chris Thompson, Hans Ulrich, Dick Vockeroth, Ding Yang and Lili Zhang for their helpful advice and assistance.

Financial Support for this study was provided by the Federal Biosystematics Group Fellowship, Dipterology Fund (2000, 2002), McGill University Margaret Duporte Fellowship (2000, 2001) and a Natural Sciences and Engineering Research Council of Canada research grant to T.A. Wheeler.

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Appendix 1. Characters and character codings used in the analysis.*Head*

1. Dorsal setae of scape: (0) absent; (1) present.
2. Antenna of male: (0) with scape and pedicel unmodified; (1) with enlarged globular scape and reduced, funnel-shaped pedicel.
3. Pedicel condyle: (0) absent or weakly developed; (1) present, well-developed (at least in female); (2) present and exposed on medial surface.
4. Apical segment of arista: (0) pubescent or bare; (1) plumose, dorsal and ventral hairs longer than lateral hairs.
5. Arista of male: (0) 2-segmented; (1) 1-segmented.
6. Medial and/or apical lamella of male arista: (0) absent; (1) present.
7. Proboscis: (0) short; (1) greatly elongated.
8. Lower margin of clypeus: (0) rounded or pointed below (especially in males); (1) straight.
9. Clypeus of male: (0) not extending beyond lower margin of eyes; (1) extending beyond lower margin of eyes.
10. Clypeus of male: (0) not subequal to face and strongly bulging; (1) subequal or shorter than clypeus and strongly bulging (at most 1.3x longer).

Thorax

11. Prothoracic seta: (0) absent; (1) present.

- 12. Prescutellar depression: (0) present; (1) absent.
- 13. Dark spot above notopleuron: (0) absent; (1) present.
- 14. Notopleuron: (0) with 2 or more strong bristles; (1) with strong anterior seta and very weak posterior seta; (2) with 1 strong seta.
- 15. Cluster of fine hairs on pleuron in front of posterior spiracle: (0) absent; (1) present.
- 16.: Patch of fine hairs on posterolateral margin of metepisternum: (0) absent; (1) present.

Legs

- 17. Pulvilli: (0) developed normally on all legs; (1) strongly reduced on mid and hind legs; (2) strongly reduced on all legs.
- 18. Strong basiventral seta on fore femur: (0) absent; (1) present.
- 19. Ventral cluster of 2-3 strong setae on male fore femur: (0) absent; (1) present.
- 20. Distinctly elongated and fine apical seta on male fore tibia: (0) absent; (1) present.
- 21. Fore tibia of male: (0) not dorsoventrally flattened; (1) dorsoventrally flattened.
- 22. Velvety pilosity on ventral surface of male fore tarsus: (0) absent or weakly developed; (1) present, well-developed.
- 23. Apical tarsomeres of male fore tarsus: (0) not laterally flattened and broadened; (1) laterally flattened and distinctly broader than basal tarsomeres.

24. Cluster of 2-3 strong setae on anterior surface of male mid coxa: (0) absent; (1) present.
25. Ventral tubercle or swelling on male mid femur: (0) absent (1) present.
26. One or more distinct anterior preapical setae on mid femur: (0) absent; (1) present (at least in females).
27. One or more distinct posterior preapical setae in addition to terminal posteroventral on mid femur: (0) absent; (1) present, 1 seta; (2) present, 2 setae.
28. One or more anterior or anterodorsal preapical setae on hind femur: (0) absent; (1) present.
29. One or more strong setae on dorsal surface of hind basitarsus: (0) absent; (1) present.
30. Elongate comma-shaped posterobasal projection on hind basitarsus of male: (0) absent; (1) present.

Wing

31. Vein Sc: (0) fused to Costa or incomplete; (1) Sc inserting into R₁.
32. Anteroproximal stub vein on vein M: (0) absent; (1) present.
33. Vein M₂: (0) present, complete; (1) present, as a stub vein; (2) absent.
34. Vein M curvature: (0) straight or with weak anterior bend (at least in female); (1) with distinct S-shaped bend; (2) with strong anterior bend towards R₄₊₅ apically.

Male abdomen and genitalia

- 35. Large membranous region posteriorly on male tergite 5: (0) absent; (1) present.

- 36. Tergite 6 of male: (0) setose; (1) bare.

- 37. Segment 7: (0) with sternite and tergite forming a sclerotized peduncle; (1) with sternite & tergite reduced and separated; (2) entirely membranous.

- 38. Segment 7: (0) bare; (1) setose.

- 39. Epandrium: epandrial foramen: (0) not developed; (1) developed.

- 40. Epandrium: basiventral epandrial lobes (0) not elongate, symmetrical and digitiform; (1) elongate, symmetrical and digitiform (Figs. 30A-C, 31A-C, 32A-C).

- 41. Epandrium: pointed or frayed, knob-like tip on one or both basiventral epandrial lobes: (0) absent; (1) present (Figs. 14A-C, 15A,C,D, 31A-C, 32A-C).

- 42. Epandrium: apicoventral epandrial lobe: (0) not elongate and setose; (1) elongate and densely setose (Figs. 30A,C, 31A,C).

- 43. Epandrium: membranous, textured sac near base of apicoventral epandrial lobe: (0) absent; (1) present (Figs. 15A,B,D, 33A-C, 34A-C).

- 44. Epandrium: frayed or branched seta on apicoventral epandrial lobe: (0) absent; (1) present (Figs. 22A,C, 36A,C).

- 45. Epandrium: acute process between apicoventral epandrial lobe and surstylus: (0) absent; (1) present (Fig. 35A,C).

46. Surstylus: (0) with at least one lobe not extremely elongate and slender; (1) both lobes extremely elongate and slender with narrow apices (Figs 30B, 31B).
47. Surstylus: 1-2 plumose setae on dorsal surstylar lobe: (0) absent; (1) present (Fig. 35A,B).
48. Surstylus: dorsal surstylar lobe: (0) not notched apicodorsally with keel-like projection and expanded apex; (1) distinctive structure, notched apicodorsally and usually with keel-like projection and expanded apex (Figs. 9B, 10B, 11B).
49. Sperm pump: basal sclerite of sperm pump: (0) not elongated (1) elongated and tubular or flattened (Figs. 16C, 22B, 23B).
50. Sperm pump: (0) not enlarged and spherical; (1) enlarged and spherical.
51. Sperm pump: (0) not folded back on itself; (1) folded back on itself (Fig. 8C).
52. Basal projection of ejaculatory apodeme: (0) not elongate and flexed towards base of phallus; (1) elongate and flexed towards base of phallus (Figs. 13B, 36B).
53. Ejaculatory apodeme: (0) rod-like, apex unmodified (e.g., Figs. 6B, 15B, 18B, 32B); (1) rod-like, apex flared and T-shaped in dorsal view (Figs. 9C, 10C); (2) rod-like, apex rounded in dorsal view and dorsoventrally flattened; (3) distinctly flattened laterally (e.g., Figs. 20B, 21B, 26B).
54. Hairy, medially divided or undivided apical projection near proctiger, i.e. proctiger brush(es): (0) absent; (1) present (Figs. 20B, 22B, 23B,C 28B, 29B).
55. Phallus: (0) not greatly swollen in basal part; (1) greatly swollen in basal part (Figs. 6B, 7B).

- 56.** Phallus: (0) not wrinkled; (1) wrinkled (Figs. 28B, 29A,B).
- 57.** Phallus: (0) not elbowed at base (1) elbowed at base (Figs. 31B, 32B).
- 58.** Postgonite: posterodorsal portion: (0) not broad with one or two dorsolateral lobes (1) broad with one or more dorsolateral lobes (Fig. 13B,C).
- 59.** Postgonite: preapical lateroventral lobes on posterodorsal portion: (0) absent or weakly developed; (1) present, well-developed (Figs. 21B, 26B, 27B).
- 60.** Medioventral projection on postgonite (in addition to dorsal lobe): (0) absent; (1) present (Figs. 15B, 22B).
- 61.** Postgonite: posterodorsal portion: (0) not strongly upturned and flared laterally; (1) strongly upturned and flared laterally (Figs. 33B,D,E, 34B, 35B, 36B).
- 62.** Anteroventral portion of postgonite: (0) looping around base of phallus; (1) not looping around base of phallus, weakly sclerotized to membranous, margin weakly defined; (2) not looping around base of phallus, well-sclerotized with well-defined margin (Figs. 22B, 23B, 24B).
- 63.** Hypandrium: (0) not laterally flanked by basiventral epandrial lobes, distinctly separate (1) laterally flanked by basiventral epandrial lobes, appearing tripartate in ventral view (Figs. 14C, 15C, 30C, 31C, 32C).
- 64.** Hypandrium and basiventral epandrial lobes: (0) not forming a complex of entangled, asymmetrical lobes; (1) forming a complex of entangled, asymmetrical lobes (Figs. 14C, 15C,D, 16E).

65. Hypandrium: (0) free, not fused to epandrium laterally near base of basiventral epandrial lobe/seta; (1) fused to epandrium laterally near base of basiventral epandrial lobe (Figs. 14A,C, 15B,C, 19A,C, 21AC, 26A,C, 30C, 31C, 32C).

66. Hypandrial arms: (0) connected to the hypandrium; (1) separated from the hypandrium (Figs. 6B, 7B, 16C, 17B, 22B, 23B, 24B).

67. Hypandrial apodeme: (0) absent or not distinctly separated from basal sclerite of sperm pump (e.g., Figs. 16C, 20B, 22B, 23B, 25B, 28B, 29B, 34B); (1) present, distinctly separated from basal sclerite of sperm pump (e.g., Figs. 5B, 9B, 10B, 11B, 13B, 14B, 18B, 19B, 26B, 32B).

68. Cercus: (0) not large and rounded with very long, fine setae on lateral margin (0) large and rounded with very long, fine setae on lateral margin (Figs. 11A, 12A,B, 25A, 27A).

Female terminalia

69. Tergite 6 and 7: (0) undivided; (1) both divided medially; (2) only T6 divided medially; (3) only T7 divided medially.

70. Segment 8: basal apodeme: (0) absent; (1) present, S8 and T8 fused into a narrow sclerite (Figs. 18E, 20E, 22E, 23F, 24E, 25E, 29E); (2) present, broad, S8 and T8 fused or separate (Figs. 33G, 34E).

71. Tergite 8: apical projections: (0) absent; (1) present (Figs. 6D,E, 7D,E).

72. Tergite 10: (0) medially divided into hemitergites; (1) fused medially (Figs. 6D, 7D, 19E).

73. Tergite 10: inner, medial acanthoporous spines: (0) absent; (1) present, 1 pair (Figs. 9E, 10E, 11D, 19E, 21D, 25D, 26D, 34D, 36D); (2) present, numerous spines (Fig. 38E).

74. Tergite 10: (0) not V-shaped; (1) V-shaped in dorsal view (Figs. 6D, 7D, 19E).

Appendix 2. Character state matrix for Dolichopodinae analysis. Taxon names are presented in their previously accepted combinations. Missing data are indicated by “?”; polymorphisms are indicated by “X” for states 0/1, and “Y” for states 0/3.

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234
<i>Allohercostomus rotundataus</i> (Yang & Saigusa)	1010000000	1000000001	0000010100	1020010010	0000000000	0030000000	0100001000	0000
<i>Argyrochlamys impudicus</i> Lamb	1010000100	1100000000	0000010101	1022010010	0000000000	0000100000	0200011000	1101
<i>Argyrochlamys</i> sp. 1	1010000100	1X00000000	0000010110	1022010010	0000000000	0010010000	0100001000	0101
<i>Cheiromyia palmaticornis</i> (Parent)	1010000100	1100000000	0000010100	1022010010	0000000000	1030000000	01000000??	????
<i>Colobocerus alchymicus</i> Parent	0000000100	0000000000	0000011100	102000????	??????????	??????????	??????????	????
<i>Dolichopus diadema</i> Haliday	1010000010	1100100001	0100010110	1011010010	0000000100	0010000000	0100001000	0010
<i>Dolichopus latipennis</i> (Fallén)	1010000000	1100100001	0000010110	1021010010	0000000100	0010000000	0100001100	0010
<i>Dolichopus unguulatus</i> (L.)	1010000100	1110100000	0000010110	1021010010	0000000100	0010000000	0100001000	0010
<i>Gymnopternus cupreus</i> (Fallén)	1010000100	1100100000	0000010100	1020010010	0000000000	0130000100	0100001000	0000
<i>Gymnopternus frequens</i> Loew	1010000100	1100110000	0000010100	1020010010	0000000000	0100000100	0100001000	0000
<i>Gymnopternus purpuratus</i> (Van Duzee)	101000010X	1100100001	0000110100	1020010010	0000000100	0000000000	0100001100	0010
<i>Gymnopternus violaceus</i> (Van Duzee)	1010000100	1100100001	0000010100	1020010010	0000000100	0000000000	0100001100	0010
<i>Halaiba cavicola</i> Parent	1010000100	1100000000	0000010101	1022010010	0000000000	0000100000	01000110?0	1101
<i>Hercostomus chalybeus</i> (Wiedemann)	1010000100	1100100001	0000010100	1020010010	0000000100	0000000000	0100001100	0010
<i>Hercostomus chetifer</i> Walker	1010000100	1100000000	0010011100	1020010010	1010000000	0000000001	0111111000	0000
<i>Hercostomus chrysozygos</i> Wiedemann	1010000100	1110000000	0000011100	1020010010	0000000000	0030000010	0100101000	0010
<i>Hercostomus longiventris</i> (Loew)	1010000100	1100000000	0000011100	1020010010	1000000000	0030000000	0111101000	0000
<i>Hercostomus straeleni</i> Vanschuytbroeck	1010000100	1100000001	0100011100	1020010010	0000000000	0030000010	0100101000	0000
<i>Katangaia longifacies</i> Parent	1000000010	1100002000	0000000000	1020000010	0000000010	0000000000	02000000??	????
<i>Lichtwardtia angularis</i> (Macquart)	1011000001	1100100000	0000010110	1111010010	0000000100	0010000000	0100001000	0010
<i>Lichtwardtia</i> sp. 9	1011000000	1100100001	0000010110	1111010010	0000000110	0010000000	0100001000	0010
<i>Ludovicius dufouri</i> (Macquart)	1110110100	1100000000	0000010100	1020010011	1100000000	0000001000	0110101000	0000
<i>Ludovicius impar</i> Rondani	1110110100	1100000000	000001X100	1020010011	1100010000	0000001000	0110101000	0000
<i>Metaparaclius australiensis</i> Parent	1110110100	1110000000	0000010100	1022010010	0000000100	0030000000	0200011000	0000
<i>Muscidideicus praetextatus</i> (Haliday)	1010000100	1100000000	0100011100	1020010010	0000000000	0000000000	0100001001	0000
<i>Nodicornis nodicornis</i> (Meigen)	1110110100	1100000000	0000010100	1020010011	1000000000	0000001010	0110101000	0000
<i>Ortochile nigrocoerulea</i> Latreille	1010001000	1100000000	000001X100	1020010010	0000000000	0030000000	0100101000	0111
<i>Ortochile soccata</i> Loew	1010001000	1100000000	0000011100	1020010010	0000000000	0030000000	0100101000	0010
<i>Paraclius abbreviatus</i> Becker	1010000100	1100010000	0000010100	1022010010	0000000001	0030000000	0100011000	0000
<i>Paraclius alternans</i> (Loew)	1010000100	1100000000	0000010100	1022010010	0000000001	0031000000	0100000001	0000
<i>Paraclius arcuatus</i> (Loew)	1010000100	1100000000	0000010100	1022010010	0000000000	0031000000	0100000101	0000
<i>Paraclius megalocerus</i> Robinson	1010000100	1100000000	0000010100	1022010010	0000000001	0030000000	0100000131	0000
<i>Parahercostomus zhongdianus</i> (Yang)	1010000100	1100010000	0100010110	1020010010	0000000000	0030000010	0100101000	0010

Appendix 2. Continued.

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234
<i>Pelastoneurus barri</i> Harmston	1011000001	1100000000	0100010100	1022010010	0001000010	0031000001	0200011111	0000
<i>Pelastoneurus punctipennis</i> (Say)	101X000101	1100000000	0000010100	1020010010	0000000000	00Y1011000	0200000031	0000
<i>Pelastoneurus vagans</i> Loew	1011000101	1100000000	0100010100	1022010010	0001000010	0031000001	0200010011	0000
<i>Phalacrosona amoenum</i> Becker	1010000010	1100000000	0010011100	1020010010	1010000000	0000000001	0111100000	0000
<i>Platyopsis maroccanus</i> (Parent)	1010000101	1100000000	0100012100	1020010010	0000000000	0000000000	0100000131	0010
<i>Poecilobothrus nobilitatus</i> (L.)	1010000100	1110000000	0000011100	1020010010	0000000000	0030000010	0100101000	0010
<i>Poecilobothrus regalis</i> (Meigen)	1010000100	1110000000	0000011110	1020010010	0000000000	0030000010	01001010?0	0010
<i>Polymedon inopinatus</i> Parent	1010000010	1100010000	0000010100	1022110010	0001000001	0000000000	0200011000	0000
<i>Proarchus tripartitus</i> (Aldrich)	1011000101	1110000000	0000010100	1020010010	0000000000	0030000000	0200010011	0000
<i>Pseudohercostomus echinatus</i> Stackelberg	0010000100	1100000000	0000010100	1020012010	0000000000	0000000000	0000001020	0020
<i>Pterostylus aberrans</i> (Loew)	1011000100	1110000000	00000111X0	1020010010	0000000000	0030000010	0100101100	0010
<i>Sarcionus lineatus</i> Aldrich	1011000000	1100000000	0000010100	1022010010	0000000010	0031000000	0200010011	0000
<i>Sarcionus maculipennis</i> Van Duzee	1010000100	1?00000000	0000010100	1020010010	000?000000	1030000000	01000000??	????
<i>Steleopyga dactylocera</i> Grootaert & Meuffels	1010000100	1100000000	0010011000	1020010010	0000000010	00?0000000	01?1?100??	????
<i>Stenopygium nubeculum</i> Becker	1010000101	1100000000	0000010100	1020010010	0000000000	0001011000	02000000??	????
<i>Sybistroma discipes</i> (Germar)	1010000100	1100000000	0010010100	1020010011	1100010000	0000000000	0110101000	0000
<i>Sybistroma obscurellum</i> (Fallén)	1010000100	1100000000	0000010100	1020010011	0100010000	0000000000	0110101000	0000
<i>Syntomoneurum alatum</i> Becker	1010000010	1102001110	0011110100	1021110010	0001000000	0110000000	1200000110	0010
<i>Syntomoneurum beckeri</i> Parent	1010000010	1102001110	0001110100	1021110010	0001000001	0110000000	1100000010	0010
<i>Tachytrechus aldrichi</i> (Van Duzee)	1010000010	1101100000	1000010100	1022010010	0000101000	0010000000	1100000010	0000
<i>Tachytrechus castus</i> (Van Duzee)	1010000010	1100000000	0000110100	1022010010	0001000000	0110000000	1100000010	0010
<i>Tachytrechus flabellifer</i> (Osten Sacken)	1010000010	1101000000	0000010100	1022010010	0001000000	0010000000	1100000010	0000
<i>Tachytrechus laevigatus</i> (Becker)	1010010010	1101000000	1000110100	1021010010	0000101100	0010000000	1100001010	0000
<i>Tachytrechus moechus</i> Loew	1110010000	1100000000	0100010100	1022010010	0010000000	0010000000	1100000012	0010
<i>Tachytrechus notatus</i> (Stannius)	1010000010	1100000000	0000110100	1020010010	0010000000	0010000000	1100000012	0000
<i>Vetimidrotus mediterraneus</i> (Becker)	0010000100	1000000000	0000010100	1020000110	0000000000	00?0000000	0?00000000	0000
OUTGROUP TAXA								
<i>Heteropsilopus cingulipes</i> (Walker)	0000000010	0100000000	0100000000	0012000110	0000000000	0000000000	0000000000	0100
<i>Nepalomyia nigricornis</i> (Van Duzee)	0010000100	1000000000	0000010100	1020010010	0000000000	0020000000	0000001000	0010
<i>Parathalassius</i> sp. 1	0000100000	0000000000	0000000000	0000000000	0000000000	0030000000	0000?00000	0000
<i>Pelorocephalus cornutus</i> (Van Duzee)	0000000100	1000000000	0000010100	1020010010	0000000010	0000000100	0100001001	0000
<i>Sympycnus annulipes</i> (Meigen)	0000000100	0X00000000	0000010100	1020001010	0000000000	0000000000	0000001000	0000
<i>Syntormon pallipes</i> (Fabricius)	0020000100	0000110000	0000011100	1020001010	0000000000	0000000000	0000001000	0000

Appendix 3. List of abbreviations used in figures.

ac proc: acute epandrial process
apv lobe: apicoventral epandrial lobe
apv setae: apicoventral epandrial setae
bas scl: basal sclerite of sperm pump
bas proj: basal projection of ejaculatory apodeme
bv lobe: basiventral epandrial lobe
bv seta: basiventral epandrial seta
cerc: cercus
dsur: dorsal lobe of surstylus
ejap: ejaculatory apodeme
ejdu: ejaculatory duct
epand: epandrium
epand fora: epandrial foramen
fur: furca
hy: hypandrium
hyap: hypandrial apodeme
hyar: hypandrial arm
pgon: postgonite
ph: phallus
prct br: proctiger brush
sac: epandrial sac
sp: sperm pump
sur: surstylus
S8: sternite 8
T8: tergite 8
T10: tergite 10
vsur: ventral lobe of surstylus

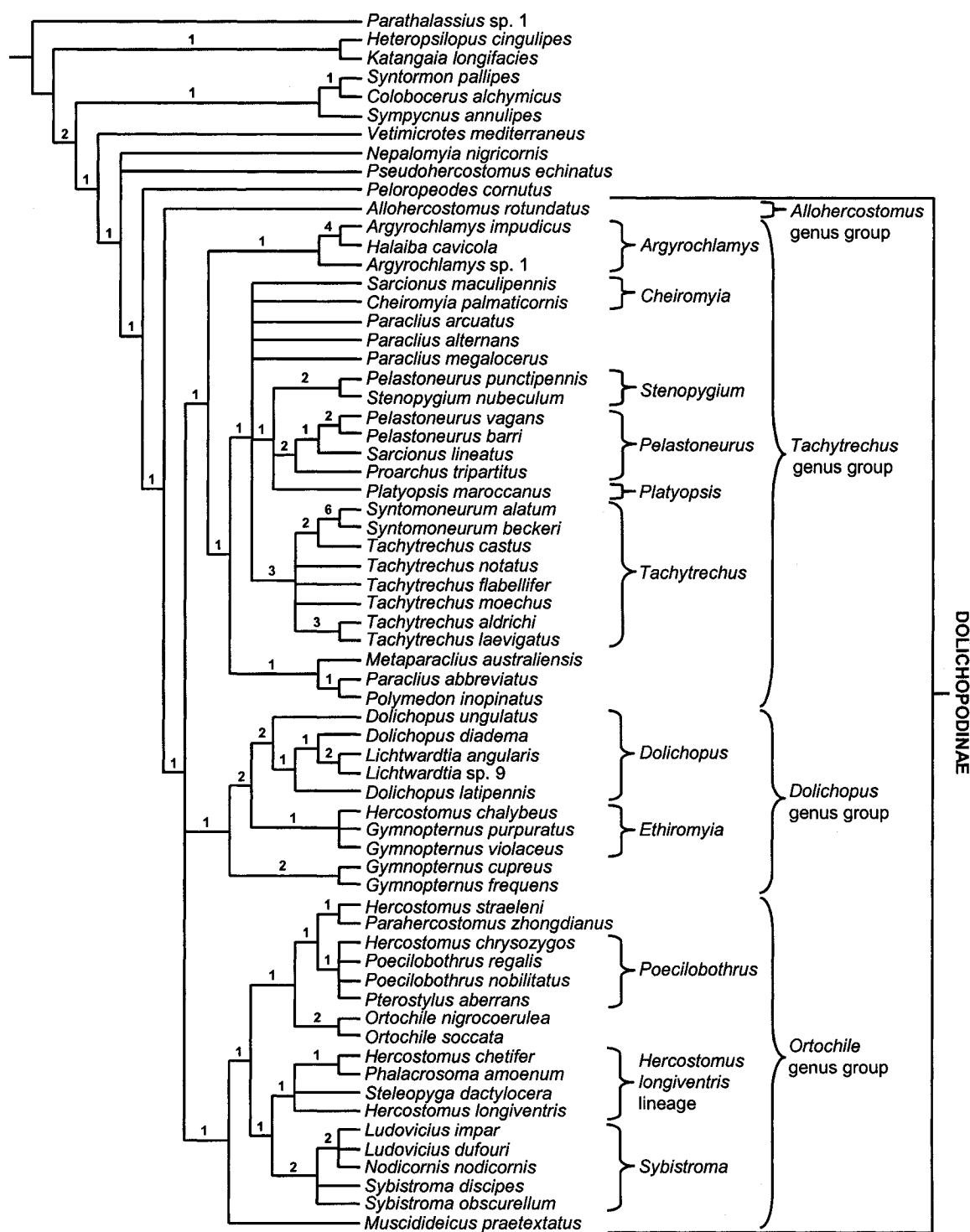


Figure 1. Strict consensus of 126 most parsimonious cladograms. Taxon names are presented in their previously accepted combinations. Newly proposed generic, genus group and subfamily limits are indicated by brackets on the right. Bremer support values are listed above each internode.

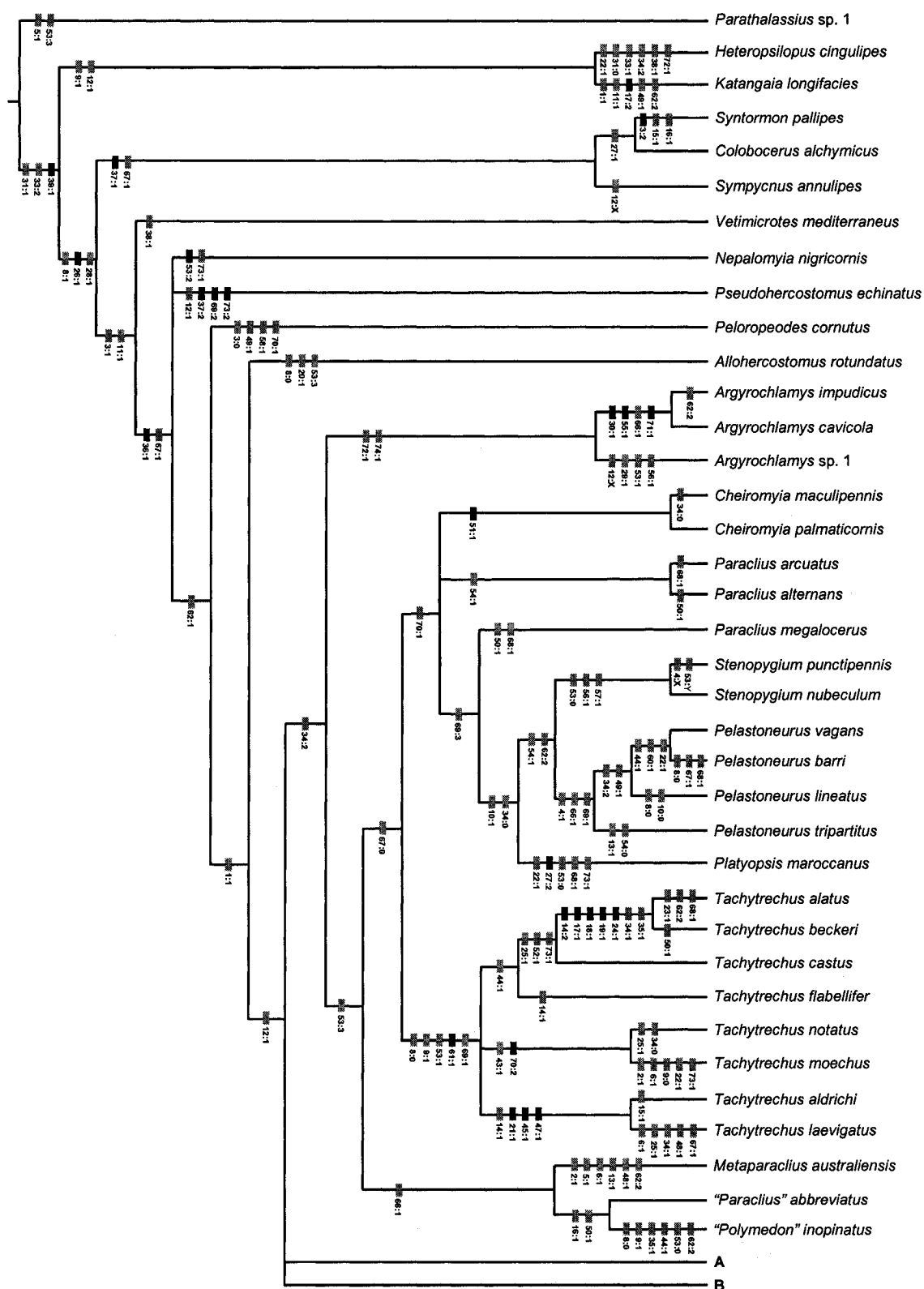


Figure 2. One of 126 most parsimonious cladograms showing character distribution (see Appendix 1 for character list). Continued in Figures 3 and 4. Taxon names are presented according to new combinations proposed in the text. Black hashmarks represent uniquely derived character states; grey hashmarks represent homoplasious character states.

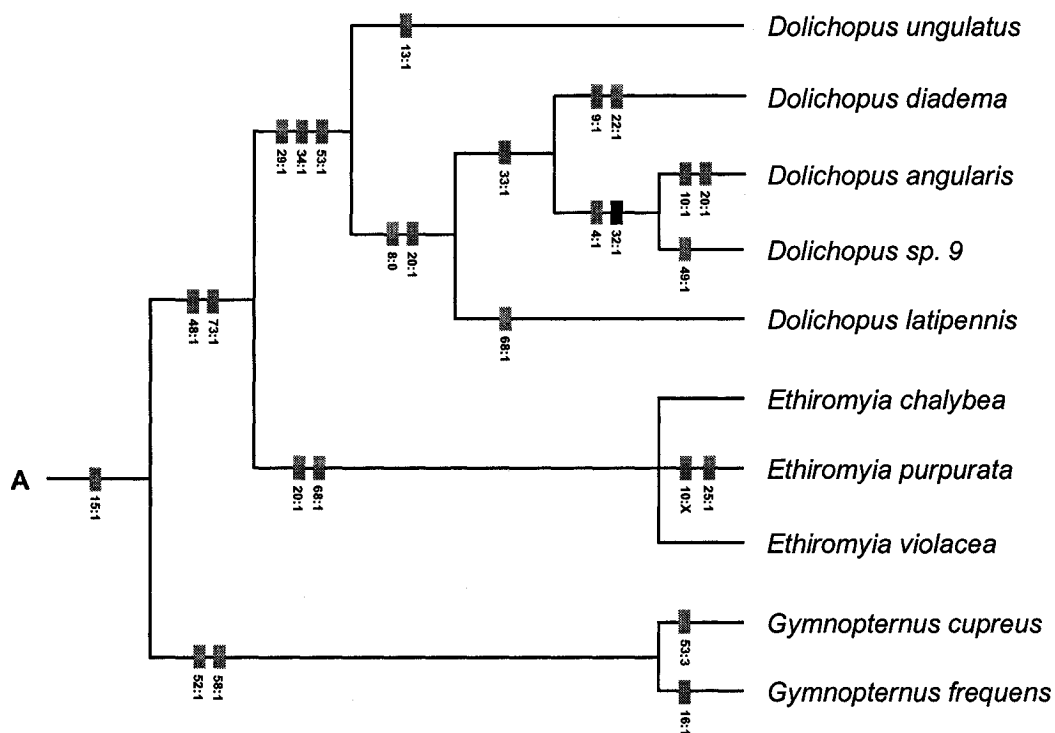


Figure 3. One of 126 most parsimonious cladograms (continued) showing character distribution (see Appendix 1 for character list). Taxon names are presented according to the new combinations proposed in the text. Black hashmarks represent uniquely derived character states; grey hashmarks represent homoplasious character states.

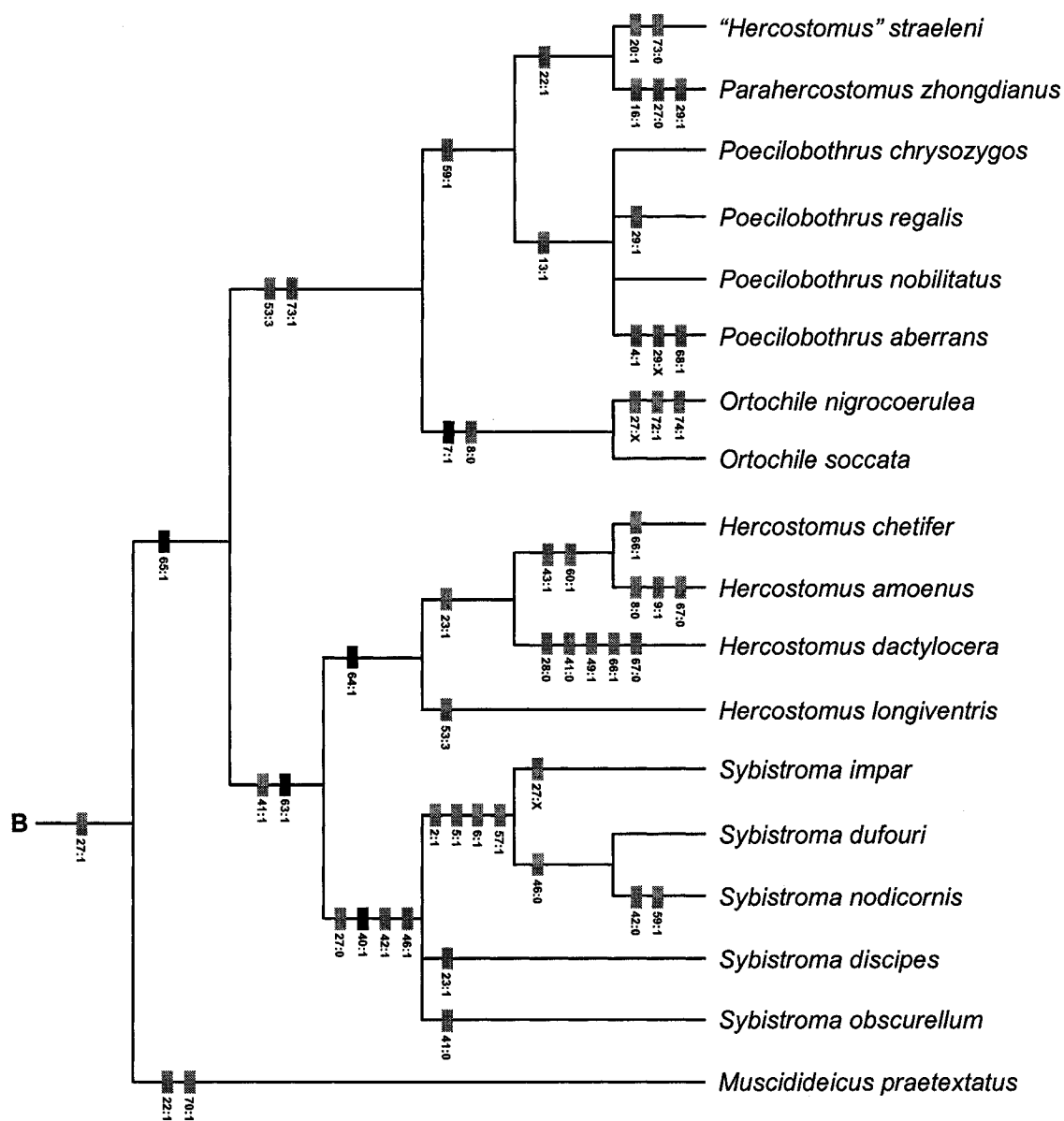


Figure 4. One of 126 most parsimonious cladograms (continued) showing character distribution (see Appendix 1 for character list). Taxon names are presented according to the new combinations proposed in the text. Black hashmarks represent uniquely derived character states; grey hashmarks represent homoplasious character states.

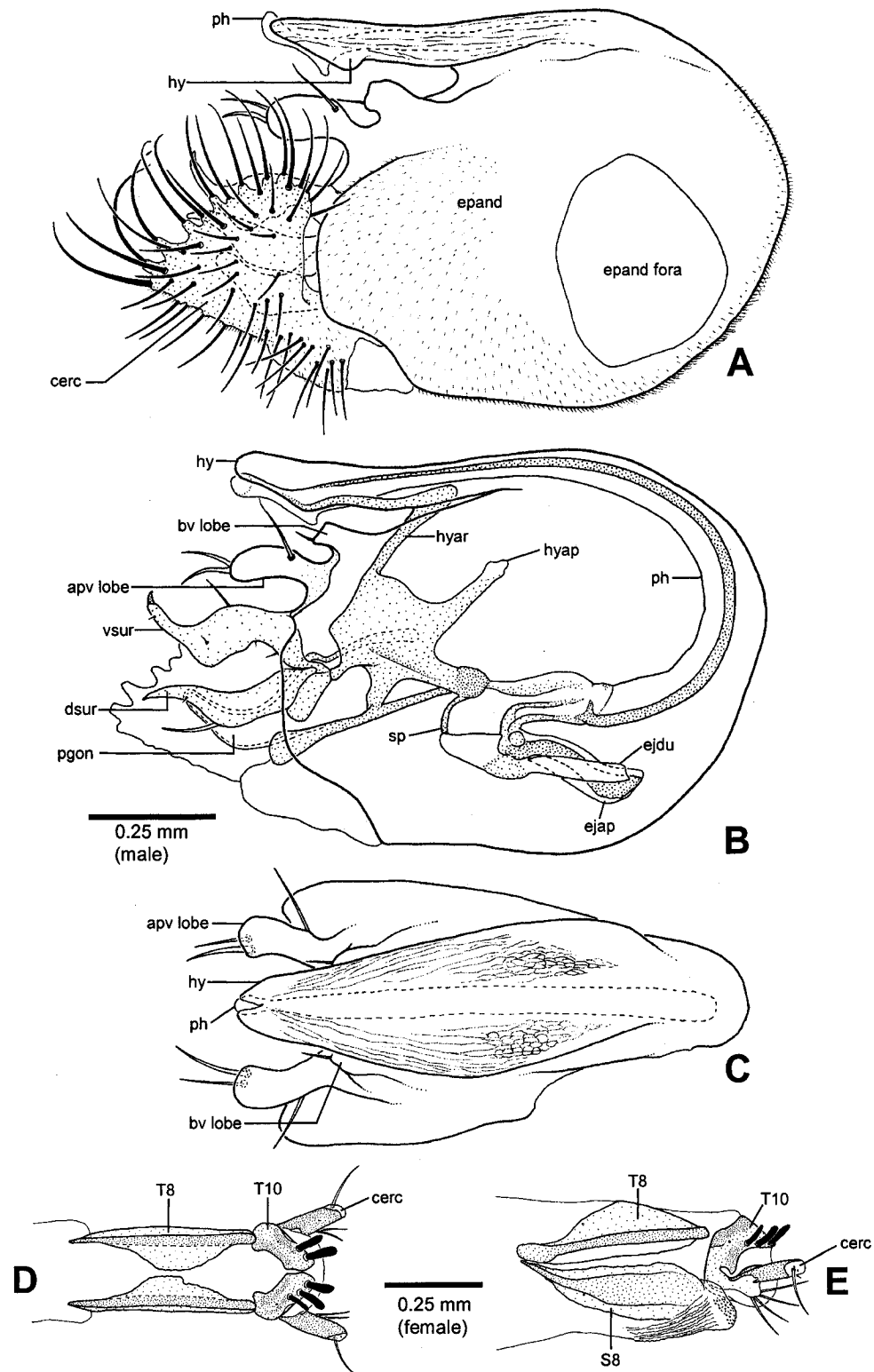


Figure 5. *Allohercostomus rotundatus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

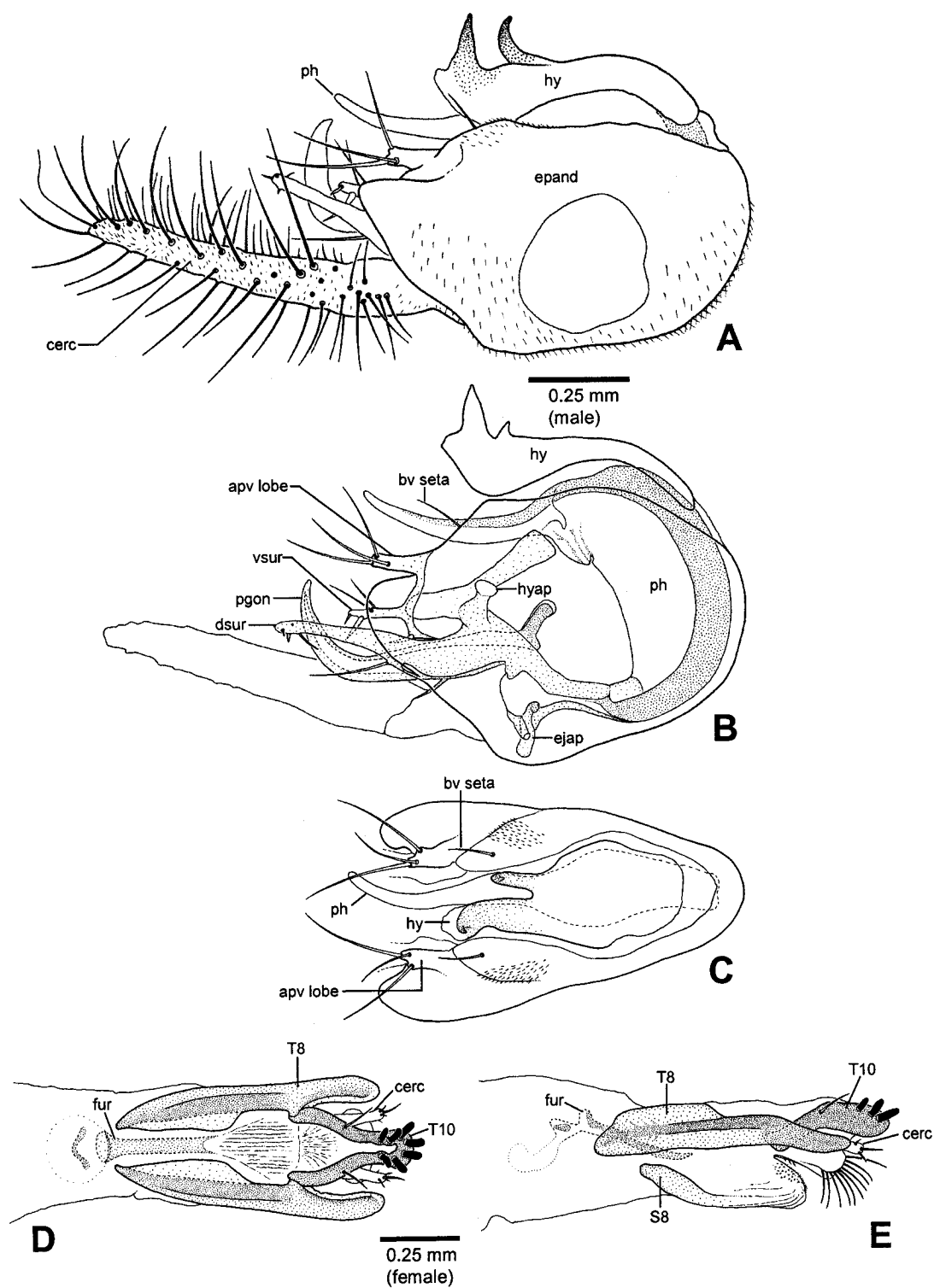


Figure 6. *Argyrochlamys impudicus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

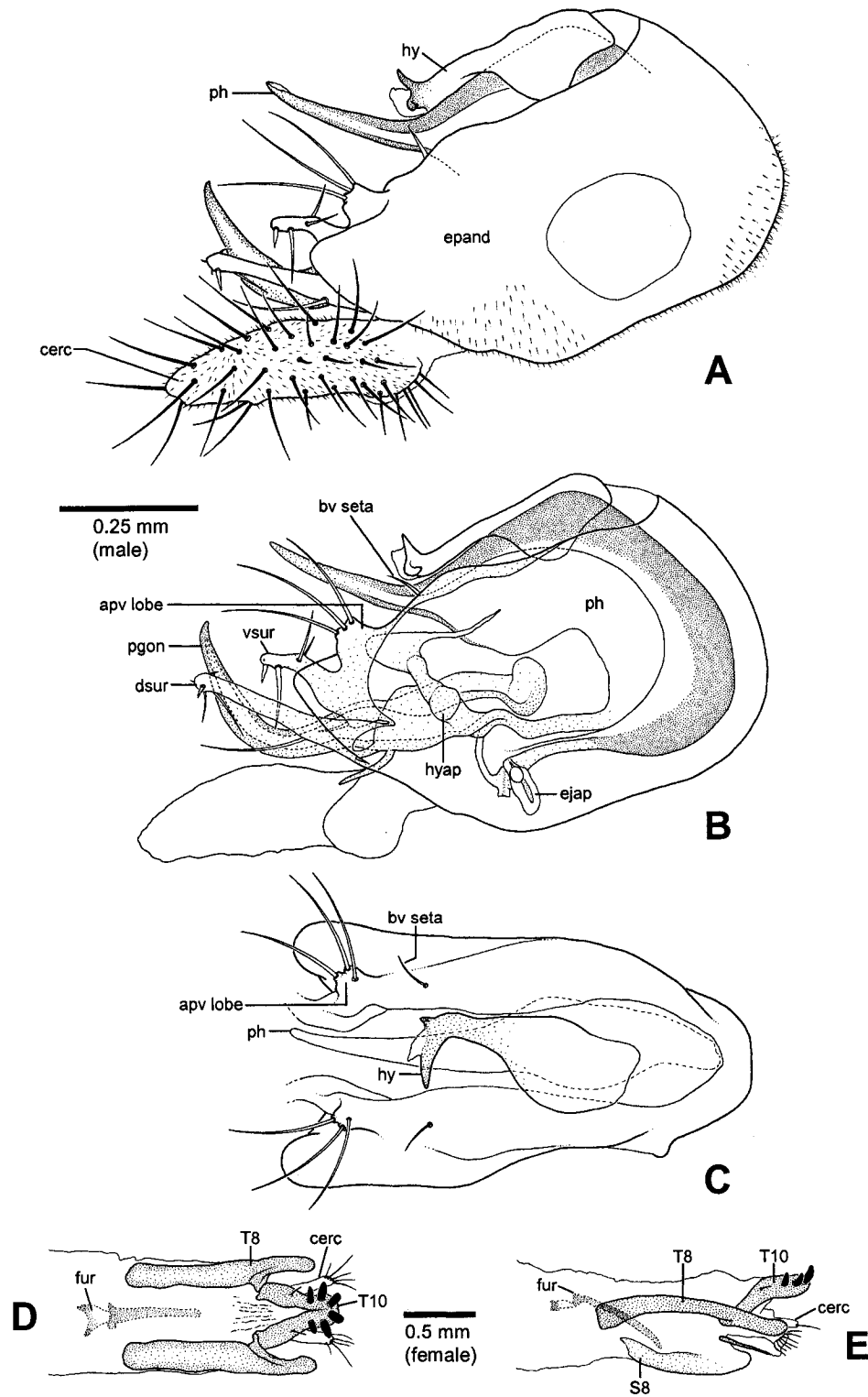


Figure 7. *Argyrochlamys cavicola*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

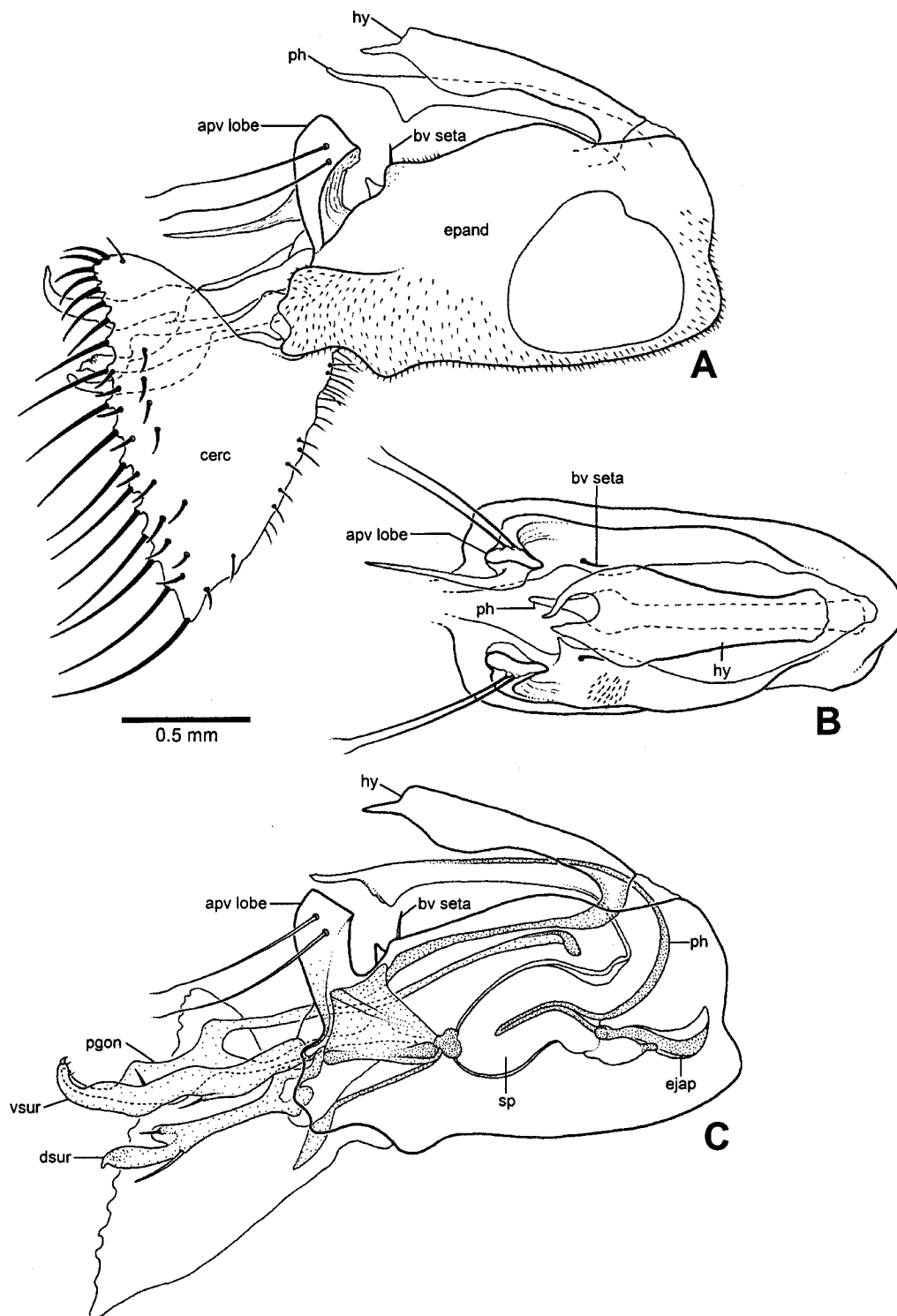


Figure 8. *Cheiromyia palmaticornis*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (C) Male genitalia, left lateral view (internal).

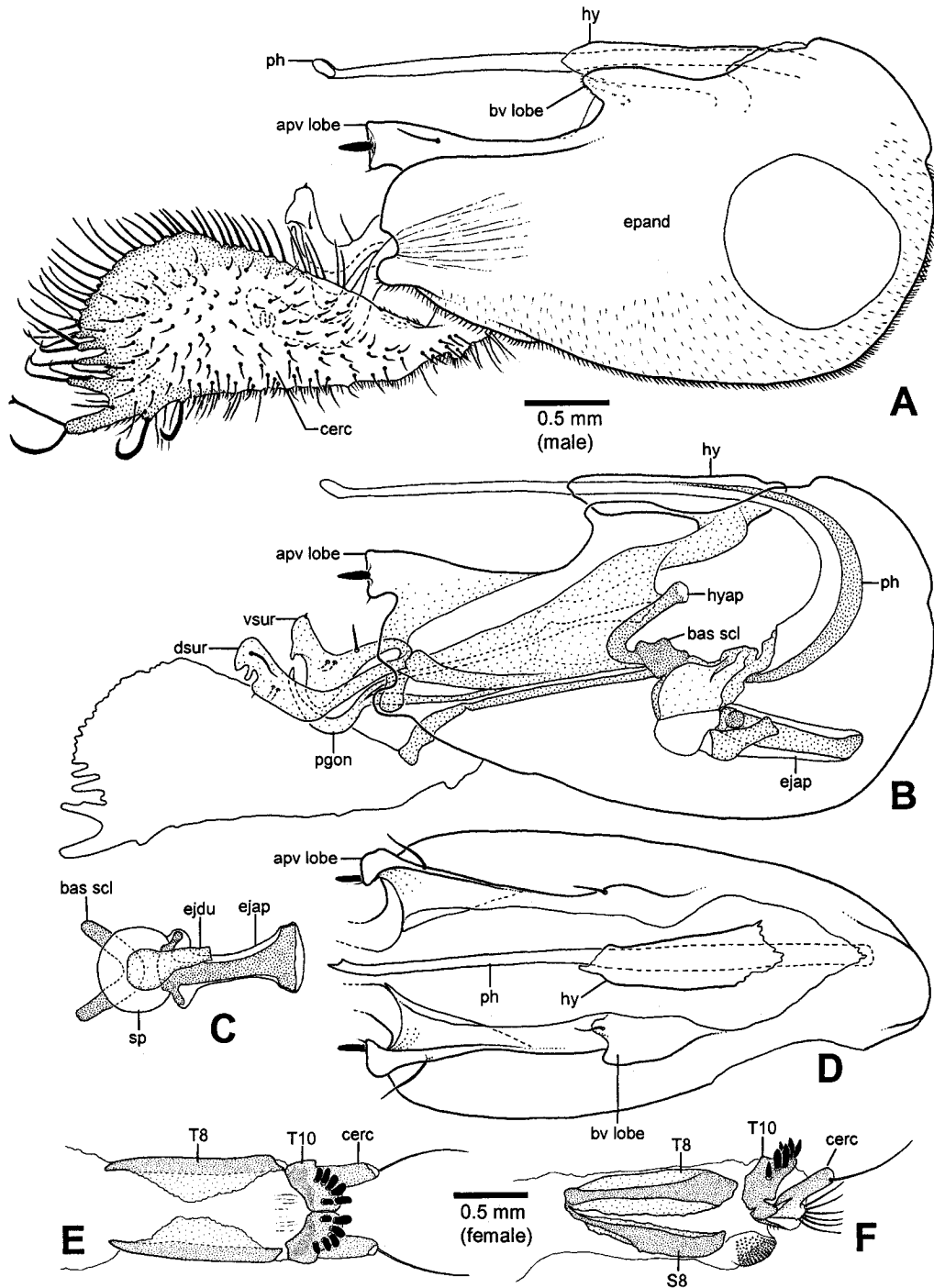


Figure 9. *Dolichopus unguulatus* and *D. diadema*: (A) *D. unguulatus*, male genitalia, left lateral view (external). (B) *D. unguulatus*, male genitalia, left lateral view (internal). (C) *D. diadema*, male genitalia, sperm pump and ejaculatory apodeme, dorsal view (D) *D. unguulatus*, male genitalia, ventral view (postgonite, surstylus and cerci not shown). (E) *D. unguulatus*, female genitalia, dorsal view. (F) *D. unguulatus*, female genitalia, left lateral view.

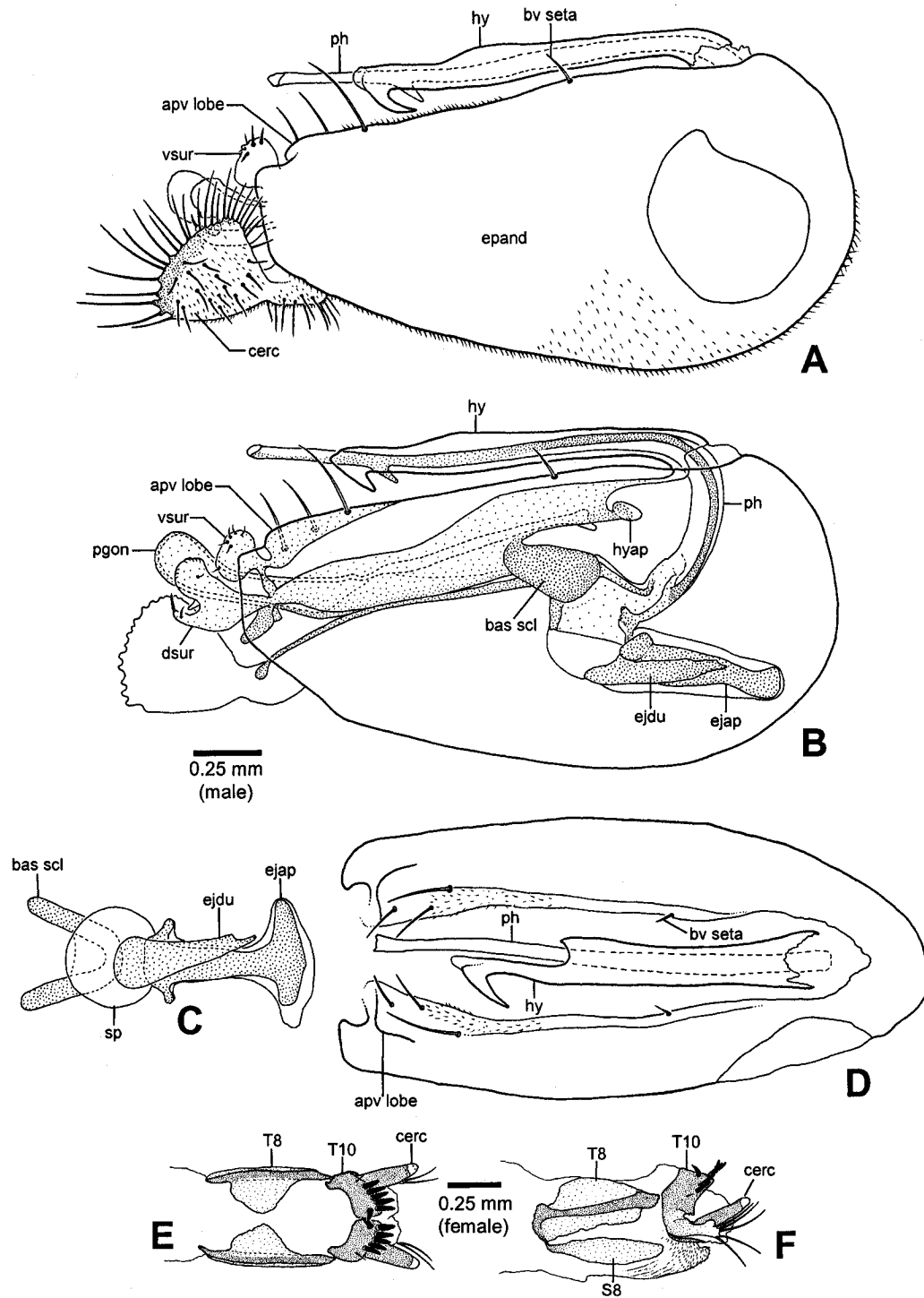


Figure 10. *Dolichopus angularis* and *Dolichopus* sp. 9: (A) *D. angularis*, male genitalia, left lateral view (external). (B) *D. angularis*, male genitalia, left lateral view (internal). (C) *D. angularis*, male genitalia, sperm pump and ejaculatory apodeme, dorsal view. (D) *D. angularis*, male genitalia, ventral view (postgonite, surstylus and cerci not shown). (E) *Dolichopus* sp. 9, female genitalia, dorsal view. (F) *Dolichopus* sp. 9, female genitalia, left lateral view.

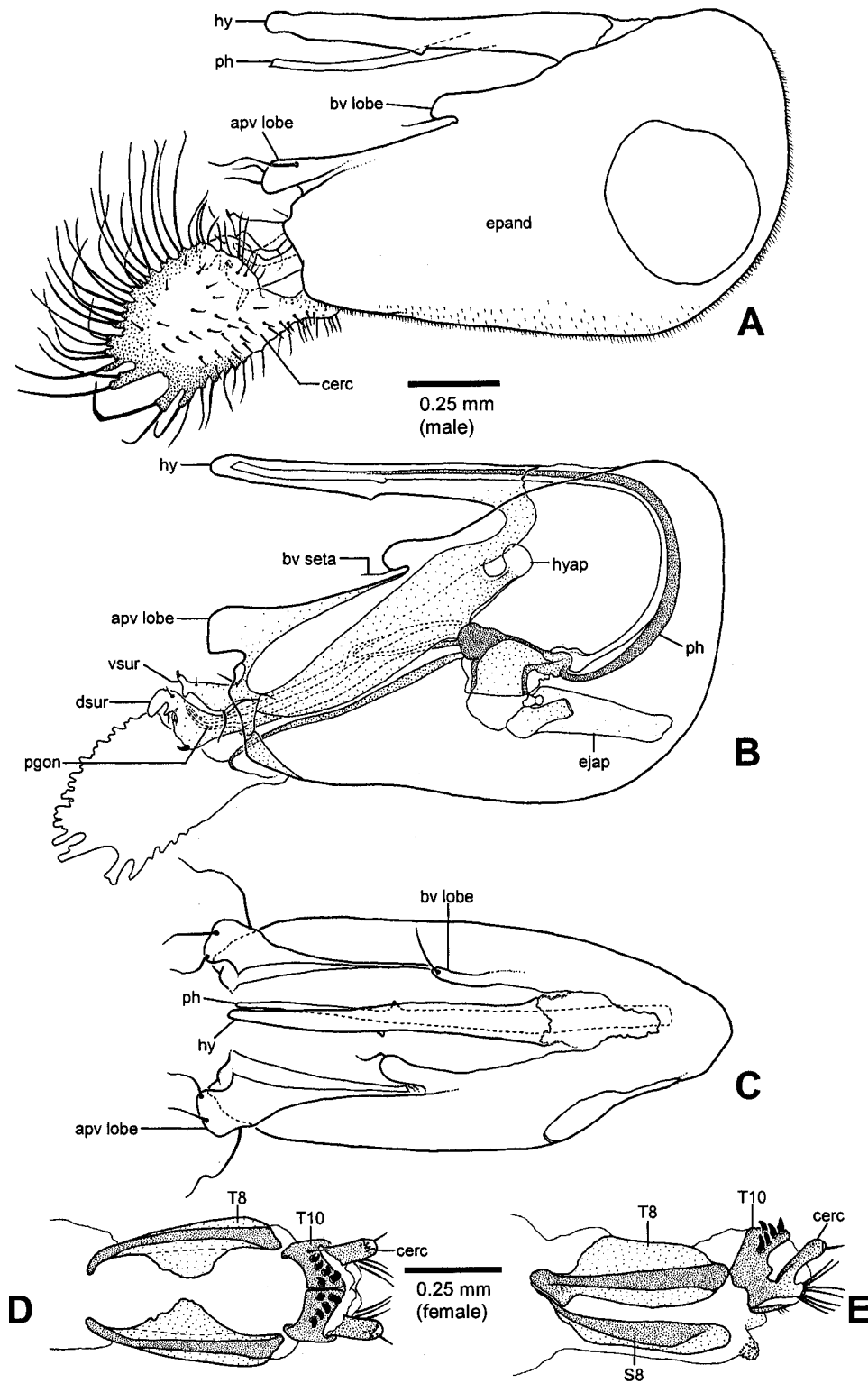


Figure 11. *Ethiomomyia purpurata*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

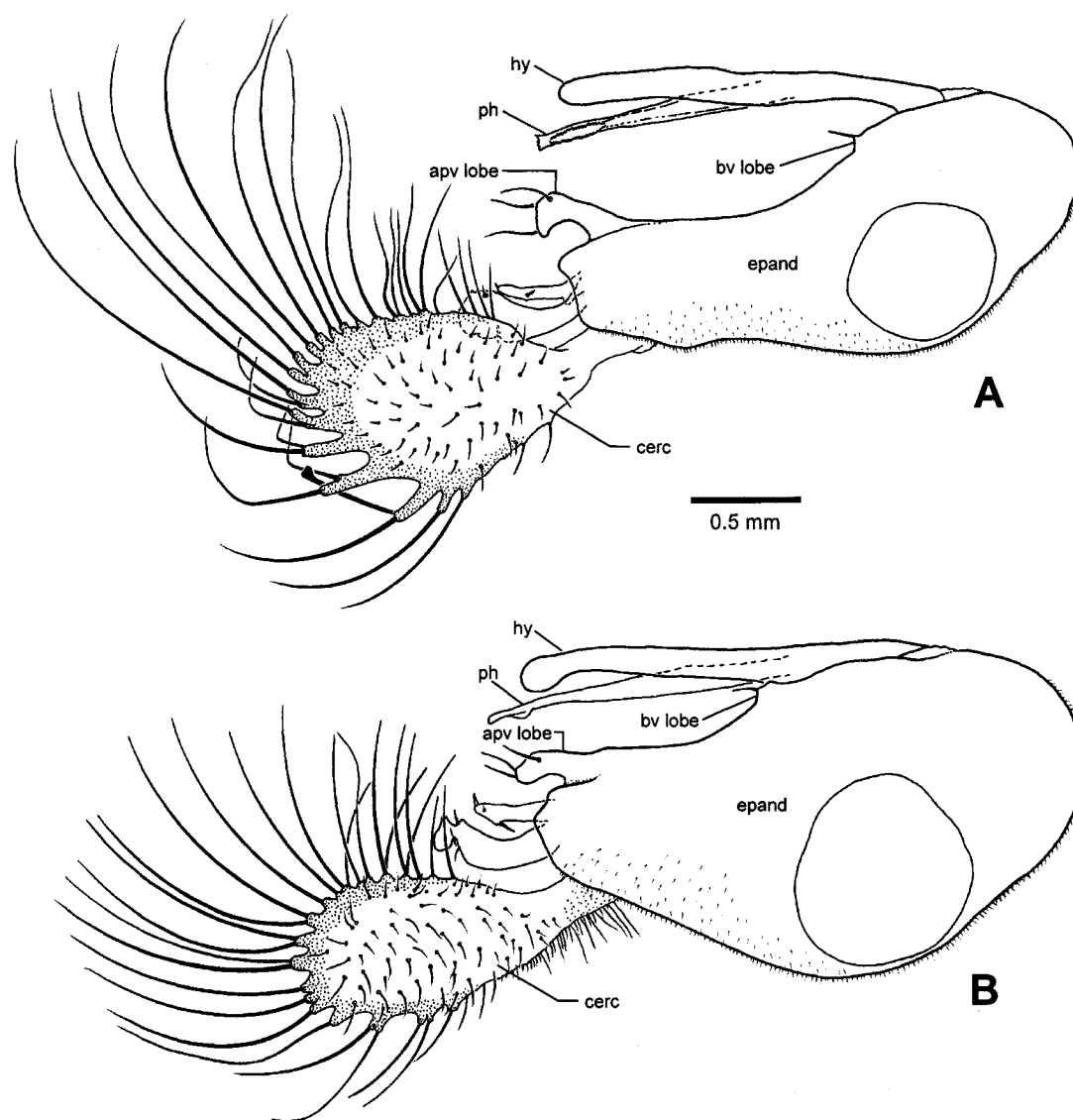


Figure 12. *Ethiomyia chalybea* and *E. violacea*: (A) *E. chalybea*, male genitalia, left lateral view. (B) *E. violacea*, male genitalia, left lateral view.

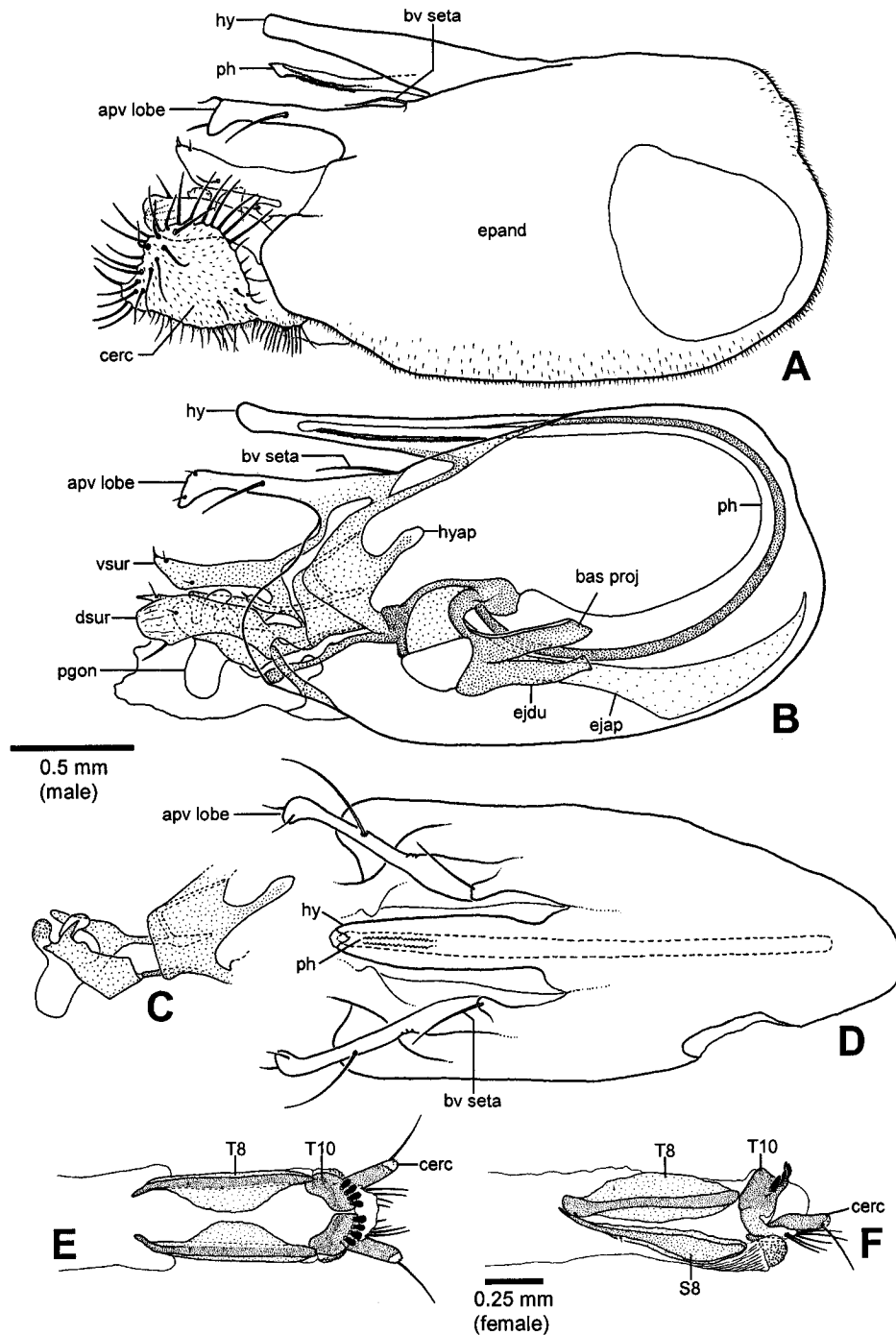


Figure 13. *Gymnopternus cupreus* and *G. aerosus*: (A) *G. cupreus*, male genitalia, left lateral view (external). (B) *G. cupreus*, male genitalia, left lateral view (internal). (C) *G. cupreus*, Male genitalia, postgonite and subepandrial sclerite/hypandrial arm complex, lateral view. (D) *G. cupreus*, male genitalia, ventral view (postgonite, surstylus and cerci not shown). (E) *G. aerosus*, female genitalia, dorsal view. (F) *G. aerosus*, female genitalia, left lateral view.

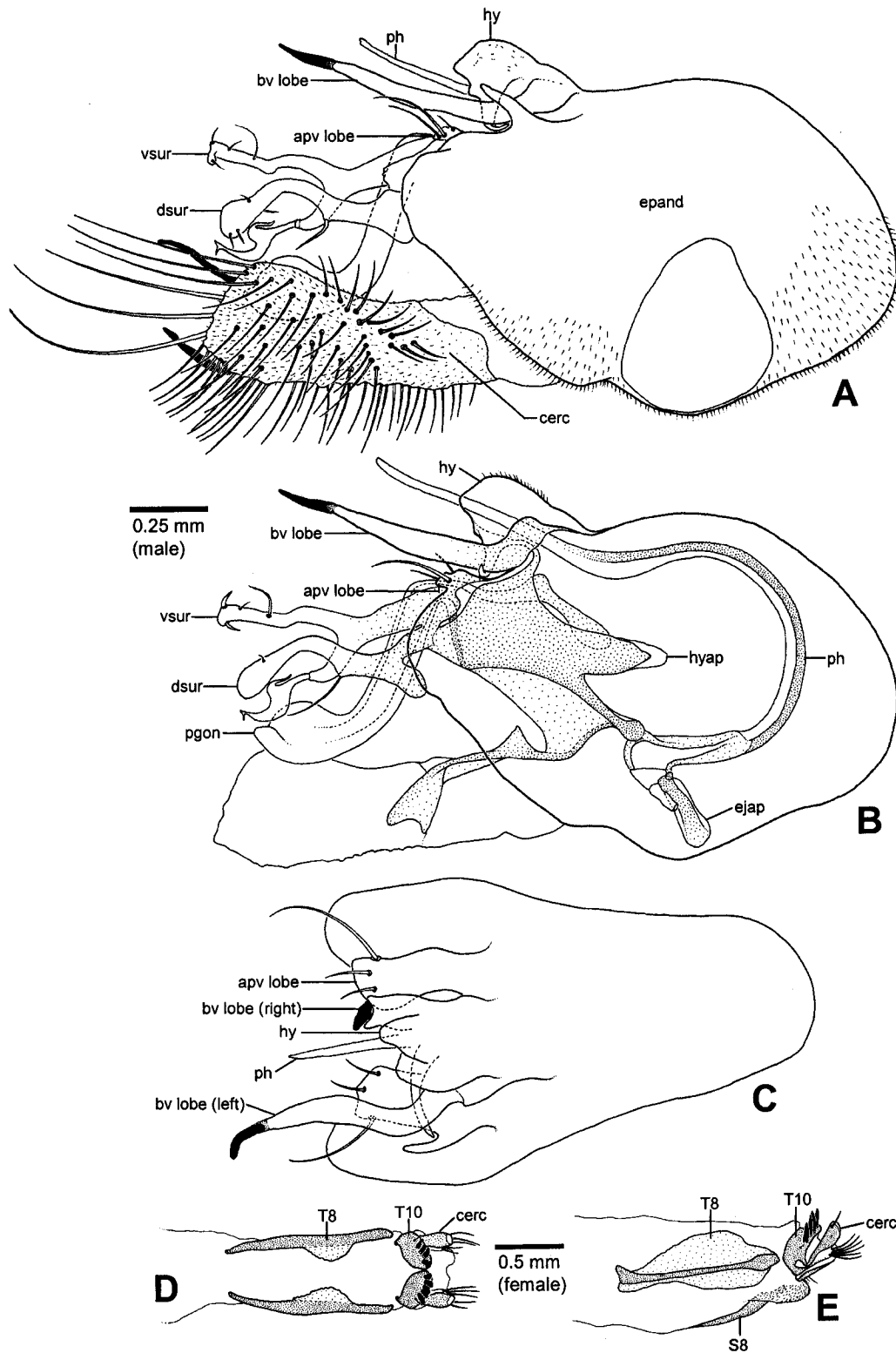


Figure 14. *Hercostomus longiventris*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

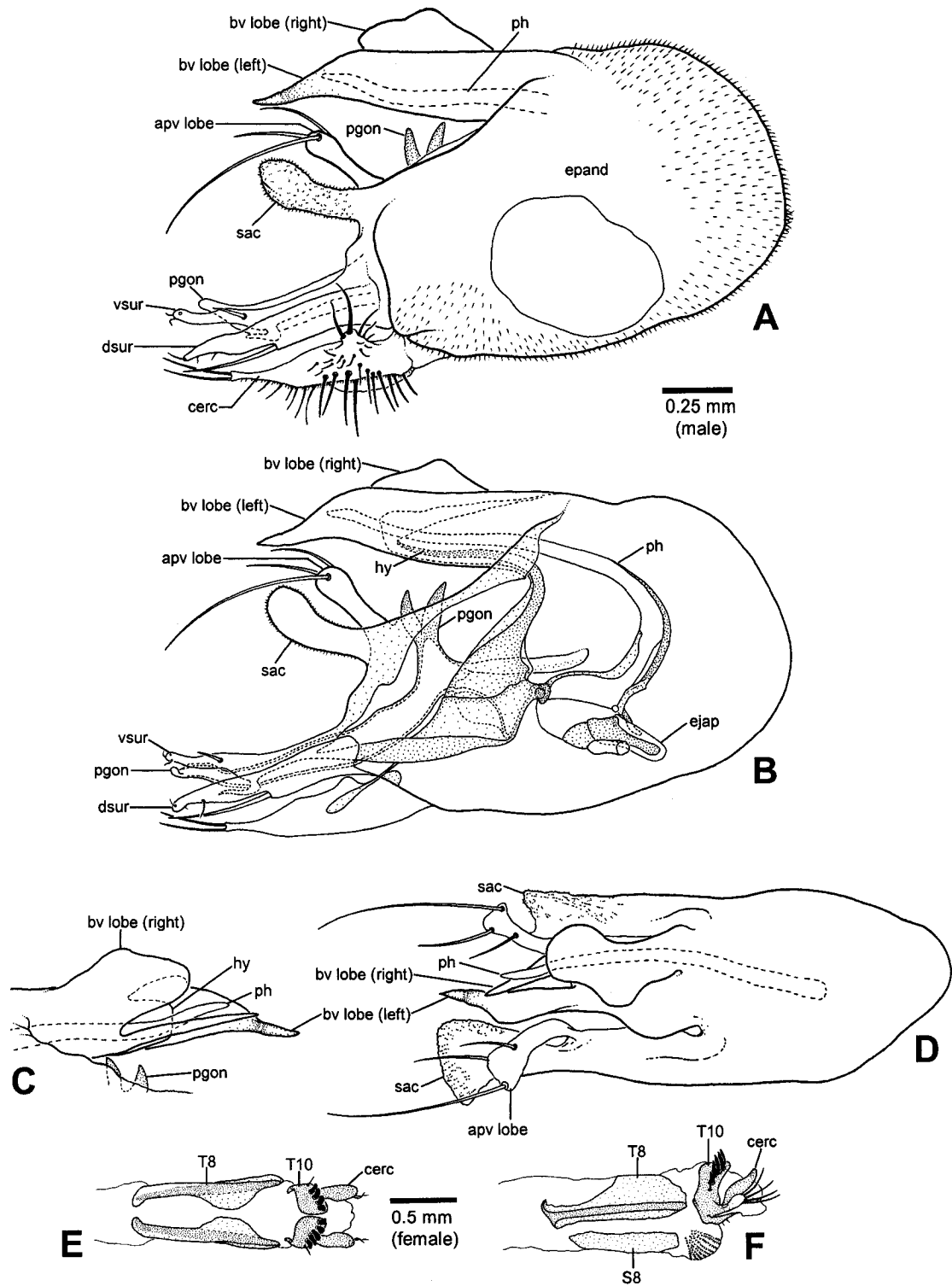


Figure 15. *Hercostomus amoenus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, basiventral epandrial lobe, hypandrium and phallus, right lateral view. (D) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (E) Female genitalia, dorsal view. (F) Female genitalia, left lateral view.

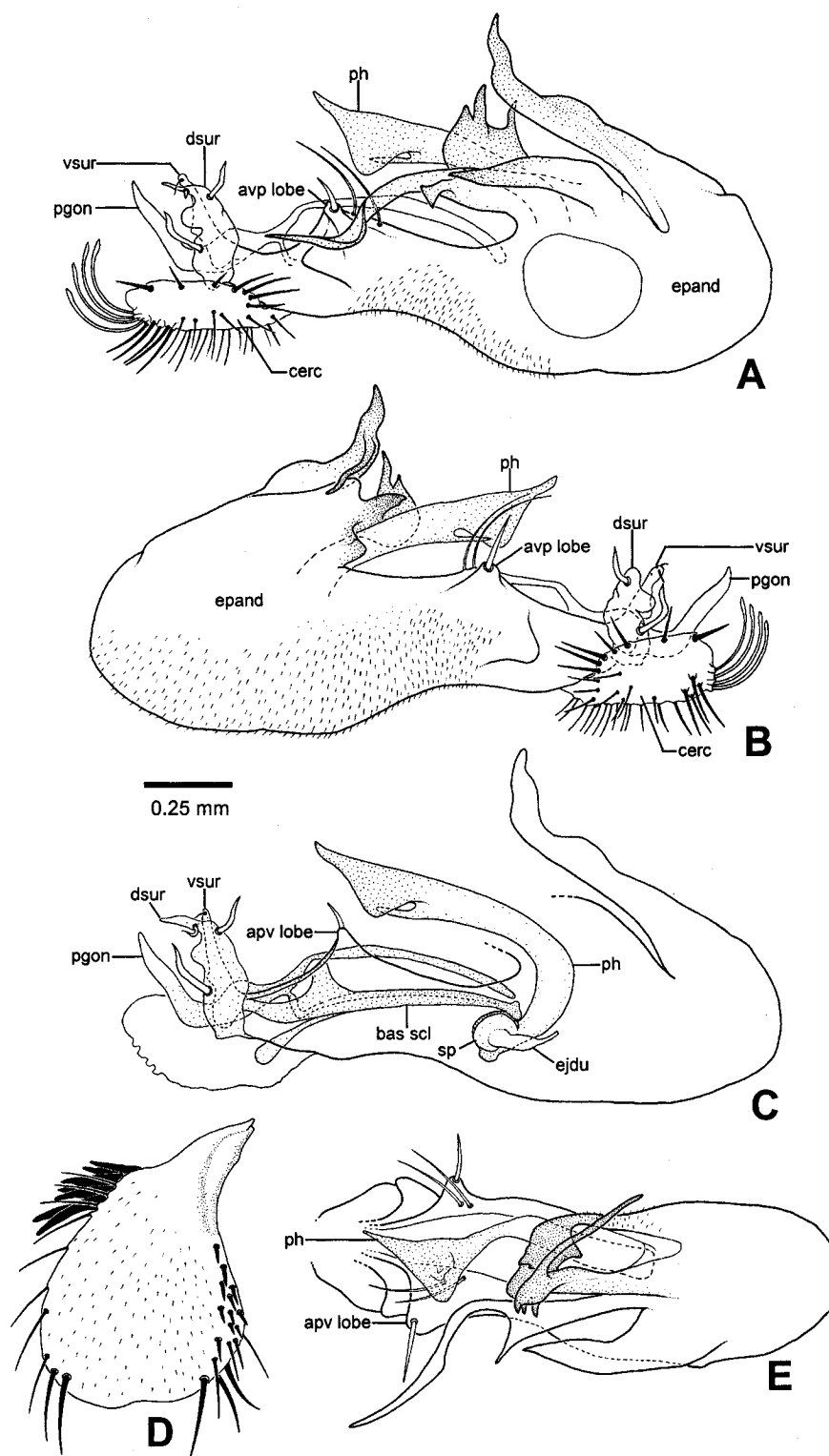


Figure 16. *Hercostomus dactylocera*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, right lateral view (external). (C) Male genitalia, left lateral view (internal, left epandrial lobes and right ventral hypopygial lobe not shown). (D) Male genitalia, sternite 8. (E) Male genitalia, ventral view (postgonite, surstylus and cerci not shown).

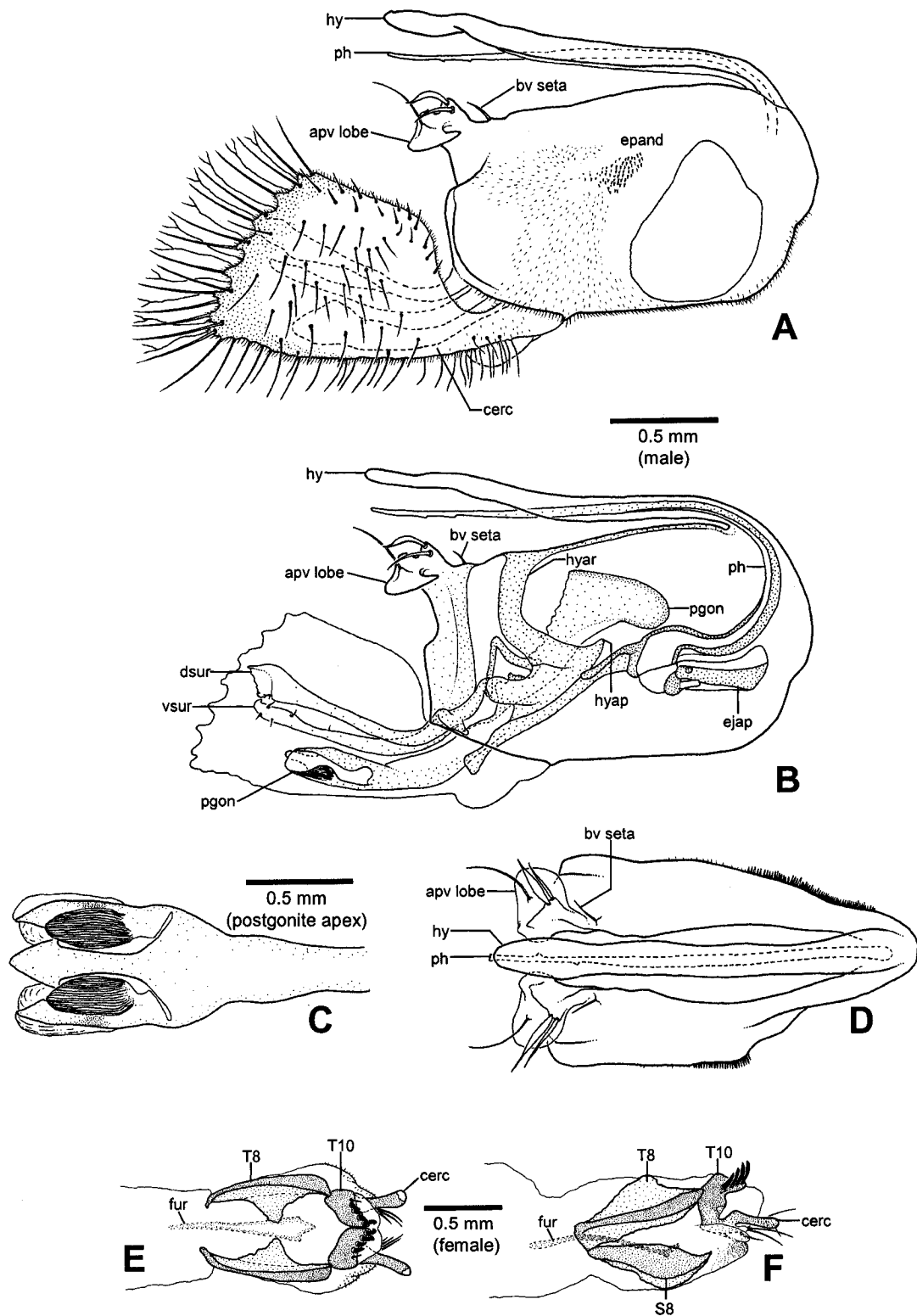


Figure 17. *Metaparaclius australiensis*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, postgonite, dorsal view of apex. (D) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (E) Female genitalia, dorsal view. (F) Female genitalia, left lateral view.

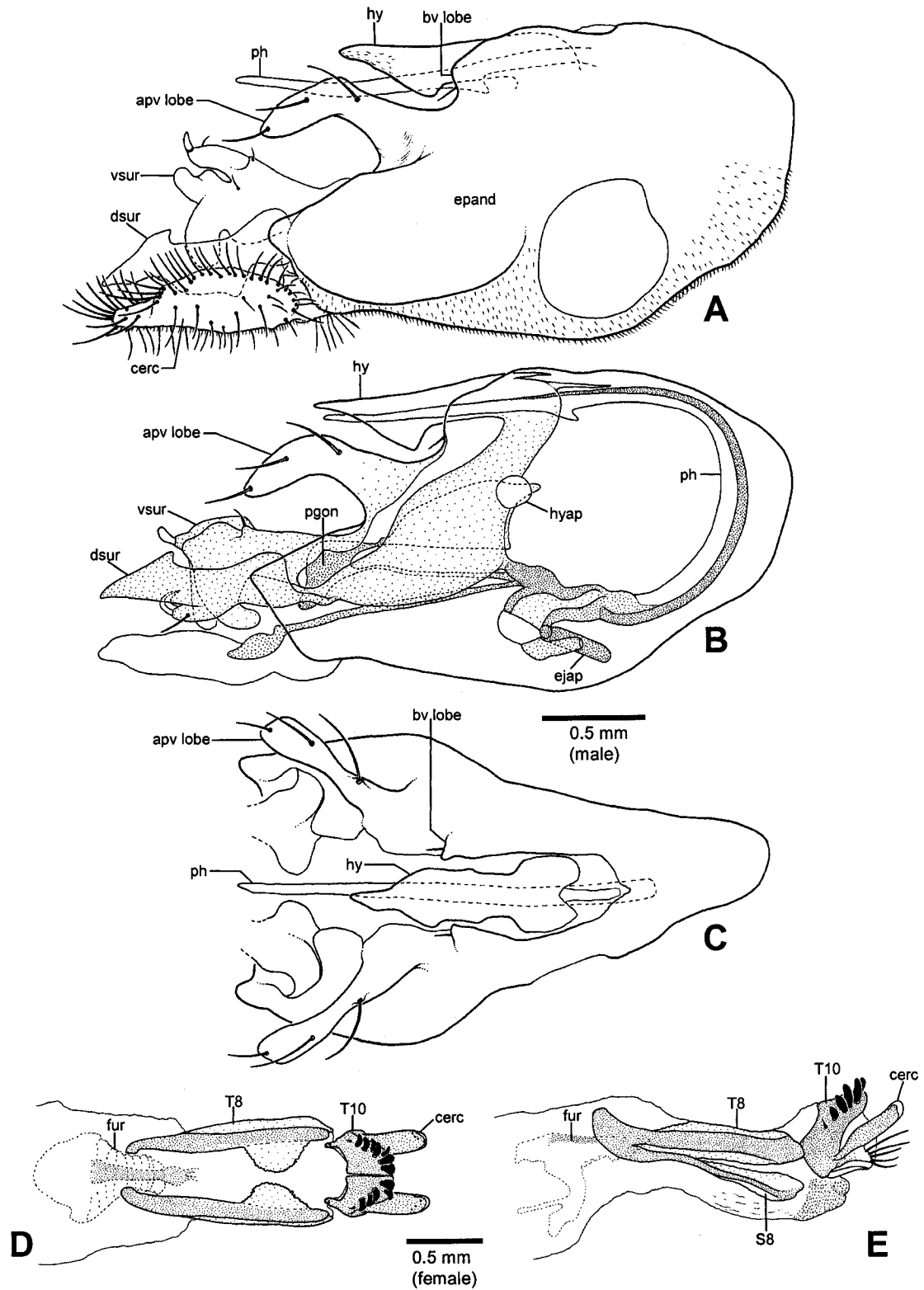


Figure 18. *Muscidideicus praetextatus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

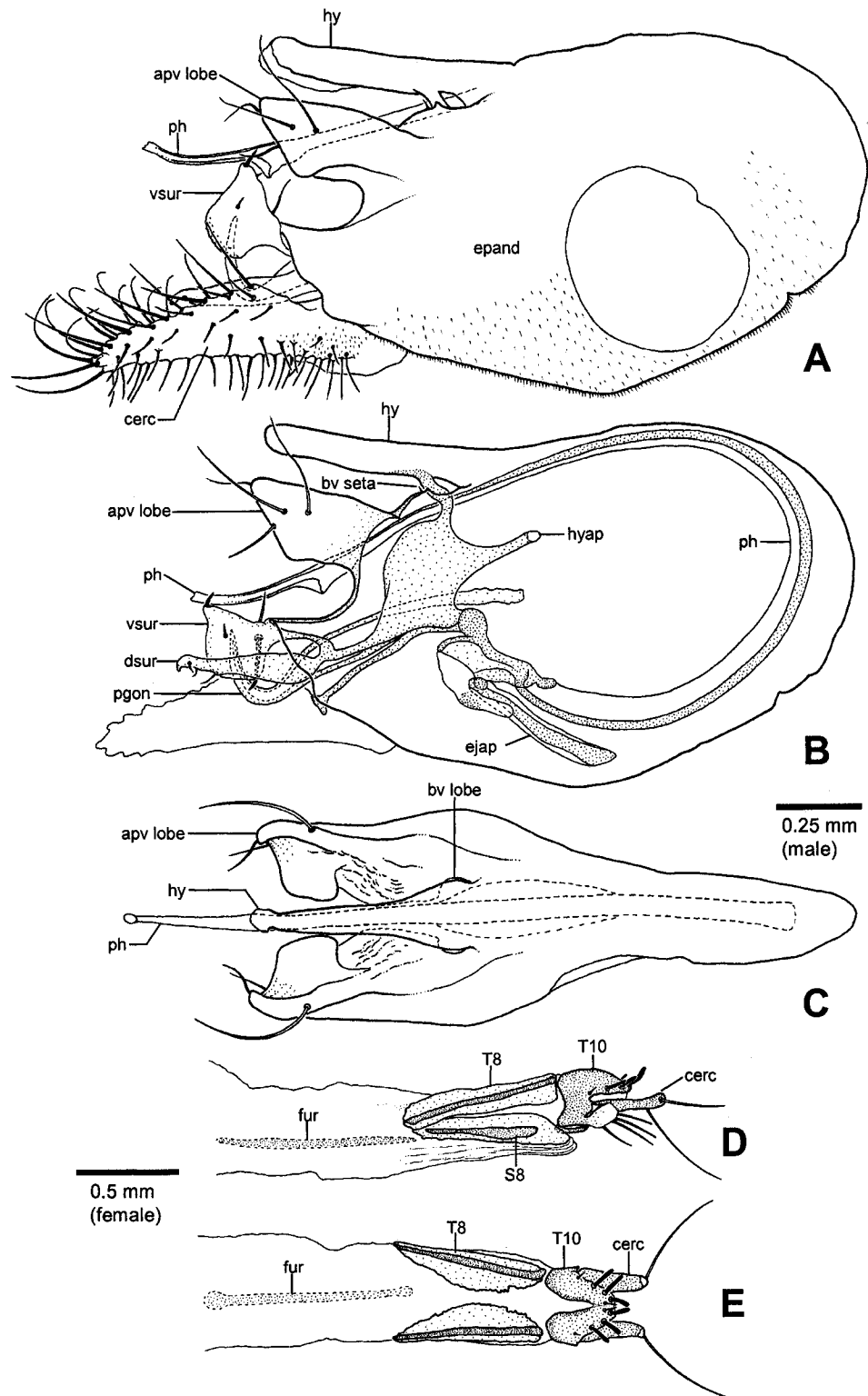


Figure 19. *Ortochile nigrocoerulea*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, left lateral view. (E) Female genitalia, dorsal view.

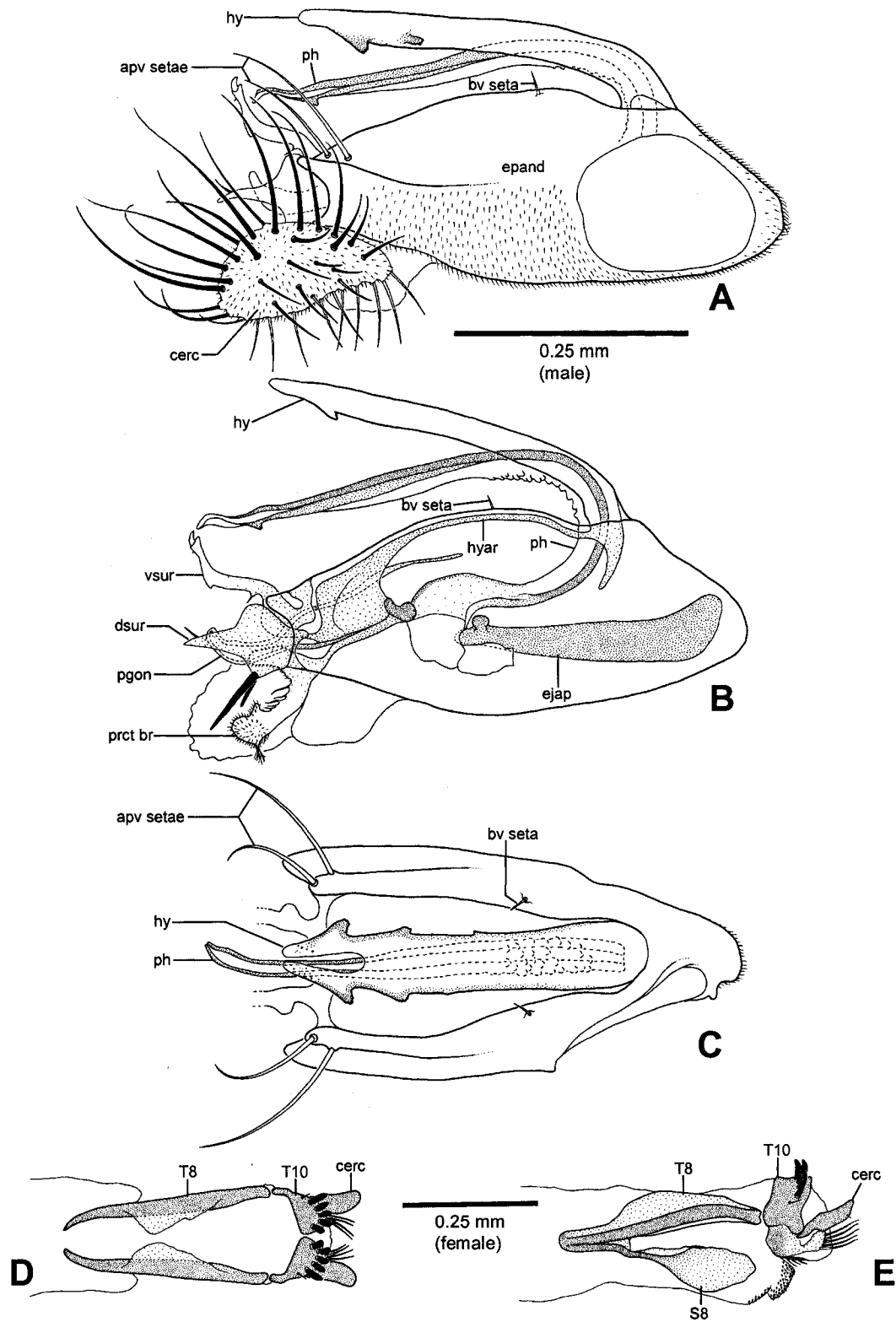


Figure 20. *Paraclius arcuatus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

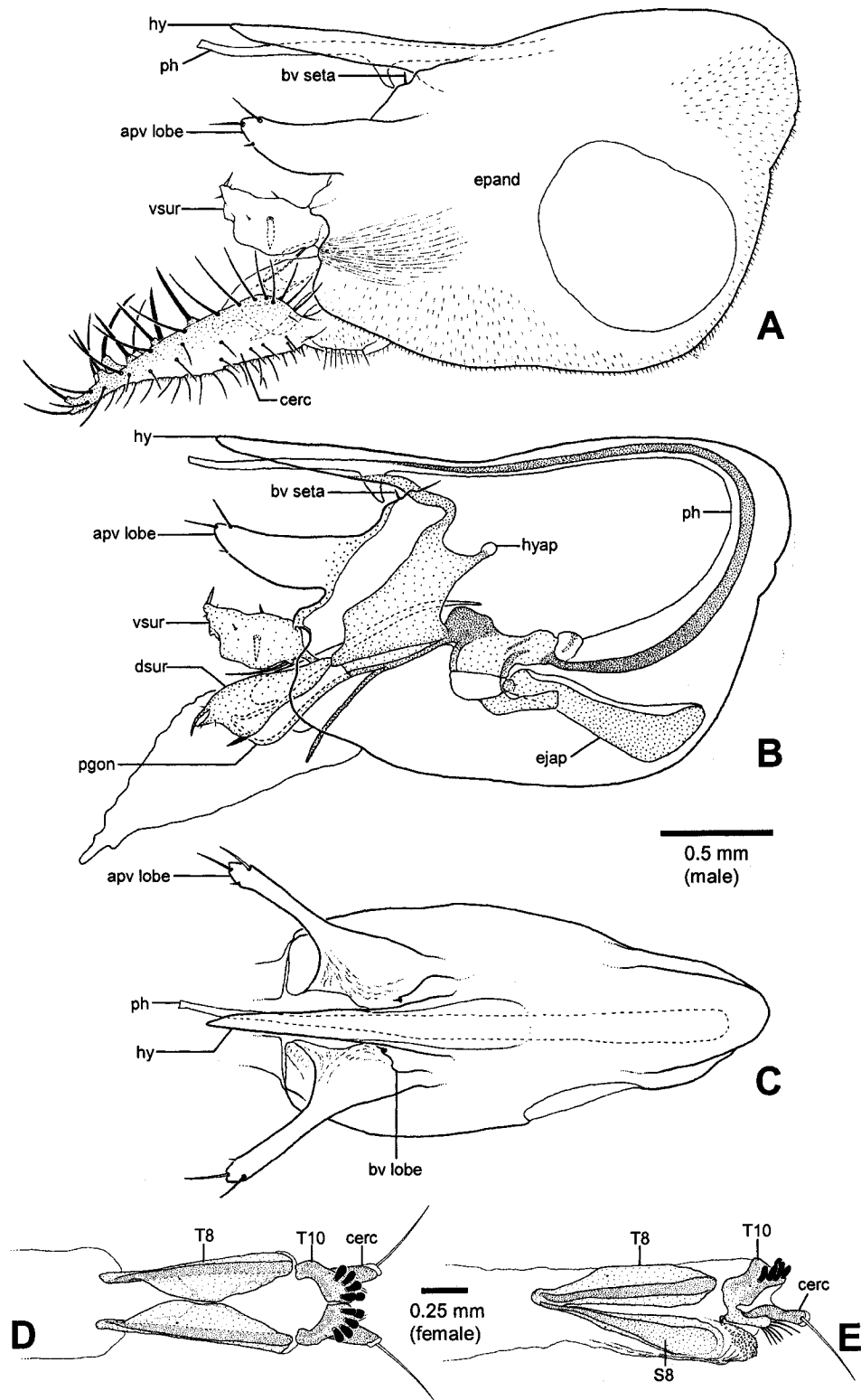


Figure 21. *Parahercostomus zhongdianus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

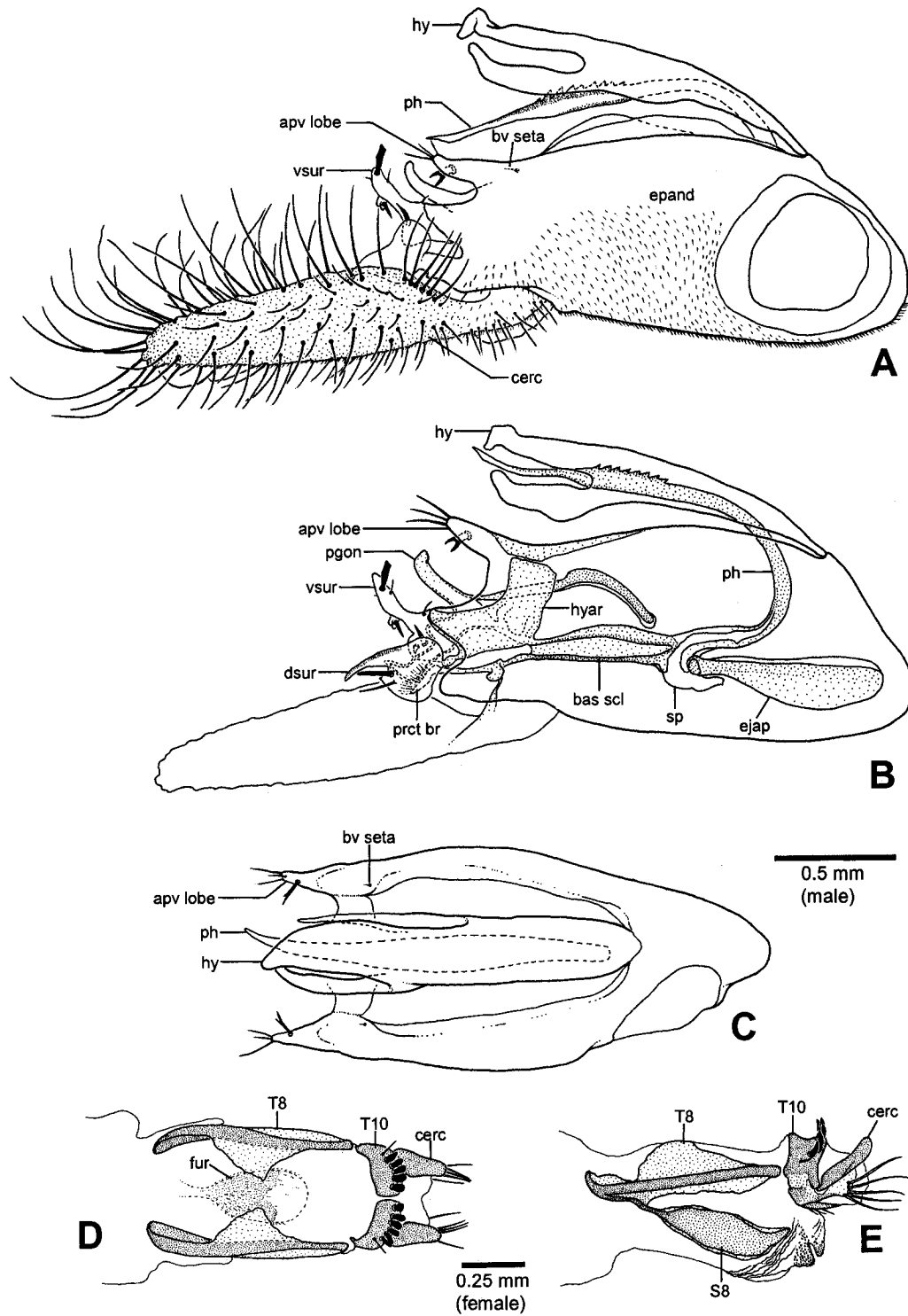


Figure 22. *Pelastoneurus vagans*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

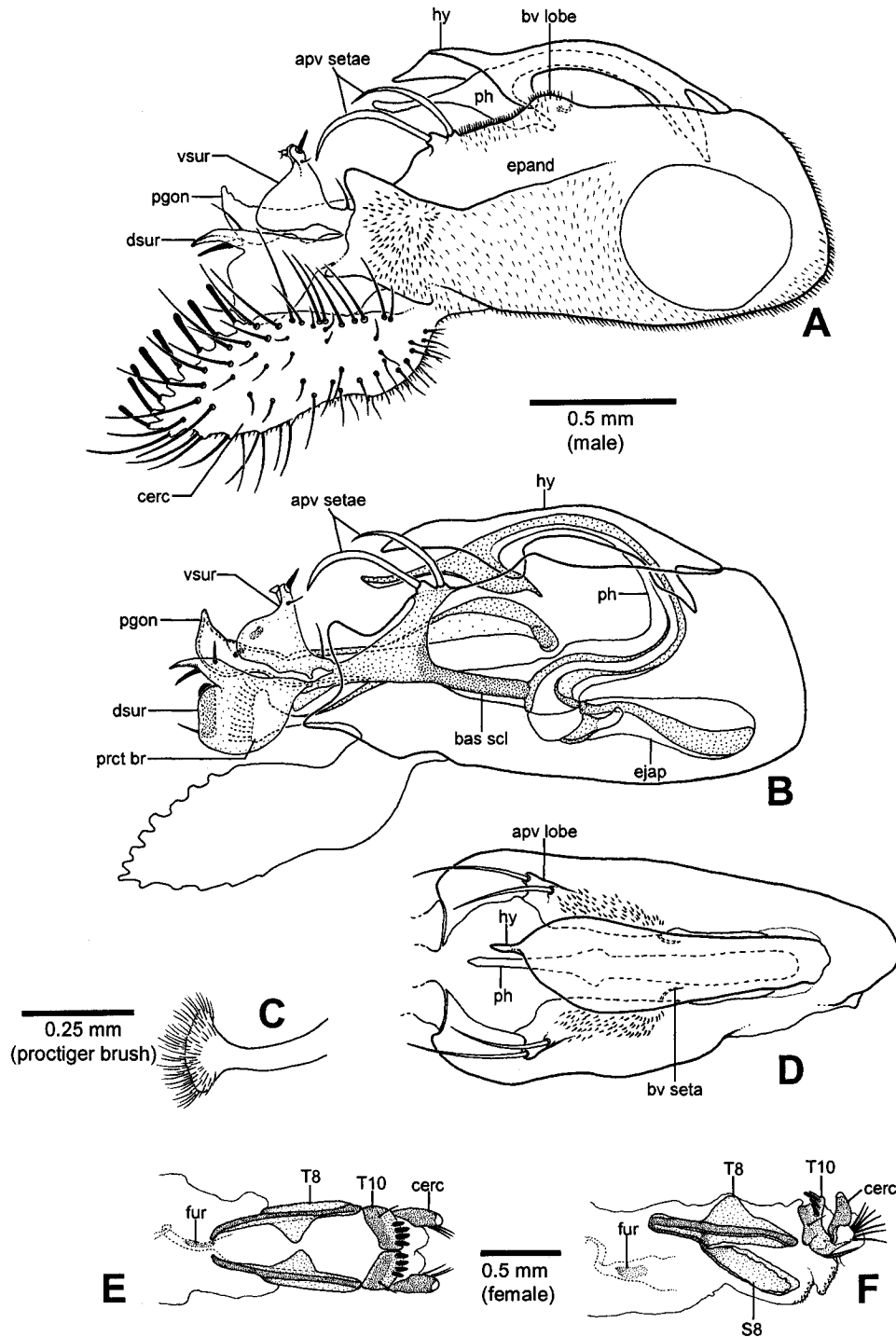


Figure 23. *Pelastoneurus lineatus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, proctiger brush, lateral view. (D) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (E) Female genitalia, dorsal view. (F) Female genitalia, left lateral view.

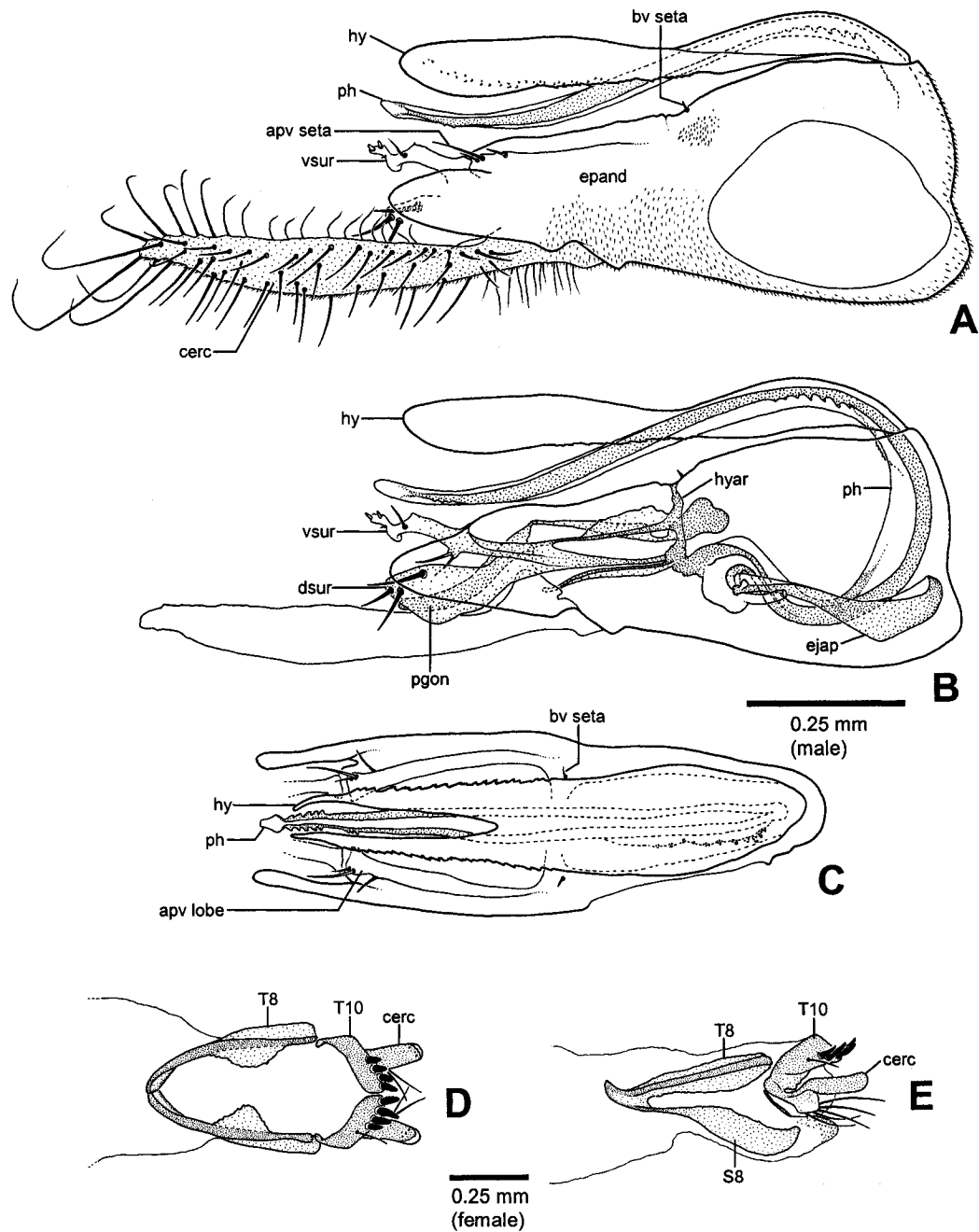


Figure 24. *Pelastoneurus tripartitus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

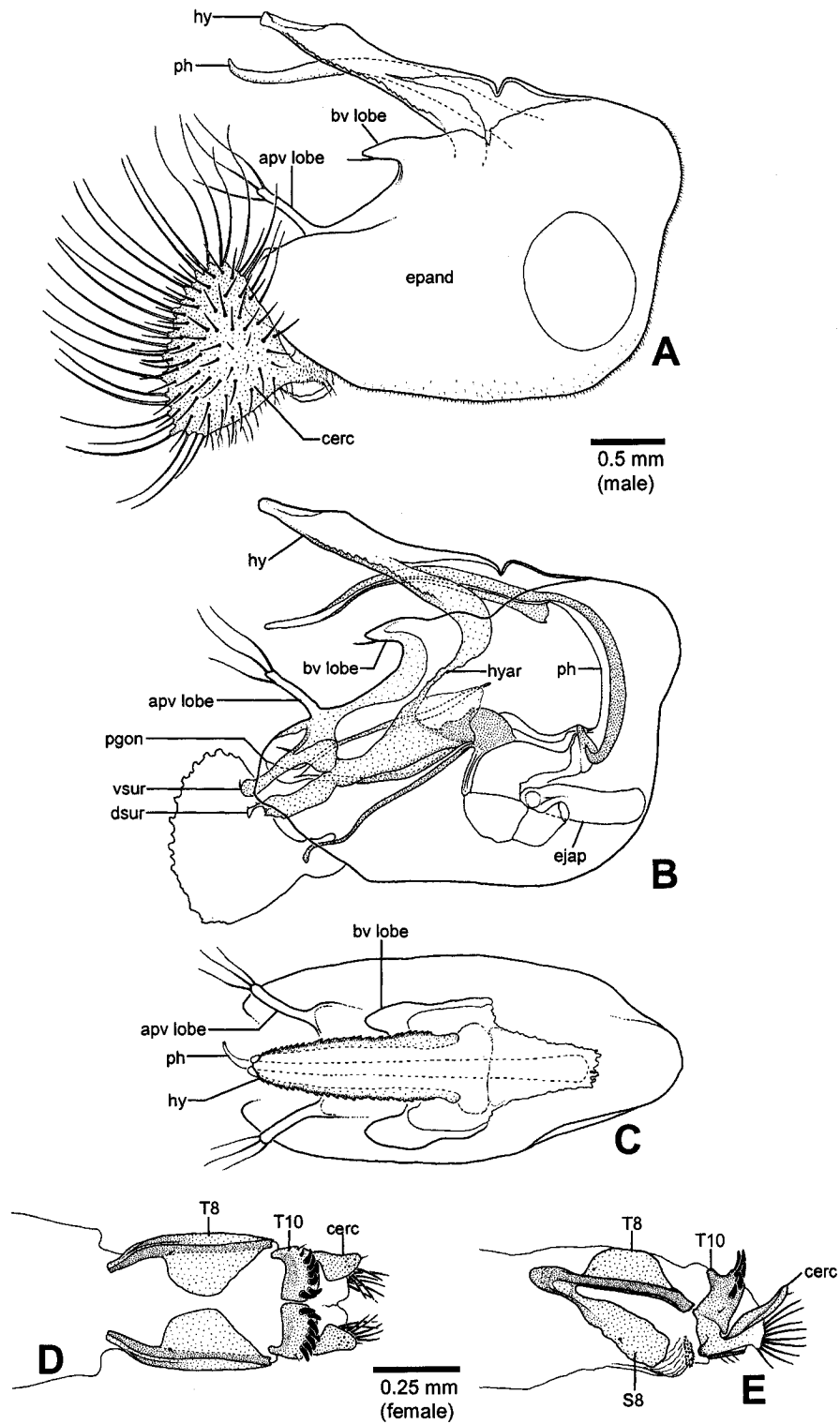


Figure 25. *Platypsopsis maroccanus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

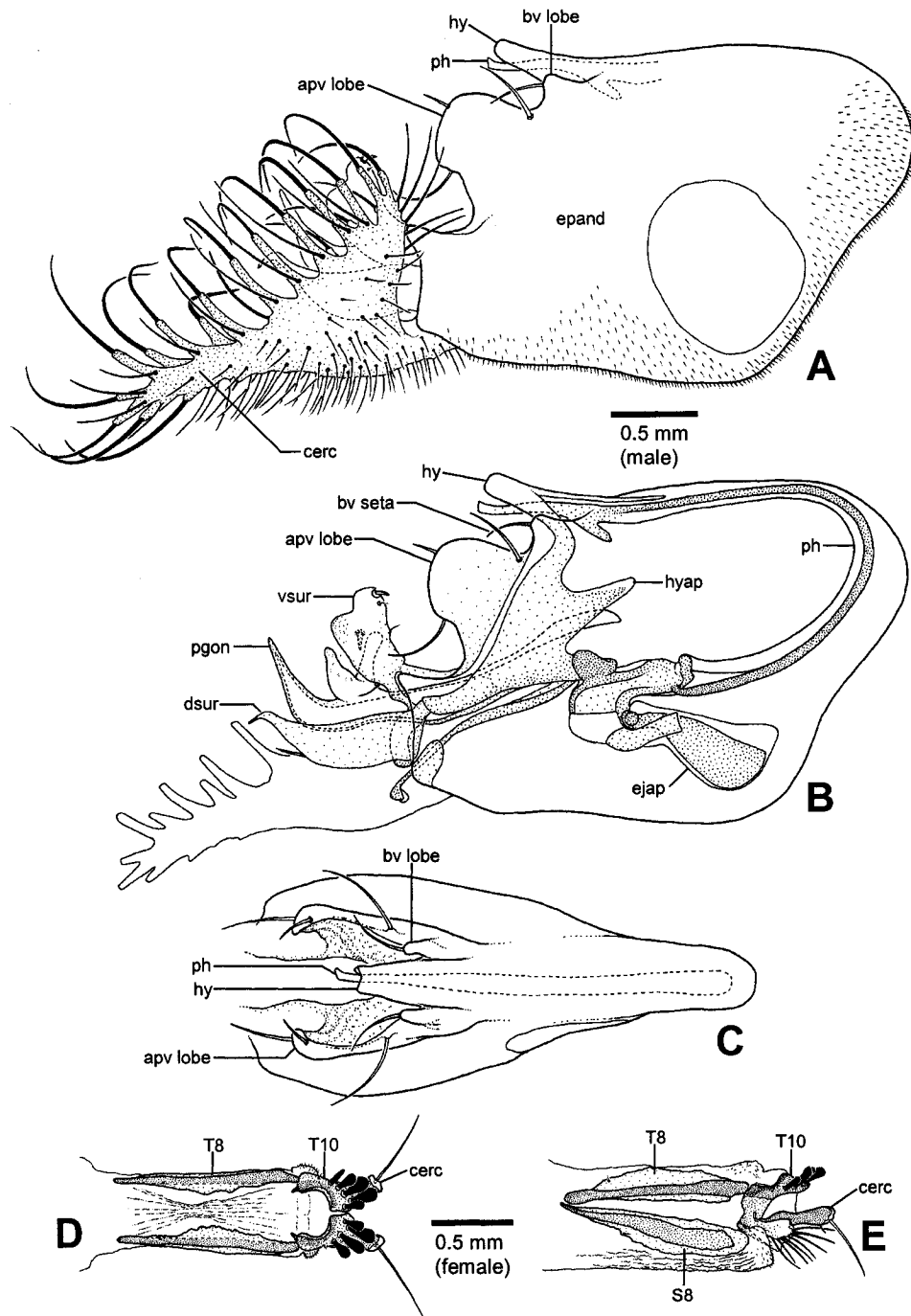


Figure 26. *Poecilobothrus regalis* and *P. nobilitatus*: (A) *P. regalis*, male genitalia, left lateral view (external). (B) *P. regalis*, male genitalia, left lateral view (internal). (C) *P. regalis*, male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) *P. nobilitatus*, female genitalia, dorsal view. (E) *P. nobilitatus*, female genitalia, left lateral view.

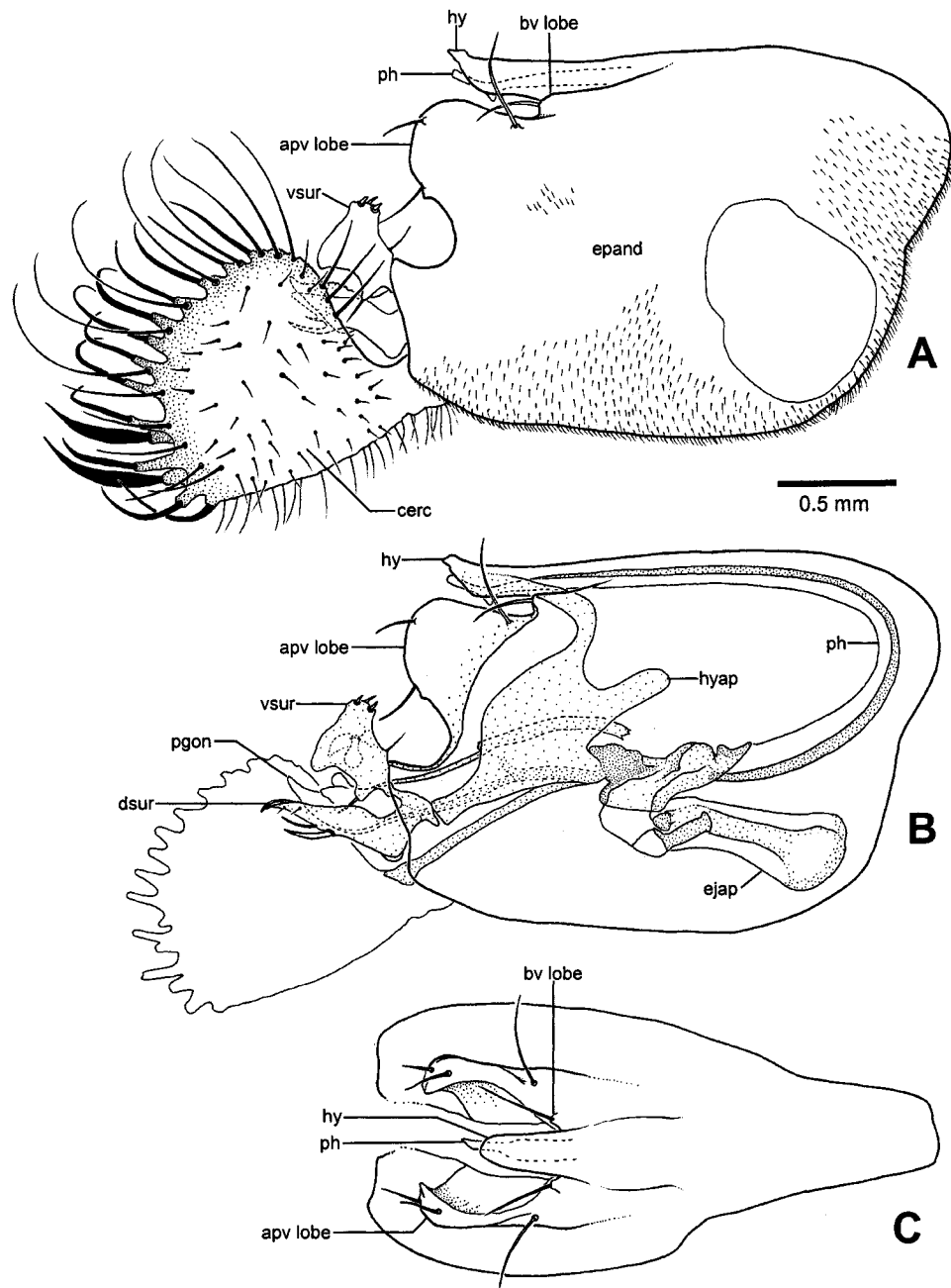


Figure 27. *Poecilobothrus aberrans*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown).

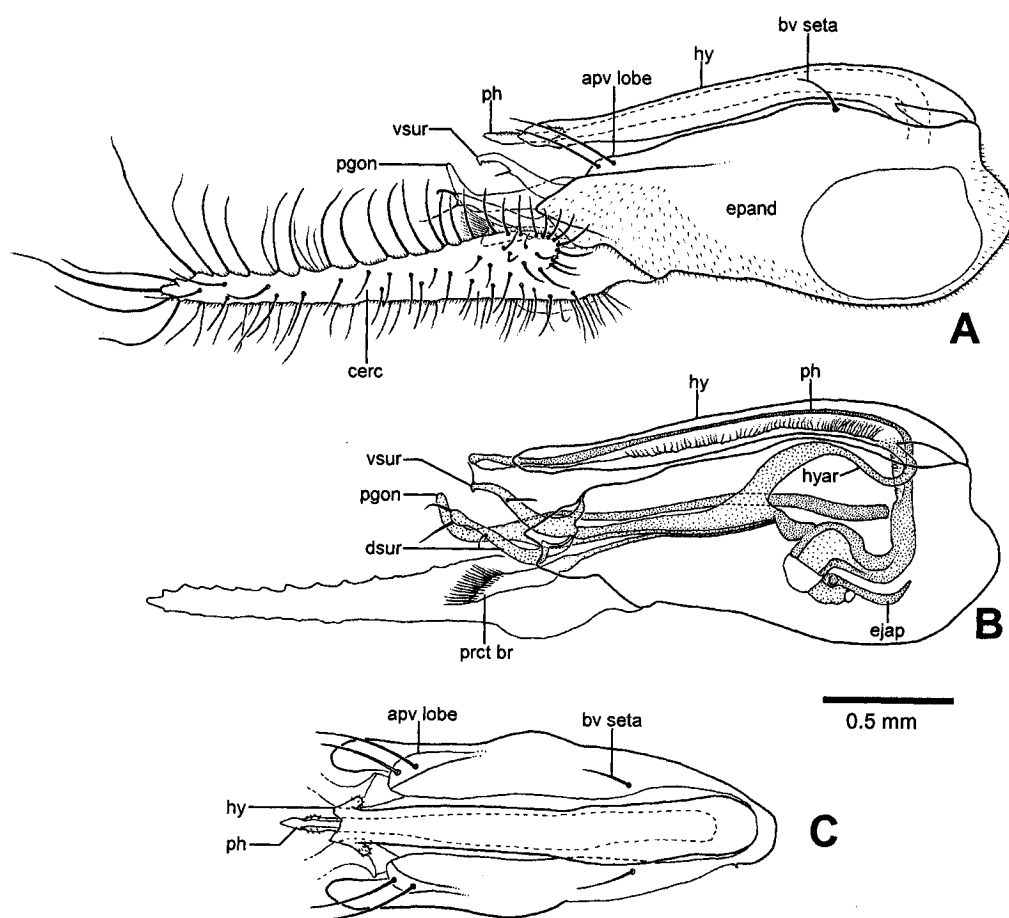


Figure 28. *Stenopygium nubeculum*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown).

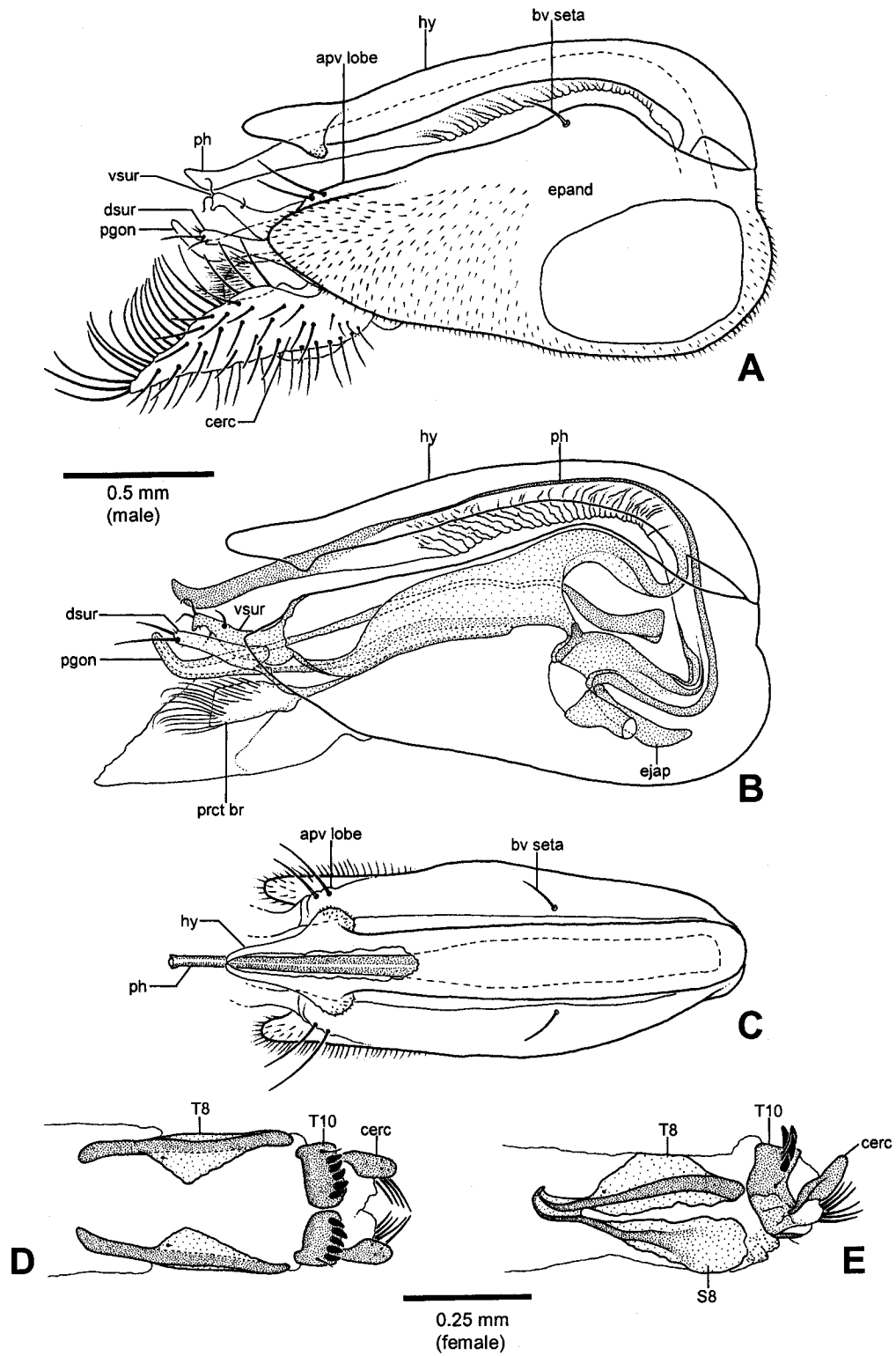


Figure 29. *Stenopygium punctipennis*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

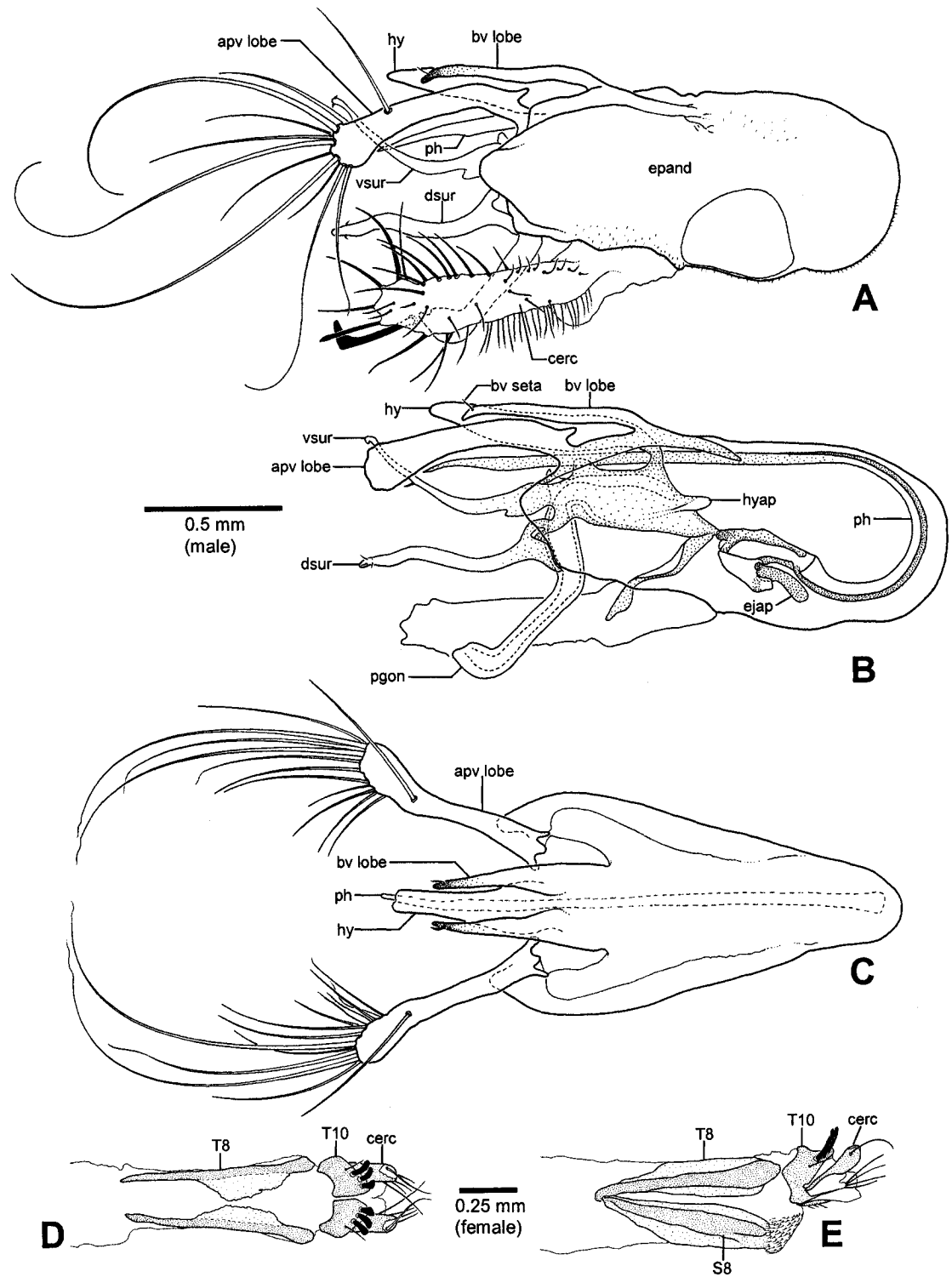


Figure 30. *Sybistroma obscurellum*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

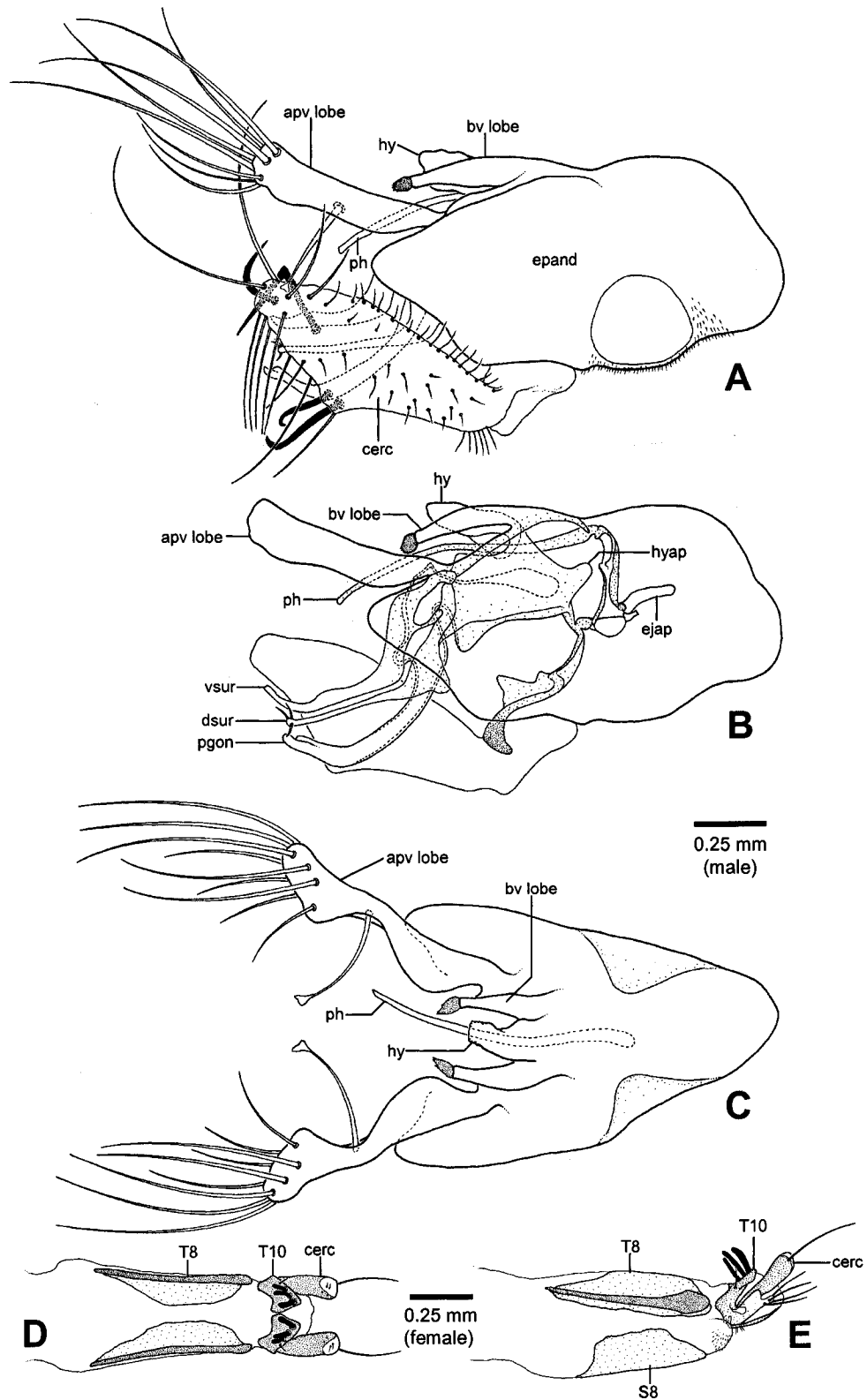


Figure 31. *Sybistroma impar*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

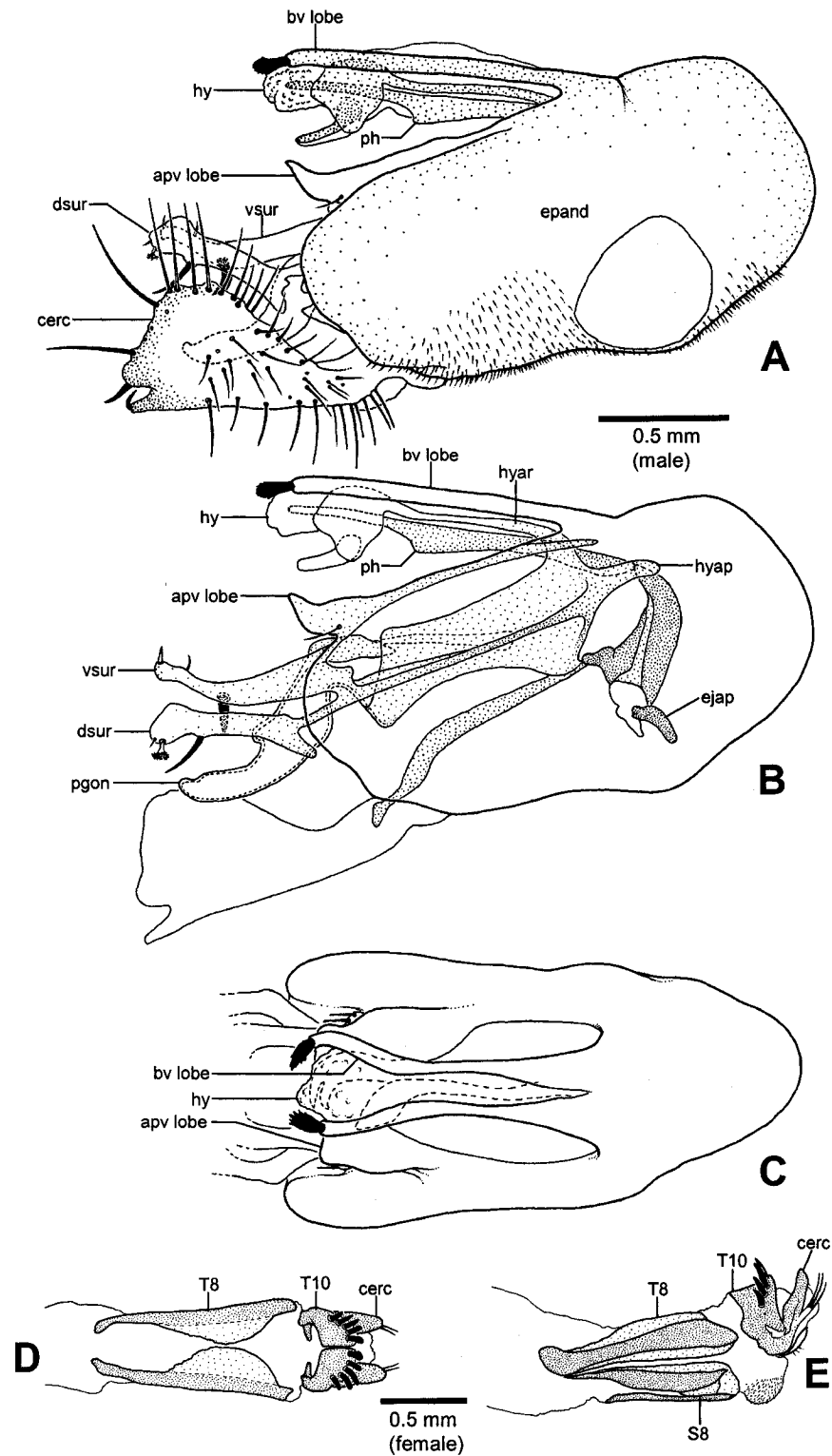


Figure 32. *Sybistroma nodicornis*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

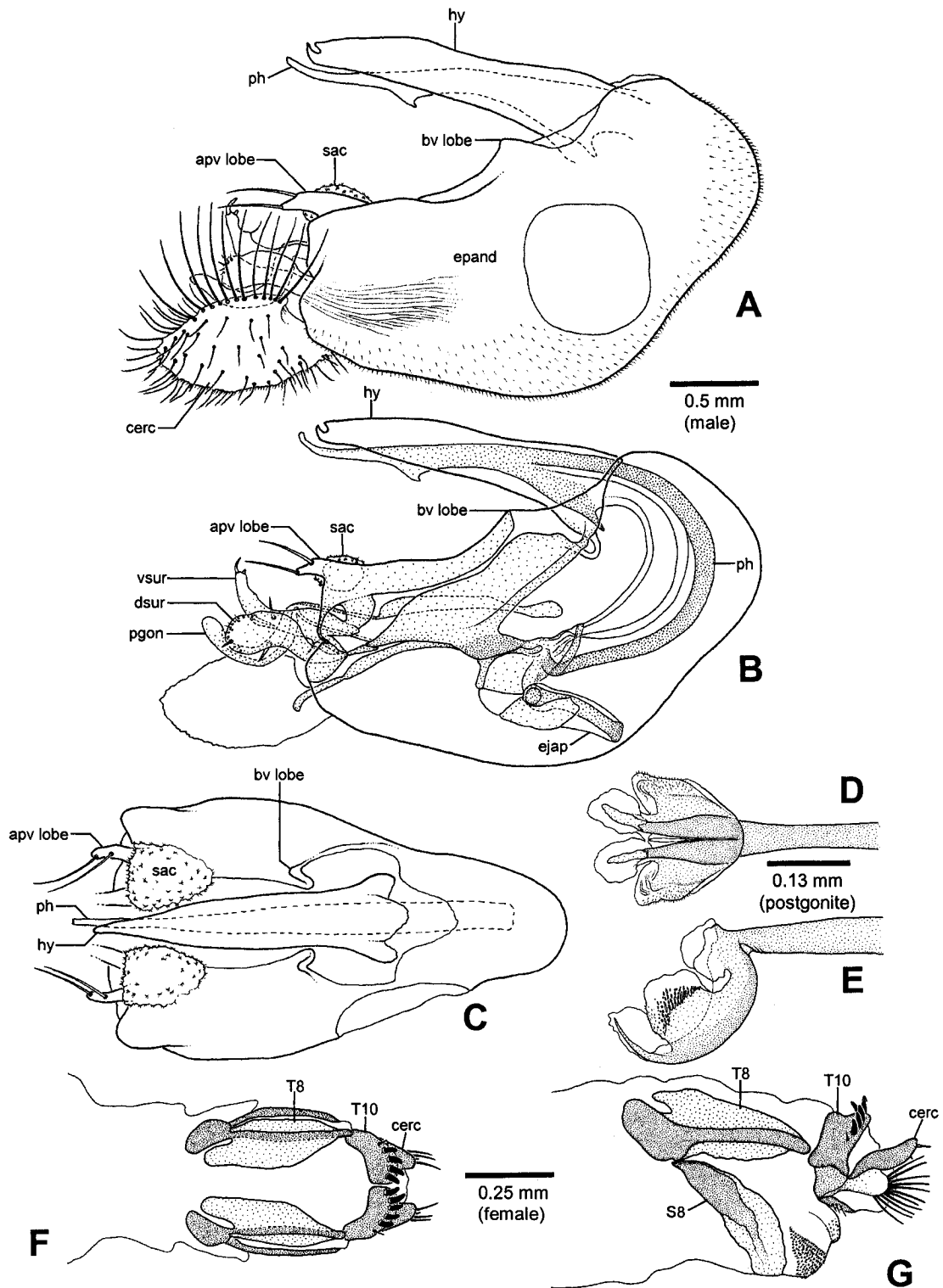


Figure 33. *Tachytrechus notatus* and *T. angustipennis*: (A) *T. notatus*, male genitalia, left lateral view (external). (B) *T. notatus*, male genitalia, left lateral view (internal). (C) *T. notatus*, male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) *T. angustipennis*, male genitalia, postgonite dorsal view. (E) *T. angustipennis*, male genitalia, postgonite lateral view. (F) *T. notatus*, female genitalia, dorsal view. (G) *T. notatus*, female genitalia, left lateral view.

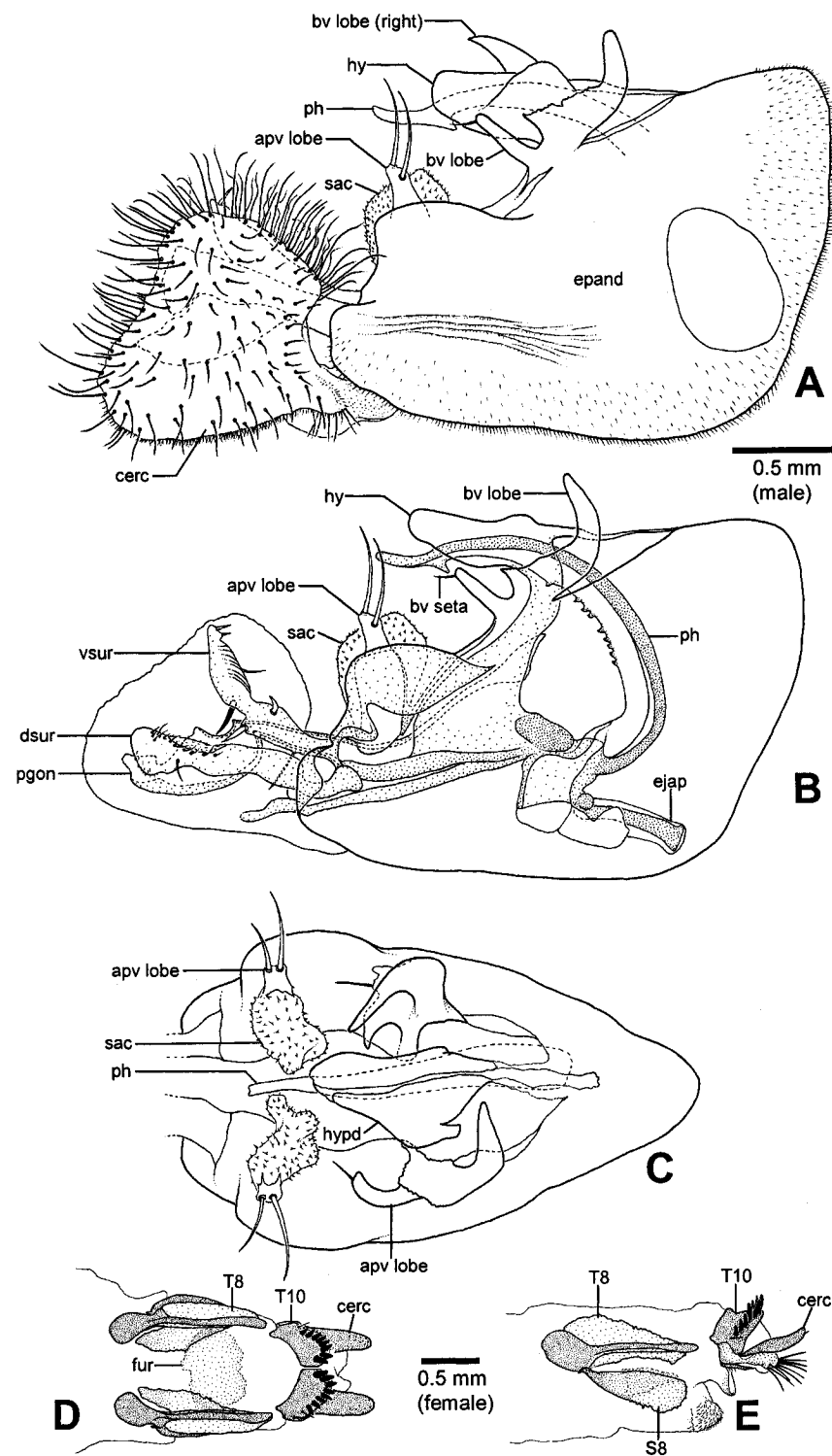


Figure 34. *Tachytrechus moechus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

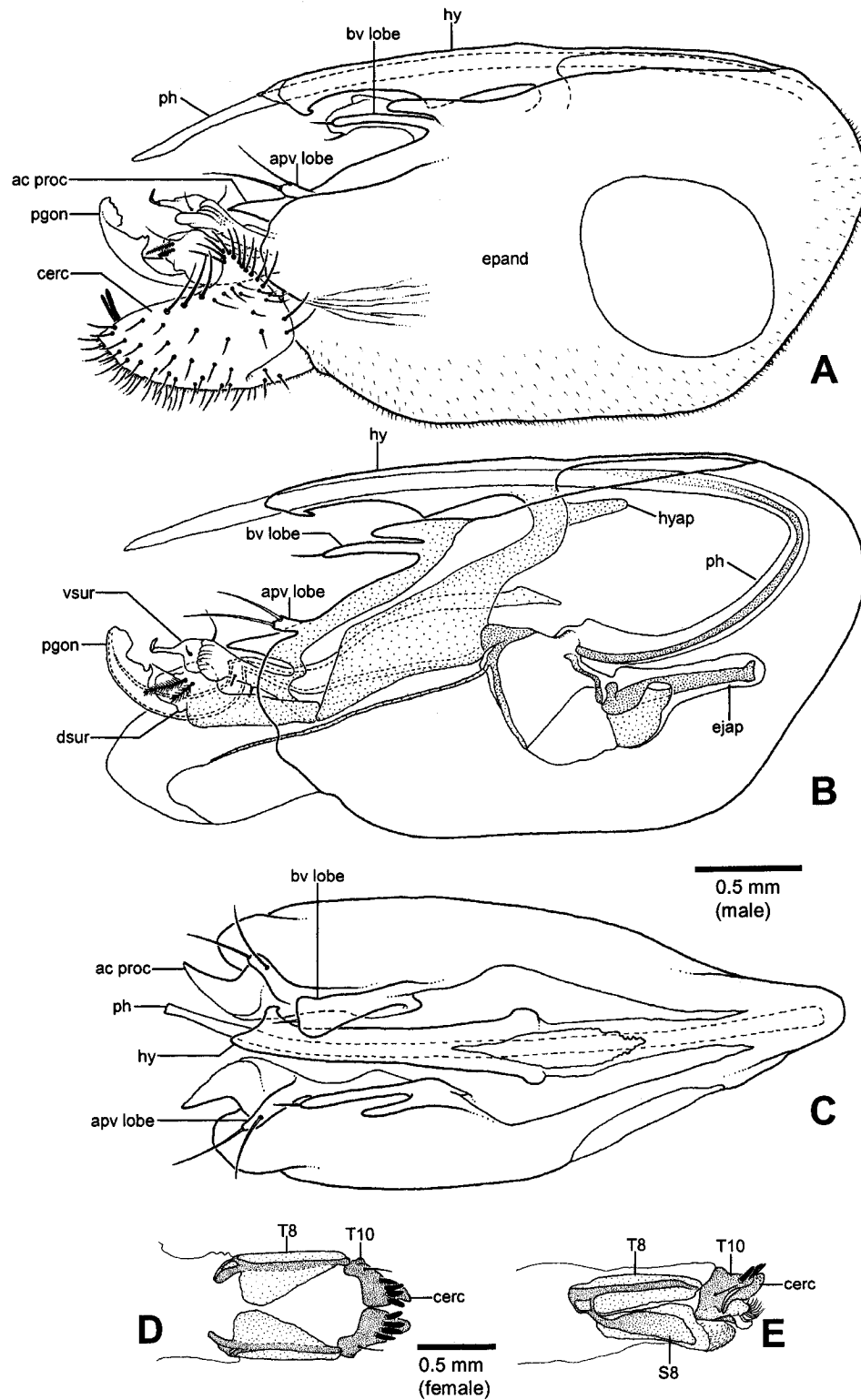


Figure 35. *Tachytrechus laevigatus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

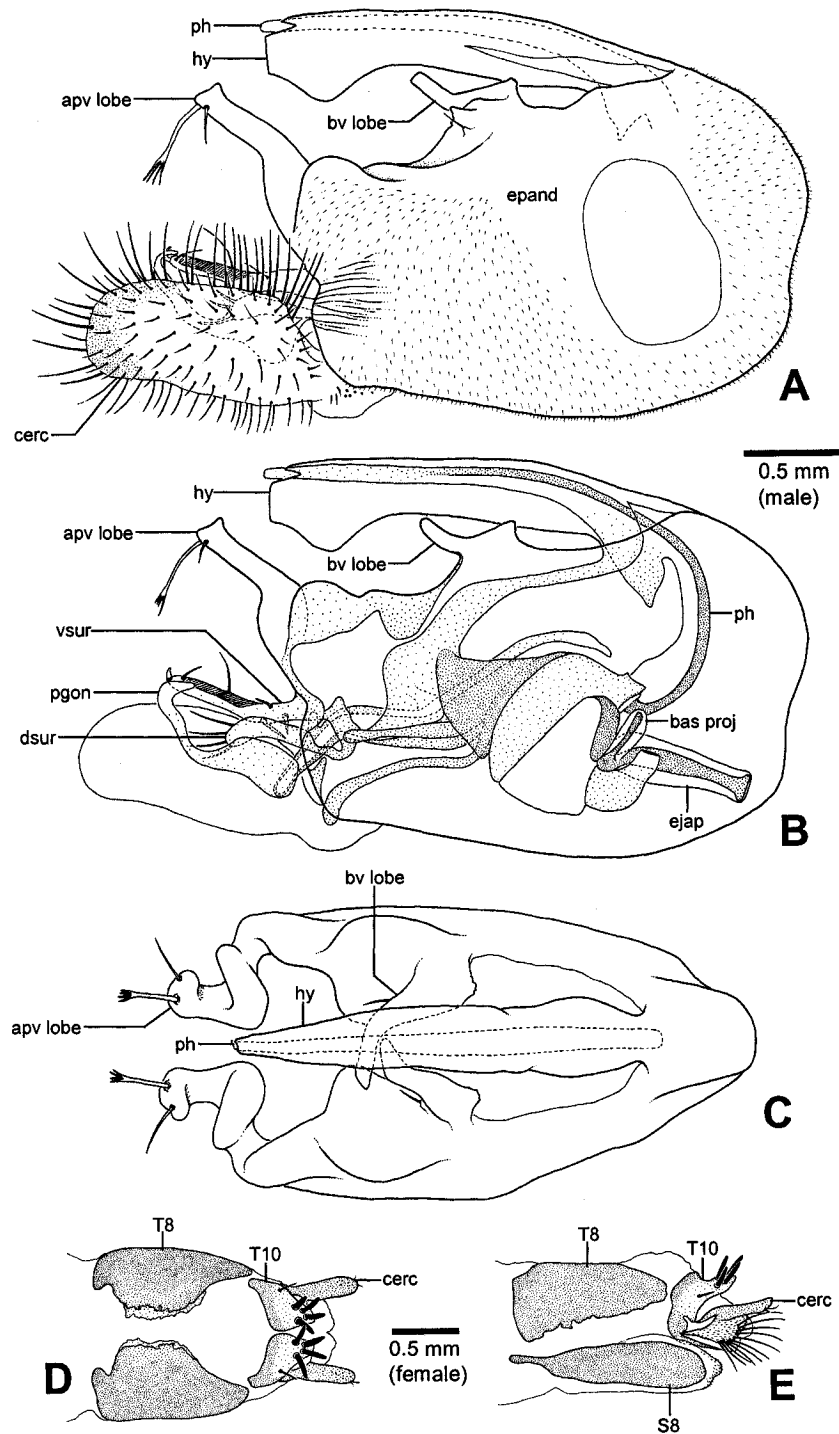


Figure 36. *Tachytrechus beckeri*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

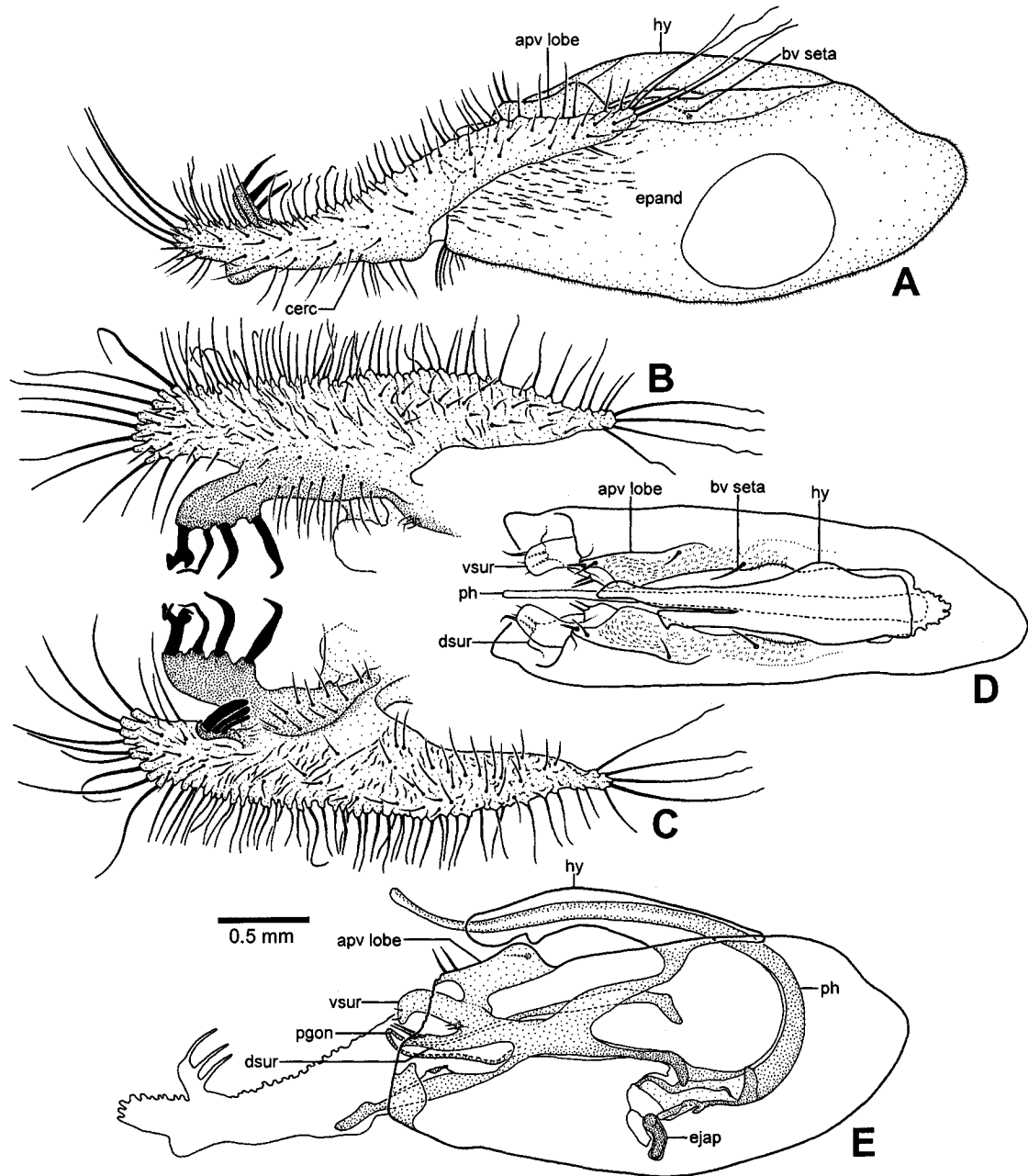


Figure 37. *Katangaia longifacies*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, right cercus (dorsal). (C) Male genitalia, right cercus (ventral). (D) Male genitalia, ventral view (postgonite, and cerci not shown). (E) Male genitalia, left lateral view (internal).

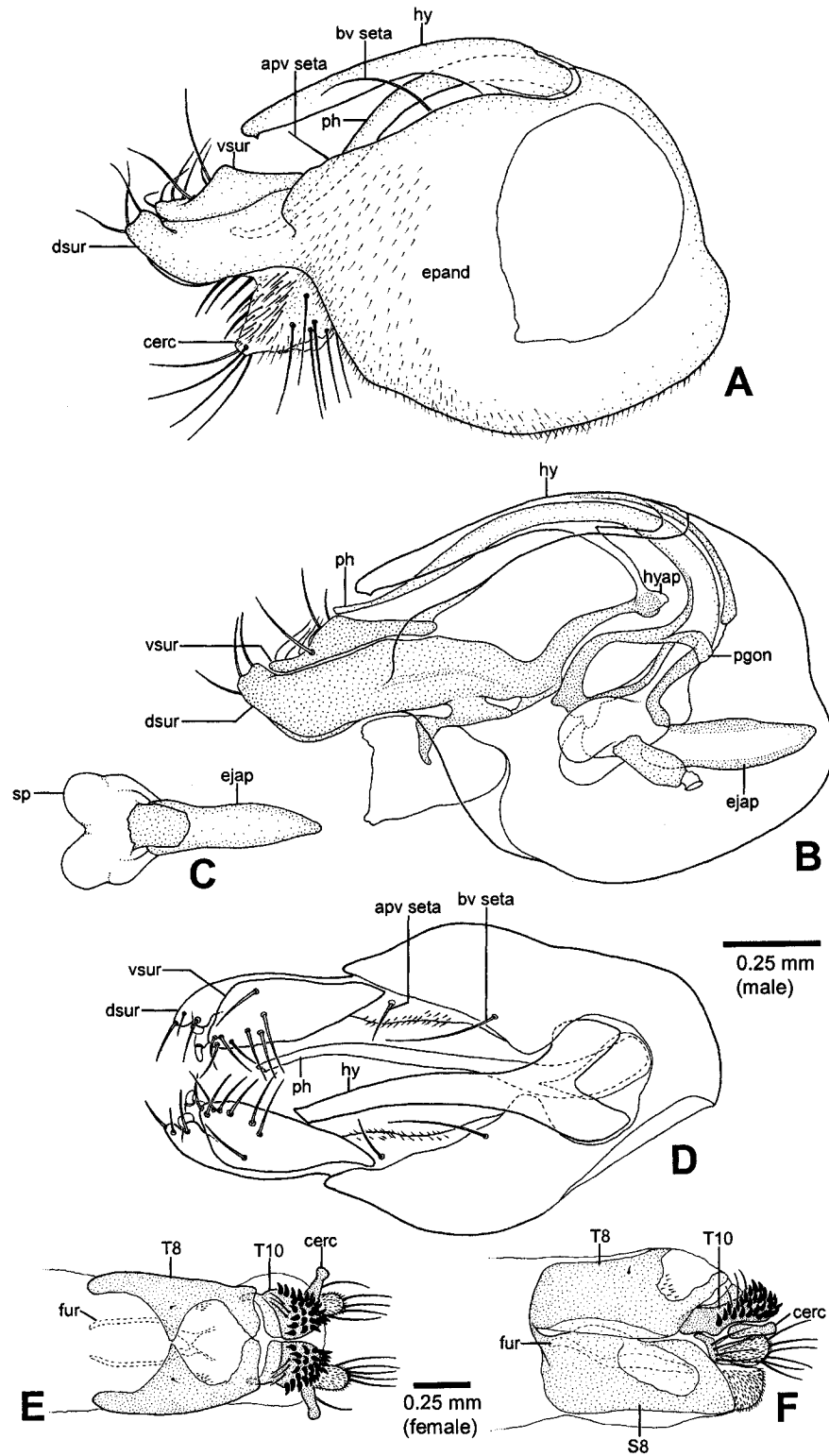


Figure 38. *Pseudohercostomus echinatus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, sperm pump and ejaculatory apodeme, dorsal view. (D) Male genitalia, ventral view. (E) Female genitalia, dorsal view. (F) Female genitalia, left lateral view.

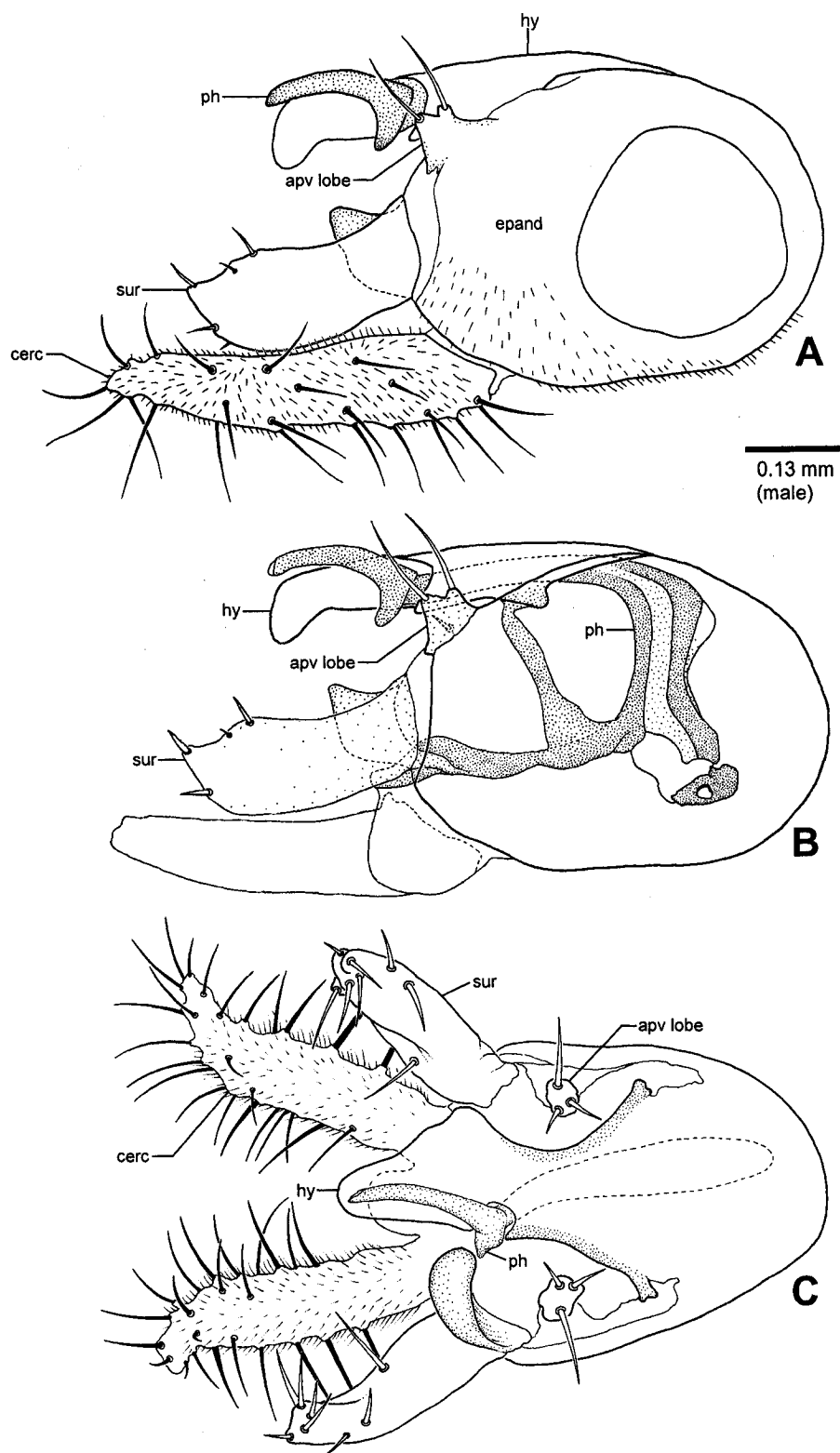


Figure 39. *Vetimicrotes mediterranneus*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view.

CONNECTING STATEMENT

In Chapter 2 it was demonstrated that the *Tachytrechus alatus* species group (formerly recognized as the genus *Syntomoneurum* Becker) is one of the best supported monophyletic lineages in the subfamily Dolichopodinae. In addition to a systematic revision of generic relationships within this subfamily, species-level revisions are also required. Such revisions provide identification tools for individual species, as well as an indication of how well a chosen exemplar represents its genus (or species group) in a higher-level analysis. In Chapter 3 the *Tachytrechus alatus* species group is revised. Chapter 3 is a modified and updated version of Brooks and Wheeler's (2002) revision of the Neotropical genus *Syntomoneurum* Becker as a result of new phylogenetic information leading to the synonymization of *Syntomoneurum* with *Tachytrechus* in Chapter 2.

CHAPTER 3. REVISION OF THE *TACHYTRECHUS ALATUS* SPECIES GROUP (DIPTERA: DOLICHOPODIDAE)

ABSTRACT. The *Tachytrechus alatus* species group (= *Syntomoneurum* Becker) is revised. The species group is defined within the genus *Tachytrechus* of the subfamily Dolichopodinae on the basis of the possession of a strong basiventral seta on the fore femur and very reduced pulvilli on the midleg and hindleg in both sexes. Males also possess a cluster of 2 - 3 strong setae on both the fore femur and mid coxa. The species group comprises five Neotropical species: *T. alatus* (Becker), *T. analis* (Parent), *T. beckeri* (Parent), *T. giganteus* (Brooks) and *T. transversus* (Van Duzee) all of which are redescribed. A key to species is provided.

INTRODUCTION

The *Tachytrechus alatus* species group is one of the most distinctive lineages within the genus *Tachytrechus* and the subfamily Dolichopodinae as a whole. Formerly this species group was recognized as the genus *Syntomoneurum* Becker. Becker (1922) originally placed *Syntomoneurum* in the subfamily Hydrophorinae based on its superficial resemblance to *Liancalus* Loew and similar wing venation to *Orthoceratium* Schrank. This subfamily placement was subsequently followed by Parent (1931, 1934, 1954) and Robinson (1970). More recently, *Syntomoneurum* was transferred to the subfamily Dolichopodinae by Negrobov (1980) and Ulrich (1981). Negrobov (1980) suggested that *Syntomoneurum* is closely related to *Phalacrosona* Becker, whereas Ulrich (1981) considered it to be close to *Tachytrechus* Haliday. Brooks and Wheeler (2002) provided evidence supporting Ulrich's hypothesis, and noted that *Syntomoneurum* may represent a species group within *Tachytrechus*, making the latter paraphyletic. The phylogenetic analysis presented in Chapter 2 verified this prediction and *Syntomoneurum* was accordingly synonymized with *Tachytrechus*.

Becker (1922) originally established *Syntomoneurum* for the single species *S. alatum* Becker from Peru. Becker's generic concept was based on the short wing vein R_{2+3} and basal position of crossvein dm-cu of males. Parent (1931) described a second Peruvian species, *S. beckeri*, from a single female and three years later described the male (Parent 1934). Parent (1934) remarked that Becker's wing venation characters were specific only to males of *S. alatum* and thus were unacceptable as defining characters for the genus; however, he did not redefine *Syntomoneurum* at that time. Parent (1954) described a third species, *S. anale*, based on a single male from Colombia and redefined the genus primarily on the basis of male characters including the possession of a white-tipped arista, a cluster of three strong setae on both the fore femur and mid coxa, and well-developed "horns" (apicoventral epandrial lobes) on the hypopygium. Recently, a fourth species, *S. giganteum* Brooks, was described (Brooks and Wheeler, 2002) also from Colombia. Following the publication of Brooks and Wheeler (2002), Harold Robinson (in litt.) pointed out that *Tachytrechus transversus* (Van Duzee) from

Guatemala and Mexico is also part of this species group. The purpose of this chapter is to revise the *Tachytrechus alatus* species group.

MATERIALS AND METHODS

This study is based on material housed in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN), Staatliches Museum für Tierkunde, Dresden (SMTD), the Museum für Naturkunde der Humboldt Universität zu Berlin (ZMHB) and the United States National Museum of Natural History, Washington, DC (USNM).

Morphological terminology for adult structures mainly follows McAlpine (1981). Terms for the structures of the male genitalia follow Cumming et al. (1995) and Sinclair (2000). Body length is measured from the base of the antenna to the tip of abdominal segment 7. Wing length is measured from the humeral crossvein to the wing apex. The relative lengths of each tarsomere are representative ratios expressed using the following formula: $t_1/t_2/t_3/t_4/t_5$, where t_1 refers to the basitarsus and t_5 refers to the 5th tarsomere.

Dark coloured, heavily sclerotized, male and female terminalia were macerated in 10% KOH which was heated on a hot plate for about 10 minutes. Lighter coloured, more weakly sclerotized male and female terminalia were macerated in 85% lactic acid heated in a microwave oven. Each microwave heating interval comprised 30 seconds and was followed by a 1-2 minute cooling period during which macerated muscle tissue was removed with a fine probe.

Label data for holotypes and lectotypes are cited verbatim. Labels are listed from the top down with data from each label in quotation marks. Lines on labels are delimited by a slash (/) and additional information is given in square brackets. The depository for each specimen is given in parentheses.

Figures showing the male genitalia in lateral view are oriented as they appear on the intact specimen (rotated 180° and lateroflexed to the right), with the morphologically ventral surface up, dorsal surface down, anterior end facing right and posterior end facing left. Figures showing the male genitalia in ventral view are correspondingly oriented with the anterior end facing right and posterior end facing left.

SYSTEMATICS

TACHYTRECHUS ALATUS SPECIES GROUP

Diagnosis. This species group is distinguished from other dolichopodids by the following combination of characters: a dorsally setose scape, a strong basiventral seta on the fore femur and hind basitarsus, and by the clypeus which projects below the lower margin of eyes in both sexes. Males are further distinguished by the possession of a cluster of 2-3 strong setae on the fore femur and mid coxa (cluster also present in females but weaker), a white-tipped arista, and large genitalia supported by a pedunculate abdominal segment 7.

Description. Body length 5.3-8.5 mm; wing length 5.2-11 mm. Head: Occiput convex. Vertex slightly (Fig. 45A) to distinctly excavated (Fig. 43A,B). Frons wider than long; 1 pair of vertical setae, weaker or stronger than postverticals. Face broad; clypeus projecting below lower margin of eyes. Palp large. Antennae: scape laterally flattened, widened distally in lateral view with setae along entire dorsal surface and ventral apex; pedicel short with apical ring of fine setulae; first flagellomere oval, round to pointed apically; arista subapical to dorsoapical, 2-articled, second article with white tip in males (also in female *T. giganteus* (Brooks)). Eyes with ommatrichia. Postocular setae mainly pale, upper 4-6 black. Lower 3-7 postoculars stronger with adjacent row of similar white setae along outer postgenal margin. Postvertical seta positioned at or slightly below level of uppermost postocular seta.

Thorax: Acrostichals biserial; 6 dorsocentrals, stronger posteriorly; 1 strong postpronotal with 2 weaker outer setae; 1 strong posthumeral; 1-2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper propleuron with cluster of fine setae; lower propleuron with several fine setae, 1 strong prothoracic seta; metaepisternum bare or with a few very fine setae. Scutellum with 1 strong inner seta and a minute outer seta.

Legs: Long and slender, especially tarsi; pulvilli of mid- and hindleg very reduced to absent. Tibia longer than femur in all legs, tarsus longer than tibia in fore- and midleg and only slightly longer in hindleg. Foreleg: Coxa with strong black setae along lower margin; femur with a single strong, curved basiventral seta close to joint with trochanter; femur of male with ventral cluster of 2-3 strong setae just beyond basiventral seta; basitarsus longer than second tarsomere. Midleg: Coxa of male with a cluster of 2-3 strong setae on anterior surface, reduced in female; femur with a weak basiventral seta close to joint with trochanter and single anterodorsal preapical seta; second tarsomere about equal to or slightly shorter than basitarsus. Hindleg: Coxa with single strong black lateral seta; femur with a weak basiventral seta close to joint with trochanter and 1-3 anterodorsal preapical setae; basitarsus with 1 strong basiventral seta and a dark hook-shaped process posterobasally, second tarsomere distinctly longer than basitarsus.

Wing: Long and narrow; costa continuous to M; M with one or two bends (Figs. 40A, 41A and 43C).

Abdomen: Cylindrical, dark metallic green to black with grey to silver pruinosity laterally. Tergites 1-5 setose in both sexes. Male: Tergite 5 slightly to strongly emarginate and membranous posteriorly; tergite 6 bare; sternite 4 with triangular membranous region posteriorly; sternite 5 emarginate and membranous posteriorly with eversible glandular structure usually present (Fig. 45B,C); sternite 6 mainly membranous; segment 7 pedunculate, shorter than wide, bare; sternite 8 subtriangular, setose posterolaterally. Hypopygium large. Epandrium subrectangular to ovoid in lateral view; basiventral epandrial lobe variable, with single pale seta; apicoventral epandrial lobe variable, with 2 setae, medial or dorsal seta branched apically. Surstylus (Fig. 44B) 2-lobed. Ventral surstylar lobe elongate, longer than dorsal lobe; ventral surface textured; 1 basal medial seta, 1 midventral seta, 1 subapical seta, 1 dorsomedial seta near basal third, 1 dorsomedial seta near middle, apex with short, blunt, curved spur. Apex of dorsal surstylar lobe rounded with several setae, medial surface produced. Postgonite (Fig. 44C,D) with apex distally upturned at a right angle and flared, dorsally bifurcate with well-developed lateral lobes. Cerci rounded or quadrate. Hypandrium long, connected to hypandrial arms laterally near base and epandrium basiventrally, hypandrial apodeme absent. Sperm pump rounded and weakly sclerotized; ejaculatory apodeme well-

developed, rod-like with apex expanded laterally; phallus with 1 or 2 dentiform to fin-like processes. Female: Tergites 6 and 7 wider than long, divided medially into quadrate halves, sternites 6 and 7 much smaller than tergites, complete or divided medially. Segment 8 heavily sclerotized; tergite 8 divided medially into subtriangular halves; sternite 8 divided medially or complete. Tergite 10 divided medially into a pair of hemitergites each bearing 4 - 6 acanthoporous spines (Fig. 42C,D).

KEY TO SPECIES OF THE *TACHYTRECHUS ALATUS* SPECIES GROUP

1. Two notopleural bristles; face and upper third of clypeus metallic greenish-copper, abruptly pale yellow in lower part of clypeus, male clypeus with strong medial carina; palp with large, stout seta on lower margin (Fig. 45A) *transversus* (Van Duzee)
 - One notopleural bristle, face and clypeus not as above, palp lacking large, stout seta on lower margin 2
2. M with two 90° bends; R_{2+3} of male very short, ending at costa before midpoint of wing; crossvein dm-cu of male close to wing base, well before midpoint of wing (Fig. 40A); crossvein dm-cu of female just before midpoint of wing, slightly shorter than last part of CuA_1 (Fig. 40B). Hypopygium: right basiventral epandrial lobe with rounded basal projection and subquadrate inner distal projection (Fig. 40D); hypandrium with a pair of sickle-shaped projections on right margin (Fig. 40D)..... *alatus* (Becker)
 - Bends in M obtuse; R_{2+3} of male ending at costa well beyond midpoint of wing; crossvein dm-cu at or slightly beyond midpoint of wing, longer than last part of CuA_1 (Figs. 41A, 43C,D). Hypopygium: right basiventral epandrial lobe lacking rounded basal projection and subquadrate distal projection; hypandrium lacking a pair of sickle-shaped projections on right margin, at most with a weak dentiform projection (Fig. 41C) 3
3. M with only a single distinct bend; R_{4+5} and M convergent distally (Fig. 43C,D); hind femur dark metallic green. Male: wing with elongate pterostigma (Fig. 43C); clypeus parallel sided and subquadrate below (Fig. 43A); hind femur with 2-3 preapical setae; basiventral epandrial lobe well-developed, elongate, curved and tapering distally,

- apicoventral epandrial lobe weakly developed (Fig. 44A,E). Large flies (body length 7.9-8.5 mm, wing length 10-11 mm) *giganteus* (Brooks)
- M with two distinct bends; R_{4+5} and M nearly parallel distally (Fig. 41A); hind femur mainly pale. Male: wing lacking pterostigma; clypeus rounded below; hind femur with 1 preapical seta; basiventral epandrial lobe weakly developed, apicoventral epandrial lobe well-developed (Figs. 41B and 42A). Smaller flies (body length 5.3-5.7 mm, wing length 5.3-5.8 mm).....4
4. Face metallic green. Male: fore tarsus with weak silver reflections anteriorly, basitarsus with curved ventral setae, tarsomeres 3 and 4 not flattened; apicoventral epandrial lobe extremely well-developed with pointed apex, medial seta positioned near base, lateral seta near middle (Fig. 41B); hypandrium wide, asymmetrical in ventral view, right margin with dentiform projection (Fig. 41C).....*analis* (Parent)
- Face brownish with weak silver-green reflections. Male: fore tarsus distinctly silver anteriorly, basitarsus lacking curved ventral setae, tarsomeres 3 and 4 flattened; apicoventral epandrial lobe with blunt apex bearing medial and outer setae (Fig. 42A,B); hypandrium narrow and symmetrical in ventral view (Fig. 42B).....*beckeri* (Parent)

***Tachytrechus alatus* (Becker)**

(Fig. 40A-D)

Syntomoneurum alatum Becker 1922: 124

Tachytrechus alatus (Becker): Brooks (2004)

Description. Male: Body length 6.4 mm, wing length 6.6 mm. Head: Frons, face and clypeus copper with green reflections; face wide and flat, narrowest near middle; clypeus slightly produced, lower margin rounded. Palp pale yellow with silvery white pruinosity and mainly pale setae, lower margin with 2-3 fine, dark setae. Antennal scape and pedicel brown, darker dorsally; scape about 0.7x as long as pedicel and first flagellomere combined; first flagellomere mainly dark brown, only yellow basiventrally, with acute

apex, about twice as long as wide; arista subapical, black with white apex, about 2.8x as long as first flagellomere. Postvertical seta stronger than uppermost postocular seta.

Thorax: Notum shining metallic blue medially, dark greenish-copper to black laterally, with silver pruinosity anteriorly and laterally; transverse suture with copper-green reflections; 1 notopleural seta. Pleuron mainly covered with silvery-grey pruinosity obscuring dark metallic green ground colour, metaepisternum bare. Scutellum greenish-black.

Legs: Fore, mid and hind femur and tibia mainly yellow with brown posterodorsal surface; hind femur darker apically. Foreleg: Coxa yellow with very fine pale pubescence, reflective silvery-white pruinosity and scattered pale and dark setae; femur with distinct ventral tubercle behind basal cluster of strong setae; tarsus brown, basal three-quarters of basitarsus and tarsomeres 3-5 flattened and silver on anterior surface, tarsomere ratio: 4.0/3.0/1.8/1.2/1.0. Midleg: Coxa concolorous with thorax, paler apically and medially, anterior surface with several weak black setae medially adjacent to cluster of strong setae; femur with distinct ventral tubercle just beyond basal third; basitarsus yellow with black apex (tarsomeres 3-5 missing on both males). Hindleg: Coxa concolorous with thorax, yellow apically and medially; femur with 1 anterodorsal preapical; tibia with dentiform process posteroapically opposite hook-shaped process of basitarsus; basitarsus brown, tarsomeres 2-5 black, tarsomere ratio: 4.1/6.9/2.1/1.0/1.0.

Wing (Fig. 40A): Costa with two adjacent swollen sections immediately proximal to insertion of R_1 ; R_1 thickened; R_{2+3} very short, ending at costa before midpoint of wing; M with two 90° bends; R_{4+5} and M parallel distally; crossvein dm-cu close to wing base, well before midpoint of wing, about $\frac{1}{4}$ as long as distal portion of CuA_1 . Calypter with black setae.

Abdomen: Tergites 1-5 black with sparse silver pruinosity laterally, tergite 5 with large membranous region posteriorly, tergite 6 and segment 7 dark brown; sternite 5 with eversible glandular structure (inverted in both examined males). Hypopygium (Fig. 40C,D): Epandrium brownish black, left basiventral epandrial lobe weakly developed; right basiventral epandrial lobe well-developed with rounded basal projection and subquadrate inner distal projection; apicoventral epandrial lobe moderately developed, subquadrate in lateral view with well-developed medial projection, medial seta branched

apically. Surstylus pale; ventral lobe slightly flattened dorsoventrally, 1 lateral seta near basal third, ventral surface with series of parallel diagonal ridges; dorsal lobe about half as long as ventral lobe. Postgonite pale, lateral lobes narrowed and curved ventrally in distal half. Cercus subquadrate, yellow with mainly pale setae, outer marginal setae stronger. Hypandrium wide and asymmetrical in ventral view, right margin with a pair of sickle-shaped projections (Fig. 40D). Phallus with weakly sclerotized projection near middle (Fig. 40C).

Female: Body length 7.1 mm, wing length 7.3-7.5 mm. Identical to male except for the following: Head: Face slightly wider; clypeus more strongly produced; palp with mainly dark setae and 1 strong black apical seta; first flagellomere rounded, mainly brown, about 1.2x as long as wide; arista about 4.5x as long as first flagellomere, apex paler than proximal portion, but not distinctly white.

Thorax: Notum dull black with weak green reflections anteriorly, coppery-black laterally, acrostichals flanked by very weak coppery vitta anteriorly. Pleuron black, metaepisternum with 2-3 fine setae. Scutellum black with copper reflections.

Legs: Fore and mid femur lacking ventral tubercle. Foreleg: tarsomeres unmodified. Midleg: tarsomere ratio: 6.3/6.2/2.0/1.0/1.2. Hindleg: tibia lacking posterodorsal dentiform process; basitarsus lacking posterobasal hook-shaped process.

Wing (Fig. 40B): Costa not swollen proximal to insertion of R_1 ; R_{2+3} ending well beyond midpoint of wing; crossvein dm-cu positioned just before midpoint of wing, slightly shorter than last part of CuA_1 .

Abdomen: Tergite 5 dark metallic green with white pruinosity. Sternites 4 and 5 also with white pruinosity. Sternite 6 complete, sternite 7 divided. Sternite 8 complete, U-shaped. Tergite 10 with 4 acanthoporous spines per hemitergite.

Type material examined. Lectotype ♂, labelled: “Peru/ 4. I. 04./ Pichis-Weg” [green label]; “Syntomoneurum/alatum B./ det. Becker”; “Zool. Mus./ Berlin” [yellow label]; “LECTOTYPE/ *Syntomoneurum/ alatum* Becker/ Des. S.E. Brooks 2002” [red label] (ZMHB). Paralectotypes (1 ♂, 3 ♀ ♀), ♂ with same locality and collection date as lectotype (SMTD); 1 ♀ with same locality and collection date as lectotype (SMTD); 1 ♀

with same locality as lectotype, dated 5. I. 04, abdomen missing (SMTD); 1 ♀ with same locality as lectotype, dated 5. I. 04 (ZMHB). All paralectotypes labelled: “PARALECTOTYPE/ *Syntomoneurum/ alatum* Becker/ Des. S.E. Brooks 2002” [yellow label].

Distribution. Peru.

Remarks. Becker (1922) did not designate a holotype for *T. alatus* from the type series. However, the single male in the SMTD bears a red label which reads “Typus/ Syntomoneu- / rum/ alatum Becker”. The two females in the SMTD also have similar red labels which read “Paratypus/ Syntomoneurum/ alatum Becker”. In contrast, the two specimens of *S. alatum* in the ZMHB lack such labels. The handwriting on the red “Typus” and “Paratypus” labels is identical to that on a label (“Typus/ Syntomoneurum/ beckeri Par.”) attached to the holotype of *S. beckeri*, also in the SMTD. The handwriting on these labels does not match that of Becker or Parent (Horn and Kahle 1935-1937) and therefore they appear to have been subsequently added to the specimens at the SMTD. In order to correct these labelling errors, U. Kallweit recently attached orange syntype labels (“SYNTYPUS/ des. U. Kallweit/ 1993”) to the three specimens of *T. alatus* in the SMTD. However, the two syntypes in the ZMHB were not similarly labelled. Brooks and Wheeler (2002) designated a lectotype and 4 paralectotypes thereby fixing the identity of *T. alatus* and removing confusion regarding the limits of the type series.

The hypopygium of the ♂ paralectotype in the SMTD has been detached from the specimen and is apparently preserved on a card in a drop of Canada balsam in the SMTD (D. Bickel, pers. comm.).

***Tachytrechus analis* (Parent)**

(Fig. 41A-C)

Syntomoneurum anale Parent 1954: 226

Syntormoneurum anale, misspelling by Parent 1954: 226.

Tachytrechus analis (Parent): Brooks (2004)

Description. Male: Body length 5.7 mm, wing length 5.8 mm. Head: Frons coppery-brown. Face and upper half of clypeus metallic green with copper reflections, lower half of clypeus copper; face wide and flat, narrowest near middle; clypeus slightly produced, lower margin rounded. Palp pale yellow with silvery white pruinosity, lower half with fine dark setae, 1-2 stronger dark setae apically. Antennal scape and pedicel brown, darker dorsally; scape about 0.7x as long as pedicel and first flagellomere combined; pedicel with black apical margin; first flagellomere dark brown, rounded apically, about 1.6x longer than wide; arista subapical, black with white apex about 3.5x as long as first flagellomere. Postvertical seta stronger than uppermost postocular seta.

Thorax: Notum shining metallic green with silver pruinosity anteriorly and laterally; acrostichals flanked by bluish-green vittae; transverse suture with coppery reflections; 1 notopleural seta. Pleuron mainly covered with silvery-grey pruinosity obscuring metallic green ground colour, metaepisternum with 1 fine seta. Scutellum metallic green.

Legs: Fore, mid and hind femur and tibia mainly yellow with metallic greenish-brown posterodorsal surface; mid femur dark metallic green posterodorsally; hind tibia brown posterodorsally. Foreleg: Coxa yellow with very fine pale pubescence, reflective silvery-white pruinosity and scattered pale and dark setae; femur with well-developed ventral tubercle behind basal cluster of strong setae; tarsus brown, basitarsus with curved setae ventrally, tarsomeres 2-4 with silvery reflections on anterior surface, tarsomeres 3 and 4 not flattened, tarsomere ratio: 4.2/2.3/2.2/1.3/1.0. Midleg: Coxa concolorous with thorax, yellow apically and medially, anterior surface with several weak black setae medially adjacent to cluster of strong setae; femur with distinct ventral tubercle just beyond basal third; basitarsus yellow, tarsomeres 2-5 dark brown, tarsomere ratio: 6.0/6.3/2.2/1.0/1.2. Hindleg: Coxa concolorous with thorax, yellow apically; femur with 1 anterodorsal preapical; tibia with dentiform process posteroapically opposite hook-shaped process of basitarsus; basitarsus yellow, tarsomeres 2-5 dark brown, tarsomere ratio: 4.3/8.2/2.5/1.0/1.2.

Wing (Fig. 41A): Costa normal, lacking pterostigma; M with two strong obtuse bends in distal half; R_{4+5} and M parallel distally; crossvein dm-cu near midpoint of wing, longer than distal section of CuA_1 . Calypter with black setae.

Abdomen: Tergites 1-5 metallic greenish-blue with dense silver pruinosity laterally, tergite 5 with large membranous region posteriorly, tergite 6 and segment 7 dark brown; sternite 5 with eversible glandular structure (inverted in male holotype).

Hypopygium (Fig. 41B,C): Epandrium dark brown; basiventral epandrial lobe very weakly developed; apicoventral epandrial lobe extremely well-developed, apex pointed, apically branched medial seta positioned near base, lateral seta near middle. Surstylus pale; ventral lobe slightly flattened dorsoventrally, 1 weak lateral seta near basal third, ventral surface with series of parallel diagonal ridges; dorsal lobe about three-quarters as long as ventral lobe. Postgonite pale, lateral lobes narrowed and curved ventrally in distal third. Cercus subquadrate, yellow with mainly pale setae, outer marginal setae stronger. Hypandrium wide and asymmetrical in ventral view, right margin with dentiform process near middle (Fig. 41C). Phallus with weak projection near middle, well-developed projection subapically.

Female: Unknown.

Type material examined. Holotype ♂, labelled: “Muzo/ Dept. Boyaca/ alt. 900 M.”; “Colombia/ 1936”; “J. Bequaert/ Collector”; “Syntormoneurum/ anale n. sp. ♂/ Type.”; “TYPE” [red label] (MNHN).

Distribution. Columbia.

Remarks. Parent (1954) indicated that only *T. analis* possesses the basiventral seta on the fore femur; however, all of the species have this seta and its presence is considered to be a synapomorphy for the species group.

Tachytrechus beckeri (Parent)

(Fig. 42A-D)

Syntomoneurum beckeri Parent 1931: 17.

Syntormoneurum beckeri, misspelling by Parent 1931: 17.

Tachytrechus beckeri (Parent): Brooks (2004)

Description. Male: Body length 5.3 mm, wing length 5.5 mm. Head: Frons green. Face and upper half of clypeus brownish with weak green reflections, lower half of clypeus yellow; face broad but narrowest near middle, weakly depressed below antennae; clypeus flat, lower margin rounded. Palp white with silvery white pruinosity, apex with a few dark setae, 1 stronger dark seta apically. Antenna: Scape, pedicel and first flagellomere brown dorsally, yellow ventrally (apex of first flagellomere damaged in single male specimen, measurements and description based on Parent (1931)); scape about 0.7x as long as pedicel and first flagellomere combined; first flagellomere weakly pointed apically, arista dorsoapical, brown with white apex, about 6x length of first flagellomere. Postvertical seta stronger than uppermost postocular seta.

Thorax: Notum metallic green with silver pruinosity anteriorly and laterally (notum damaged in single male specimen); 1 notopleural seta. Pleuron mainly covered with silvery-grey pruinosity obscuring dark metallic green ground colour, metaepisternum bare. Scutellum greenish-blue with copper reflections.

Legs: Fore, mid and hind femur mainly yellow; fore femur slightly infuscated apically; mid femur with brown posterodorsal surface. Fore, mid and hind tibia yellow, with posterodorsal surface weakly infuscated. Foreleg: Coxa yellow with very fine pale pubescence, reflective silvery-white pruinosity, and scattered dark setae medially; femur with weakly produced ventral tubercle behind basal cluster of strong setae; basitarsus yellow, anterior surface silver, tarsomeres 2-5 brown on posterior surface, anterior surface silver, tarsomeres 3 and 4 flattened, tarsomere ratio: 3.3/2.7/2.5/1.3/1.0. Midleg: Coxa mainly yellow, dark brown on outer surface and outer margin of anterior surface, anterior surface with several weak black setae medially adjacent to cluster of strong setae; femur with very weak ventral tubercle just beyond basal third; basitarsus yellow with brown apex, tarsomeres 2-4 dark brown, tarsomere ratio: 6.4/6.2/2.6/1.0/1.2. Hindleg: Coxa

mainly yellow, brown basally; femur with 1 anterodorsal preapical; tarsus brown, basitarsus paler than distal segment, tarsomere ratio: 4.2/6.7/2.7/1.0/1.0.

Wing: Costa normal, lacking pterostigma; M with two strong obtuse bends in distal half; R_{4+5} and M parallel distally; crossvein dm-cu near midpoint of wing, longer than distal section of CuA_1 . Calypter with black setae.

Abdomen: Tergites 1-5 dull green, tergite 5 with large membranous region posteriorly, tergite 6 and segment 7 dark brown. Hypopygium (Fig. 42A,B): Epandrium dark brown; basiventral epandrial lobe weakly developed, right lobe longer; apicoventral epandrial lobe very well-developed, apex blunt bearing setae, medial seta branched apically. Surstylus pale; ventral lobe slightly flattened dorsoventrally, 1 lateral seta near basal third, ventral surface with series of parallel diagonal ridges; dorsal lobe about half as long as ventral lobe. Postgonite pale, lateral lobes narrowed and curved ventrally in distal half. Cercus subquadrate, yellow with mainly pale setae, outer marginal setae stronger and darker basally. Hypandrium narrow, symmetrical in ventral view (Fig. 42B). Phallus with fin-like projection before middle (Fig. 42A).

Female: Body length 5.4 mm, wing length 5.3 mm. Identical to male except for the following: Head: Clypeus strongly produced. Palp grayish. Antenna: first flagellomere brown; arista subapical, about 5.5x length of first flagellomere, brown apically.

Thorax: Notum shining metallic green with silver pruinosity anteriorly and laterally; dull brown median vitta, acrostichals flanked by dark greenish-blue vittae; transverse suture with coppery reflections.

Legs: Fore and mid femur lacking ventral tubercle. Foreleg: Femur brown posterodorsally; tarsomere ratio: 4.2/3.2/3.2/1.2/1.0. Midleg: Coxa concolorous with thorax, yellow apically; tibia yellow, tarsomere ratio: 7.2/6.5/2.7/1.0/1.2. Hindleg: Coxa brown, yellow apically and medially; femur mainly yellow, posterodorsal surface infuscated apically; tarsomere ratio: 4.6/6.6/2.8/1.0/1.2.

Abdomen: Sternite 6 and 7 complete. Sternite 8 divided. Tergite 10 with 4 acanthoporous spines per hemitergite (Fig. 42C,D).

Type material examined. Holotype ♀, labelled: “Peru-Urubambafl./ 13. IX. 03/ Umahuankilla” [green label]; “Typus/ Syntomoneurum/ beckeri Par.” [red label]; “n. sp.”; “Syntormoneurum/ Beckeri ♀. n. sp./ O. Parent/ Parent” [underside, partially cut off] [entire label folded 4 times]; “Staatl. Museum für/ Tierkunde, Dresden”; “Coll. W. Schnuse/ 1911 – 3” [green label]; “SYNTYPUS/ des. U.Kallweit/ 1993” [orange label]; “HOLOTYPE ♀/ *Syntomoneurum/ beckeri* Parent” [red label] (SMTD).

Other material examined. 1 ♂ labelled: “MUSEUM PARIS/ PÉROU/ ?rég. côtière du N./ Dr. VERGNE” (MNHN). 1 ♀ from same locality (MNHN).

Distribution. Peru.

Remarks. The single female specimen of *T. beckeri* in the SMTD has an orange syntype label (“SYNTYPUS/ des. U.Kallweit/ 1993”) in addition to the red “Typus” label (see “Remarks” under *T. alatus*). According to Article 73.1.2 of the International Code of Zoological Nomenclature (4th Edition), this specimen is the holotype, fixed by monotypy, as there is sufficient evidence in Parent (1931) to conclude that the description of *T. beckeri* was based on a single specimen. Accordingly, a new holotype label has been attached.

In his description of the male of *T. beckeri*, Parent (1934: 273) used the notation “n. sp.”; however, this must be considered an error as he referred to the original description (i.e. Parent 1931: 17) in his description of the female (Parent 1934: 274).

The eversible glandular structure present in the other species was not found in the single male specimen of *T. beckeri*. However, the abdomen of this specimen was partially damaged prior to my examination and dissection, and the eversible gland, if present, may have been lost as a result.

***Tachytrechus giganteus* (Brooks)**

(Figs. 43A-D, 44A-G)

Syntomoneurum giganteum Brooks in Brooks and Wheeler 2002: 321

Tachytrechus giganteus (Brooks): Brooks (2004)

Description. Male: Body length 8.5 mm; wing length 10.7 mm. Head (Fig. 43A): Frons metallic greenish-blue with silver-grey pruinosity. Face and clypeus silver, face parallel-sided, strongly depressed, with a distinct vertical median line; lower half of clypeus slightly produced, clypeus parallel sided and subquadrate below. Palp pale yellow with silvery white pruinosity, distal half with fine pale setae becoming longer along lower margin, 1-3 stronger dark setae apically. Antennal scape black, about 1.25x as long as pedicel and first flagellomere combined; pedicel mainly black, yellow basoventrally; first flagellomere black, rounded apically, about 1.5x as long as wide; arista black with white apex, about 3.7x as long as first flagellomere. Postvertical seta about as strong as upper postocular seta.

Thorax: Notum shining metallic green with silver pruinosity anteriorly and laterally; acrostichals flanked by brownish-coppery vittae; notopleuron and transverse suture with deep purple reflections; 1 notopleural seta. Pleuron almost entirely covered with silvery-grey pruinosity which obscures dark metallic green ground colour, metaepisternum bare. Scutellum metallic green.

Legs: Foreleg: Coxa yellow with very fine pale pubescence, reflective silvery-white pruinosity and scattered pale and dark setae; femur mainly yellow, posterodorsal surface dark metallic green, yellow in basal fifth, lacking tubercle behind cluster of strong setae; tibia yellow anteroventrally, metallic greenish-brown posterodorsally; tarsus brown, each tarsomere with a pair of short thick apicoventral setae, tarsomere ratio: 3.5/2.2/1.5/1.0/1.0. Midleg: Coxa concolorous with thorax, yellow apically, anterior surface with cluster of weak black setae above and medial to the cluster of strong setae; femur mainly yellow with metallic greenish-brown band running basiventrally to apicodorsally, ventral surface with distinct tubercle just beyond basal third; tibia mainly yellow, posterior surface dark brown with metallic reflections, basitarsus dark brown, tarsomeres 2-5 black, tarsomere ratio: 6.1/4.2/1.7/1.0/1.2. Hindleg: Coxa concolorous with thorax, yellow apically; femur almost entirely dark metallic green, 2-3 anterodorsal preapicals; tibia almost entirely metallic black, paler ventrally, dentiform process

posteroapically opposite hook-shaped process of basitarsus; tarsus black, tarsomere ratio: 5.0/6.0/2.0/1.0/1.5.

Wing (Fig. 43C): Pterostigma present along middle third of costa extending to insertion point of R_{2+3} , well beyond midpoint of wing, with very fine setae along anterior margin; M with weak obtuse bend in distal half; R_{4+5} and M convergent; crossvein dm-cu slightly beyond midpoint of wing, longer than distal section of CuA_1 . Calypter with black setae.

Abdomen: Tergites 1-5 metallic green with dense silver pruinosity laterally and weaker pruinosity dorsally, tergite 5 with large membranous region posteriorly, tergite 6 and segment 7 dark brown; sternite 5 with eversible glandular structure (inverted in both examined males). Hypopygium (Fig. 44A-E): Epandrium dark brown, basiventral epandrial lobe very well-developed, elongate, curved and pointed apically; apicoventral epandrial lobe weakly developed, pale, apex rounded and bearing setae, medial seta branched apically. Surstylus pale; ventral lobe dorsoventrally flattened, lacking lateral seta near basal third, ventral surface denticulate; dorsal lobe about half as long as ventral lobe. Postgonite pale, lateral lobe with subtriangular apex. Cercus round, yellow with mainly pale setae, distal margin with strong, black setae. Hypandrium asymmetrical in ventral view (Fig. 44E), rugose distally. Middle third of phallus with weak dentiform projection proximally and rounded fin-like projection distally (Fig. 44A).

Female: Body length 7.6 mm; wing length 11 mm. Identical to male except for the following: Head (Fig. 43B): Face dull metallic green with grey sides, not depressed; clypeus strongly produced, lower margin sharply rounded, mainly covered with silver-grey pruinosity, apex pale brown. Palp with mainly dark setae. Antennal scape about equal to length of pedicel and first flagellomere combined; arista black with white apex (as in male), distal segment about 8.5x longer than basal segment. Upper 5 - 7 postocular setae black.

Thorax: Notum shining metallic greenish-copper.

Legs: Foreleg: Coxa with a few black setae medially. Midleg: femur lacking tubercle near basal third; tarsus black; tarsomere ratio: 5.7/3.8/1.7/1.0/1.1. Hindleg: femur with single anterodorsal preapical seta; tibia lacking posterodorsal dentiform

process, basitarsus lacking posterobasal hook-shaped process, tarsomere ratio: 4.7/5.5/2.1/1.0/1.2.

Wing (Fig. 43D): Pterostigma absent.

Abdomen: Sternites 1-5 dark grey with silver pruinosity. Sternite 6 and 7 divided. Sternite 8 complete, heavily sclerotized, with deep medial invagination. Tergite 10 with 5-6 acanthoporous spines per hemitergite (Fig. 44F,G).

Type material examined. Holotype ♂, labelled: “COLOMBIA: Ant./ 10km E. Medellin/ rd. to Las Palmas/ 21 Feb 1984/ C.M. & O.S. Flint, Jr.”; “HOLOTYPE ♂ / *Syntomoneurum/ giganteum/ Brooks*” [red label] (USNM). Paratypes, 1 ♂ and 2 ♀, from same locality as holotype (USNM).

Distribution. Colombia.

Remarks. The type series of *T. giganteus* was collected at an elevation of about 2000m, near a pair of small streams, each about 30cm wide and a few centimeters deep. The streambeds were bedrock, boulders, gravel and sand, and the streams were overhung by bush in a wet forested area (O. Flint, pers. comm).

***Tachytrechus transversus* (Van Duzee)**

(Fig. 45A-E)

Polymedon transversus Van Duzee 1928: 52.

Tachytrechus transversus (Van Duzee): Robinson, 1970: 56 (catalog).

Description. Male: Body length 5.5 mm, wing length 5.4 mm. Head: Frons and surface immediately posterior to ocellar tubercle metallic violet with blue reflections. Face and upper third of clypeus metallic green with copper reflections, abruptly pale yellow in lower part of clypeus; face broad and flat, sides subparallel; clypeus produced, narrowing below, with sharp medial and lateral carinae (Fig. 45A), lower margin apparently truncate

(male holotype with apex of clypeus covered by anterior part of labellum). Palp pale yellow with silver white pruinosity, lower half with fine setae, lower margin with 1 stout black seta (Fig. 45A). Antennal scape and pedicel dark brown dorsally, pale below; scape about 0.8x as long as pedicel and first flagellomere combined; first flagellomere dark brown, rounded apically, about 1.4x longer than wide; arista dorsoapical, black with white apex about 4.4x as long as first flagellomere. Postvertical seta stronger than uppermost postocular seta.

Thorax: Notum dark metallic bluish-green dorsally, metallic green anteriorly and laterally with whitish pruinosity; red-violet reflections on both sides of transverse suture; 2 notopleurals, posterior seta weaker. Pleuron mainly covered with silvery-grey pruinosity, metaepisternum with 3 fine setae. Scutellum metallic bluish-green.

Legs: Fore, mid and hind femur and tibia mainly yellow; mid femur with brown infuscation posterodorsally; hind tibia brown posterodorsally. Foreleg: Coxa yellow with very fine pubescence, silvery-white pruinosity and scattered pale and dark setae; tarsus brown, unmodified, tarsomere ratio: 4.2/2.4/1.7/1.1/1.0. Midleg: Coxa concolorous with thorax; femur with weak ventral tubercle near basal third, setae longer anteroventrally; basitarsus yellow with darkened apex, tarsomeres 2-5 dark brown, tarsomere ratio: 4.9/4.3/2.0/1.0/1.0. Hindleg: Coxa concolorous with thorax; femur with 1 anterodorsal preapical; tibia with dentiform process posteroapically opposite hook-shaped process of basitarsus; basitarsus mainly dark brown with pale base, tarsomeres 2-5 dark brown, tarsomere ratio: 3.6/5.4/2.2/1.0/1.0.

Wing: Anterior surface of costa with two adjacent flap-like swellings (pterostigma) immediately proximal to insertion of R_1 ; proximal swelling pale concolorous with basal section of costa; M with two strong obtuse bends in distal half; R_{4+5} and M parallel distally; crossvein dm-cu near midpoint of wing, longer than distal section of CuA_1 . Calypter with black setae.

Abdomen: Tergite 1 dark grey, posterior margin protruding dorsolaterally on both sides, concave medially (possibly a specimen artifact), tergites 2-5 metallic green with coppery reflections and dense silver pruinosity laterally, tergite 6 and segment 7 brown. Sternite 5 with large complex eversible glandular structure (Fig. 45B), apex wide in anterior view (Fig. 45C). Hypopygium (Fig. 45D,E): Epandrium brownish-black with

metallic green reflections; right and left basiventral epandrial lobes well-developed, digitiform, projecting dorsally and lying adjacent to medial surface of apicoventral epandrial lobe, right lobe with bent apex; apicoventral epandrial lobe well-developed, flared apically, laterally flattened, dorsal seta branched apically. Surstylus pale; ventral lobe slightly flattened dorsoventrally, ventral surface with series of parallel diagonal ridges; dorsal lobe about half as long as ventral lobe. Postgonite pale, lateral lobes narrowed apically and curved ventrally. Cercus subquadrate, yellow with mainly pale setae, outer marginal setae stronger and brown. Hypandrium moderately wide and asymmetrical in ventral view, leaning to the left in ventral view, right margin with rounded process near middle (Fig. 45E). Phallus with extremely strong fin along middle third, weak dentiform projection subapically.

Female: Body length 5.8-6.2 mm; wing length 5.6 mm. Identical to male except for the following: Head: Distinct transverse suture at boundary of face and clypeus; clypeus lacking medial carina on yellow portion, rounded below. Antennae with first flagellomere slightly shorter; apex of arista usually black, sometimes indistinctly white at extreme apex.

Thorax: Notum lacking red-violet reflections on both sides of transverse suture.

Legs: Midleg: Femur lacking weak ventral tubercle near basal third. Hindleg: Tibia lacking posteroapical dentiform process; basitarsus lacking hook-shaped process.

Wing: Costa not swollen proximal to insertion of R_1 .

Abdomen: Tergite 1 with posterior margin lacking dorsolateral protrusions, flat medially. Sternite 6 complete, sternite 7 and 8 divided. Tergite 10 with 5 acanthoporous spines per hemitergite.

Type material examined. Holotype ♂, labelled: "ElJicara/ ZacapaGuat/ May 11, 1926."; "Type No./ 41062/ U.S.N.M." [red label]; "Polymedon/ transversa/ Holotype. Van Duzee" (USNM). Paratypes (3 ♀ ♀) with same locality and collection date as lectotype (USNM).

Distribution. *Tachytrechus transversus* is known from the type locality in Guatemala and also from a single male collected by Harold Robinson near Arriaga, Chiapas, Mexico (H. Robinson, pers. comm.).

Remarks. Van Duzee (1929) originally described *T. transversus* in *Polymedon* Osten Sacken, which was later synonymized with *Tachytrechus* by Robinson (1970).

Tachytrechus transversus differs from the other species by the possession of two notopleural bristles instead of only one, and may represent the basal species of the *T. alatus* species group.

DISCUSSION

The *Tachytrechus alatus* species group is one of the most well-supported monophyletic lineages in the subfamily, based on the synapomorphic possession of a basiventral seta on the fore femur and reduced pulvilli on the midleg and hindleg in both sexes. Male-associated synapomorphies include the possession of 2-3 strong setae on both the fore femur and mid coxa. Based on the examination of over 340 exemplar species, it appears that none of these apomorphic states occur in other members of the Dolichopodinae. The possession of a basiventral seta or series of setae on the fore femur is known to occur outside of the Dolichopodinae in *Hydatostega* Philippi and some species of *Achalcus* Loew and *Sciapus* Zeller.

This species group appears to be restricted to the northern Neotropics from southern Mexico and Guatemala, south to the tropical Andes of Colombia and Peru within an elevational range of 300 – 2000m (Papavero 1973, O. Flint pers. comm.). Specimens of this species group also appear to be rare in collections.

The male genitalia of the *T. alatus* species group, particularly *T. alatus*, show a very strong resemblance to that of *Tachytrechus castus* (Wheeler) from Utah and Arizona. This species shares a number of other characters in common with the *T. alatus* species group including an enlarged palp, a broad face, a ventral tubercle on the midfemur and its large size. *Tachytrechus alternans* (Curran) and *T. bracteatus* (Wiedemann) from

the Afrotropics also possess a ventral tubercle on the midfemur but this appears to be independently derived in these species. As such, *T. castus* may represent the sister group of the *T. alatus* species group.

ACKNOWLEDGEMENTS

Thanks to Christophe Daugeron (MNHN), Uwe Kallweit (SMTD), Hella Wendt (ZMHB) and Norm Woodley (USNM) for the loan of specimens. Marc Pollet (Royal Belgian Institute of Natural Sciences) and Rüdiger Wagner (Max-Planck Institute) provided specimens of *Phalacrotopa amoneum*. Thanks also to Dan Bickel (Australian Museum), Jeff Cumming (Canadian National Collection of Insects), Marc Pollet and Jade Savage (McGill University) for reviewing the manuscript. Oliver Flint (USNM) provided information on the type locality of *T. giganteus*, and Harold Robinson (USNM) provided information on the distribution of *T. transversus*. Financial support for this study was provided by a Dipterology Fund grant to S.E. Brooks and a Natural Sciences and Engineering Research Council of Canada research grant to T.A. Wheeler.

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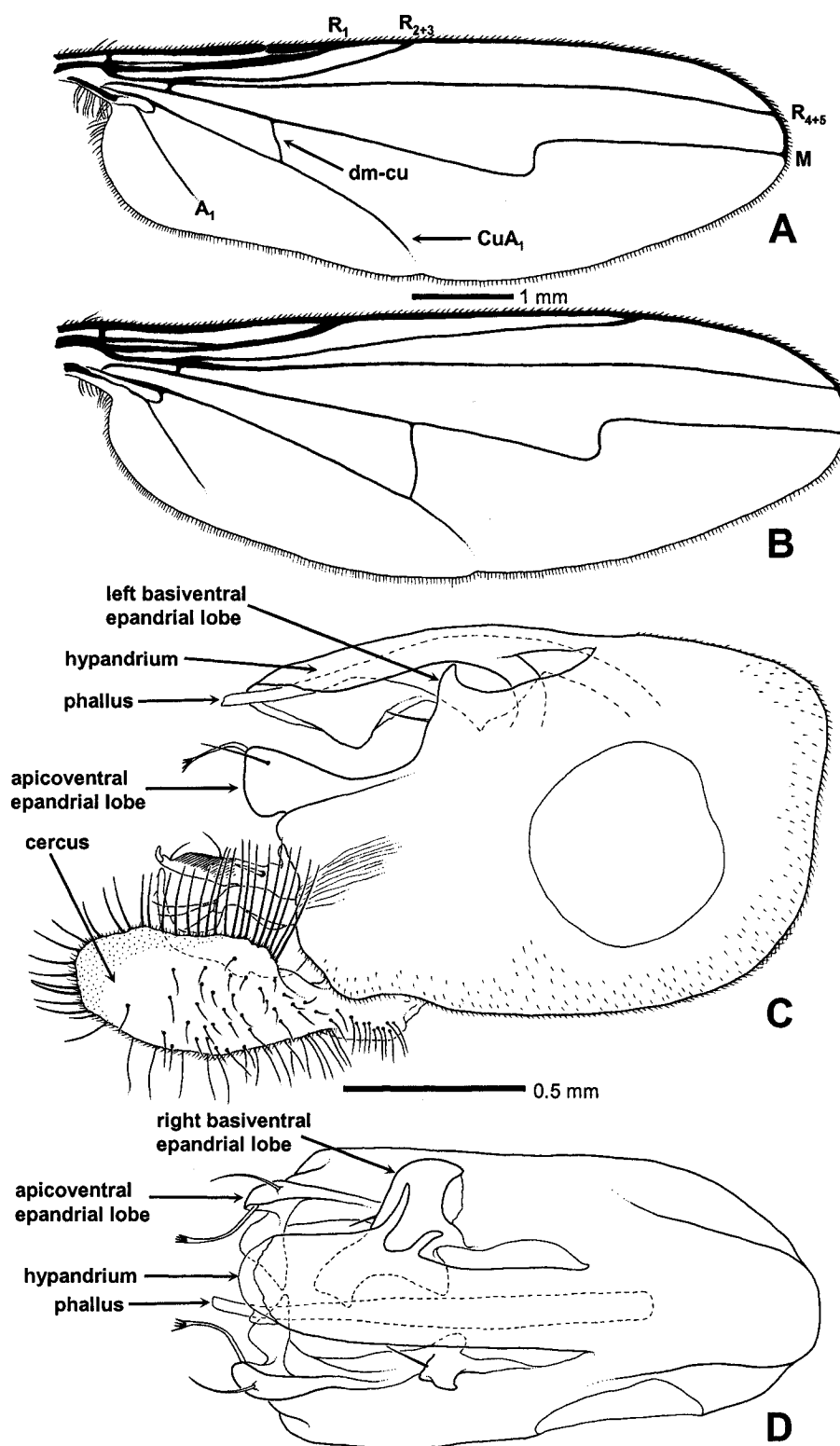


Figure 40. *Tachytrechus alatus*: (A) Male wing. (B) Female wing. (C) Male genitalia, left lateral view. (D) Male genitalia, ventral view (surstyli, postgonite and cerci not shown).

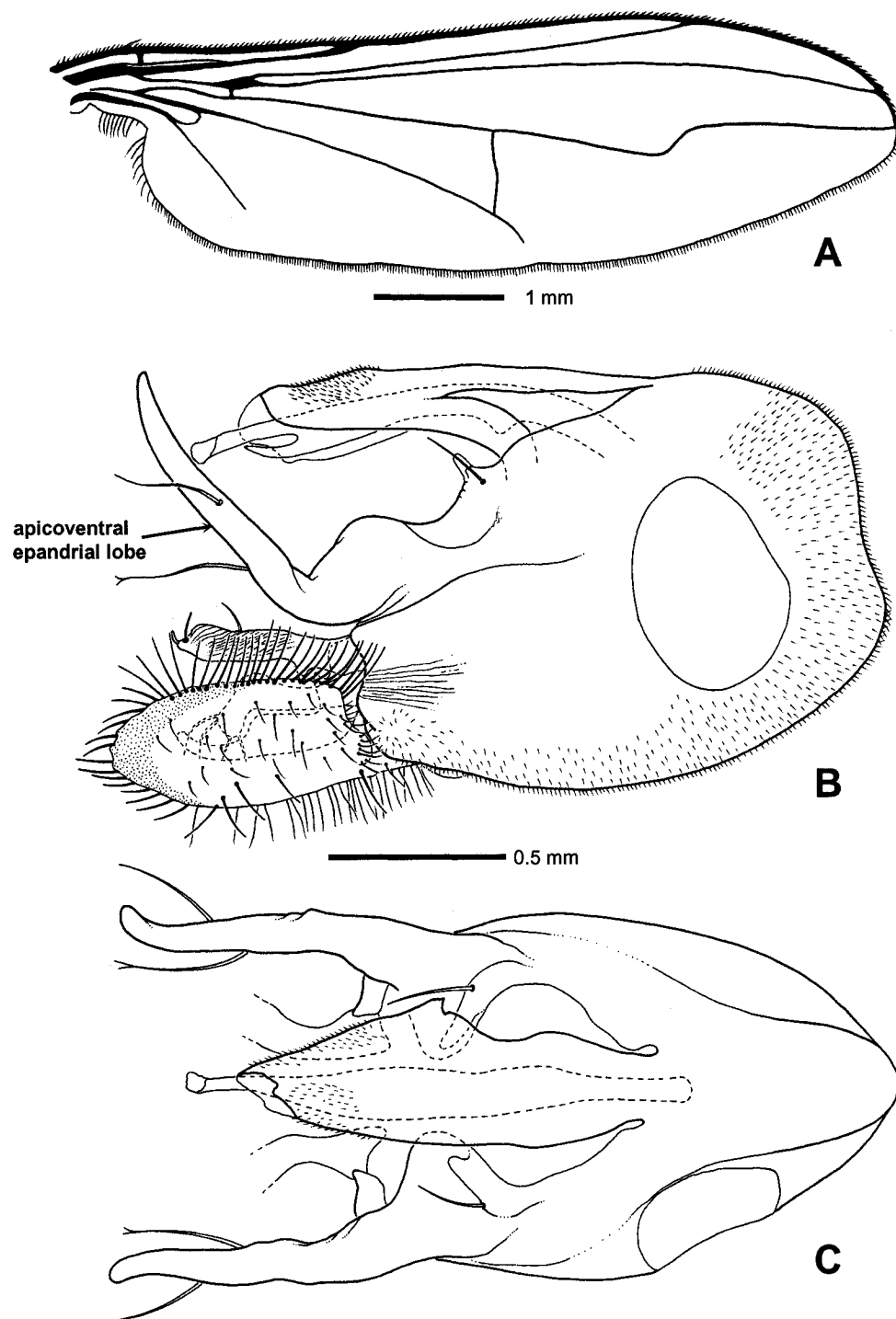


Figure 41. *Tachytrechus analis*: (A) Male wing. (B) Male genitalia, left lateral view. (C) Male genitalia, ventral view (surstyli, postgonite and cerci not shown).

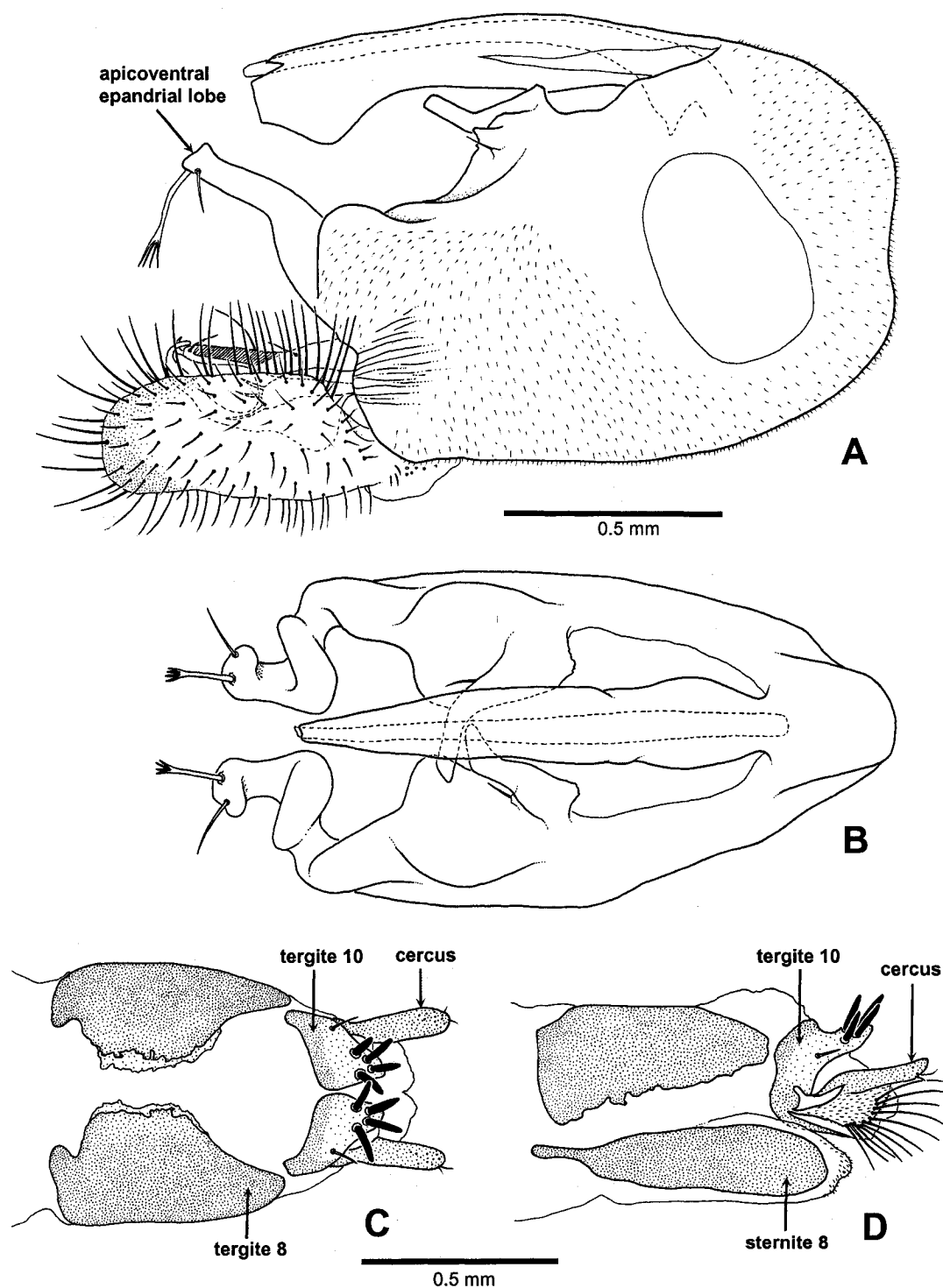


Figure 42. *Tachytrechus beckeri*: (A) Male genitalia, left lateral view. (B) Male genitalia, ventral view (surstyli, postgonite and cerci not shown). (C) Female genitalia, dorsal view. (D) Female genitalia, left lateral view.

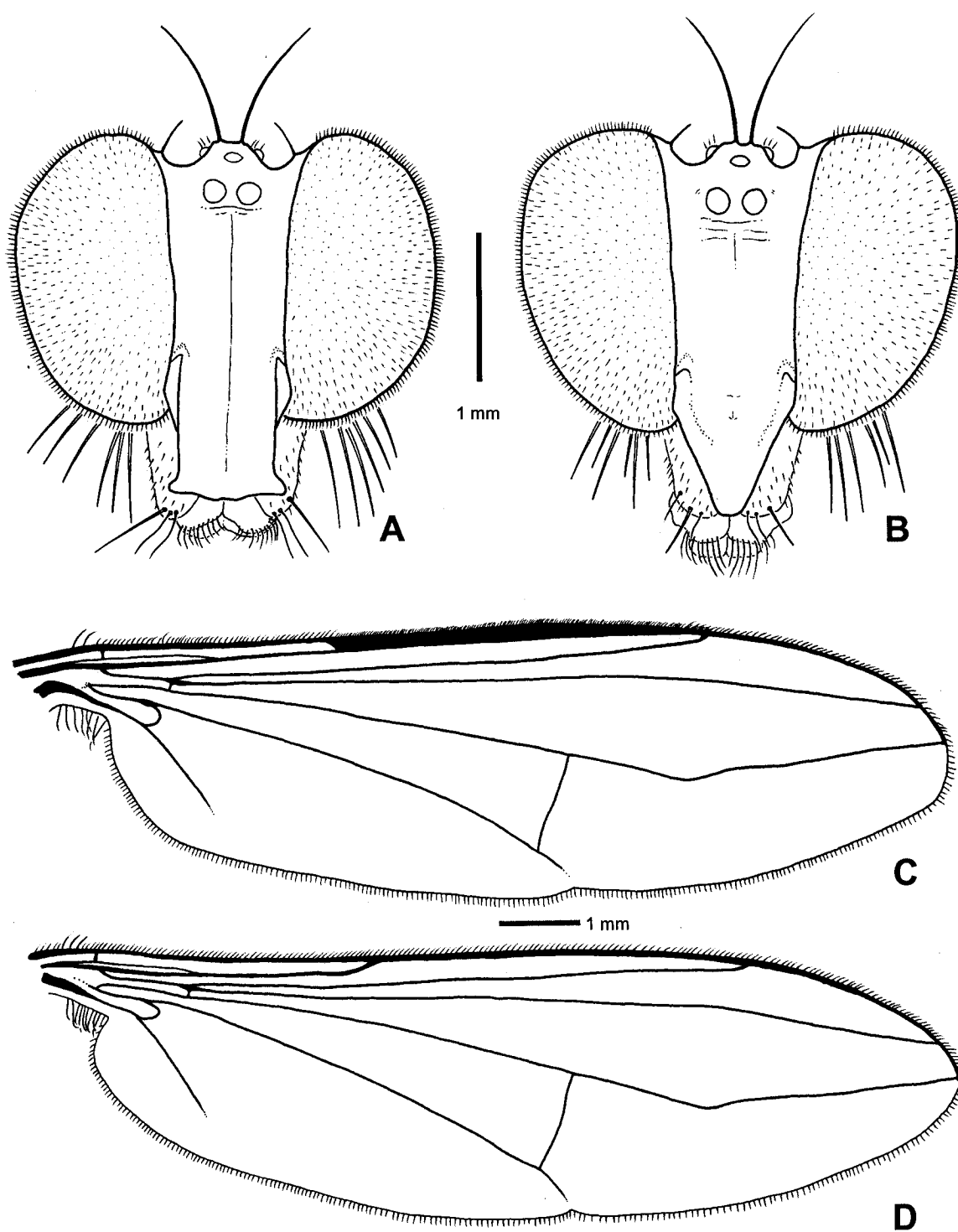


Figure 43. *Tachytrechus giganteus*: (A) Male head. (B) Female head. (C) Male wing. (D) Female wing.

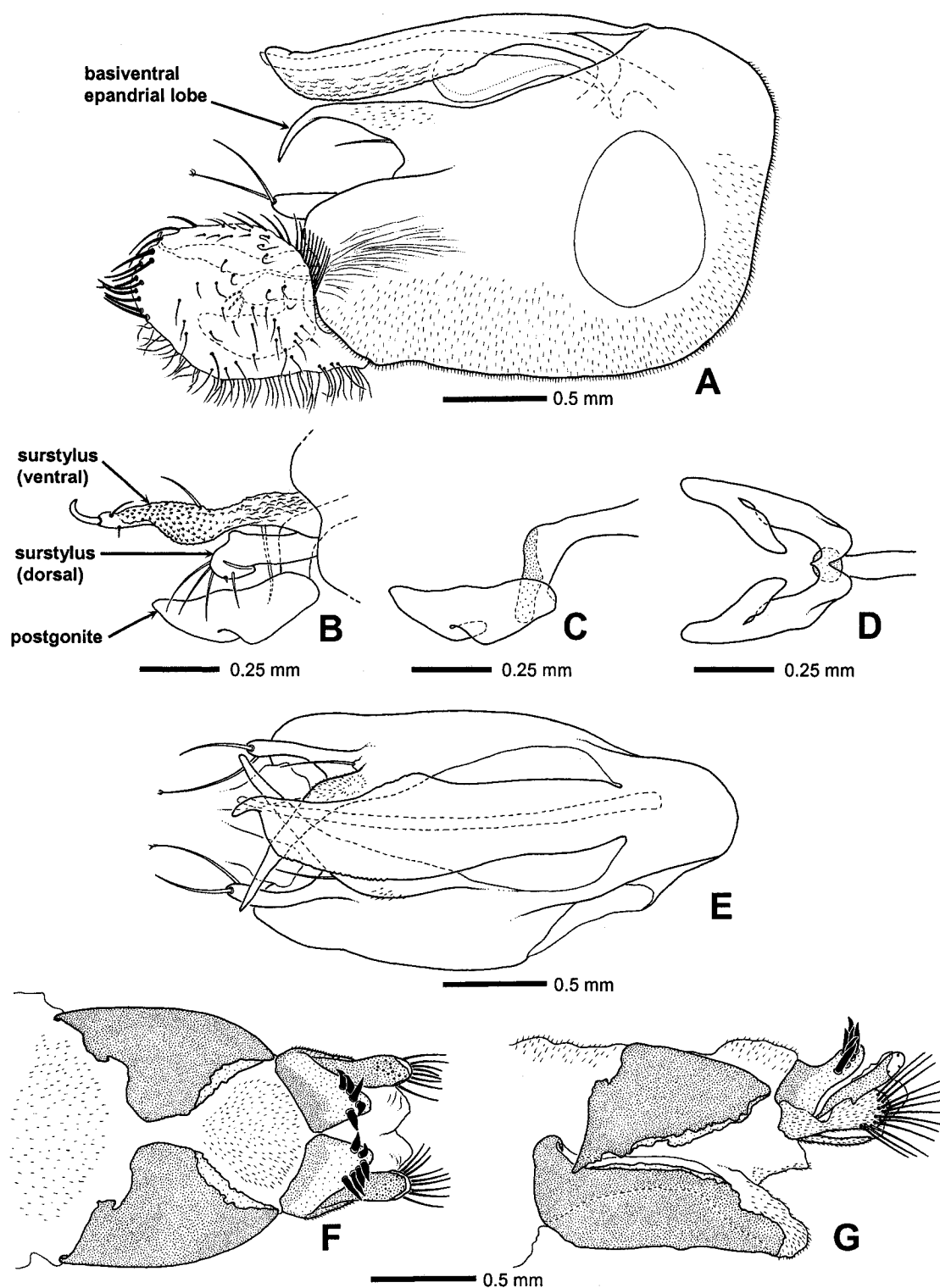


Figure 44: *Tachytrechus giganteus*: (A) Male genitalia, left lateral view. (B) Surstylus and postgonite, lateral view. (C) Postgonite, lateral view. (D) Postgonite, dorsal view. (E) Male genitalia, ventral view (surstyli, postgonite and cerci not shown). (F) Female terminalia, dorsal view. (G) Female terminalia, left lateral view.

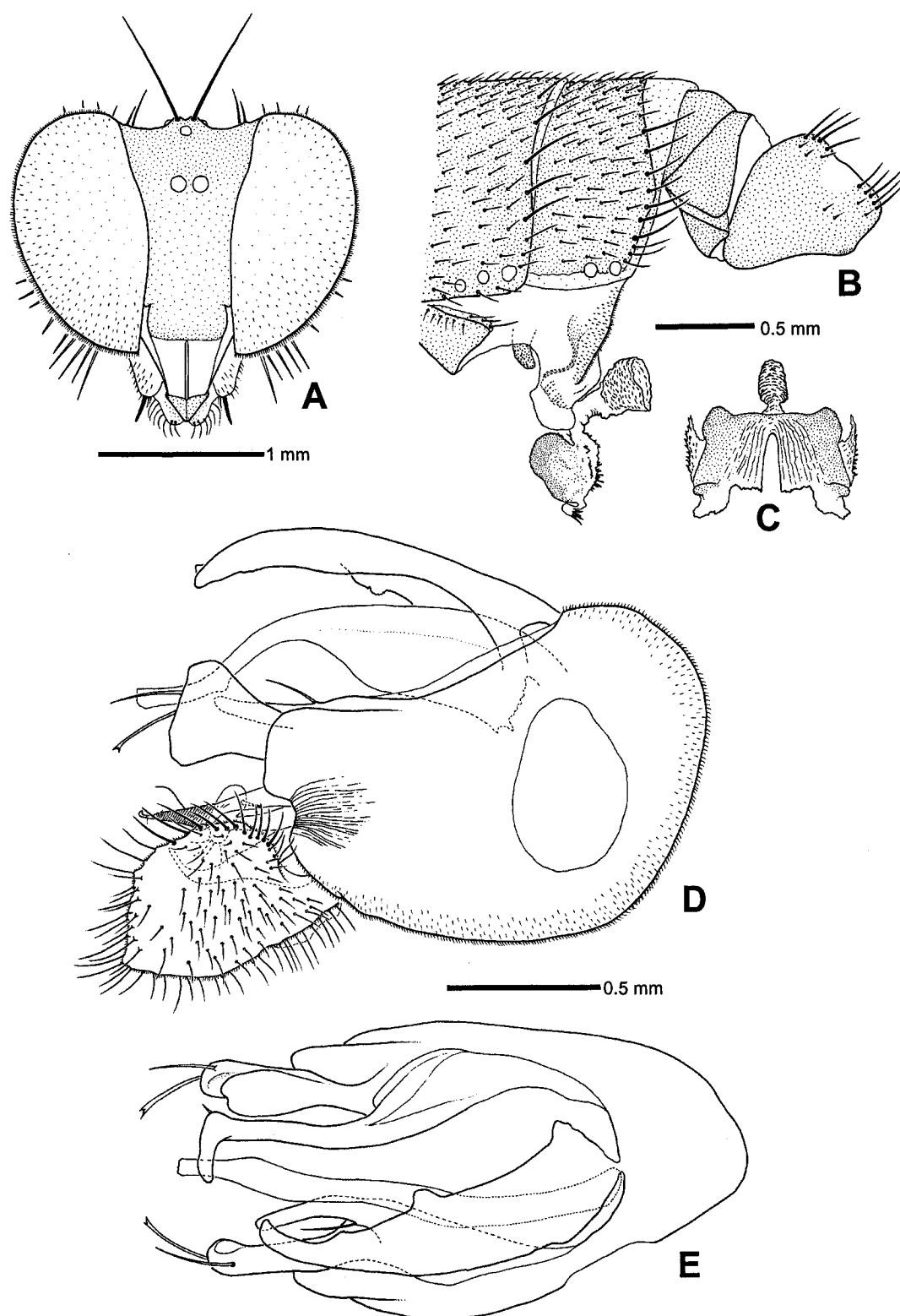


Figure 45: *Tachytrechus transversus*: (A) Male head. (B) Male abdomen, lateral view (hypopygium removed). (C) Glandular projection of sternite 5, ventral view of apex. (D) Male genitalia, lateral view. (E) Male genitalia, ventral view (surstyli, postgonite and cerci not shown).

CONNECTING STATEMENT

The phylogenetic analysis in Chapter 2 led to the establishment of a new genus of Dolichopodinae, i.e. *Ethiomyia* Brooks. Like the previous chapter, which revised the species of the *Tachytrechus alatus* group, Chapter 4 is a species-level revision of *Ethiomyia*, in which all of the included species are redescribed and illustrated. Chapter 4 also provides a key to identify the species of *Ethiomyia*.

CHAPTER 4. REVISION OF *ETHIROMYIA* BROOKS (DIPTERA: DOLICHOPODIDAE)

ABSTRACT. *Ethiomyia* Brooks, a Holarctic genus of dolichopodid flies in the subfamily Dolichopodinae is revised. *Ethiomyia* is distinguished by the following features: wing vein M straight and subparallel to R_{4+5} ; thoracic pleuron with a cluster of fine hairs in front of the posterior spiracle; fore tibia of males with an elongate apicoventral seta; cercus of males whitish with black border and long, fine marginal setae; dorsal surstylus with preapical dorsal notch and keel-like projection; female terminalia with inner medial pair of acanthoporous spines on T10. The genus comprises three species, including *Ethiomyia purpurata* (Van Duzee) and *Ethiomyia violacea* (Van Duzee) from the eastern Nearctic, and *Ethiomyia chalybea* (Wiedemann) from Europe. All species are redescribed and a key is provided to facilitate their identification.

INTRODUCTION

Ethiomyia Brooks was established in Chapter 2 for the enigmatic Holarctic species group that includes the Nearctic species *Gymnopternus purpuratus* (Van Duzee) and *Gymnopternus violaceus* (Van Duzee), and the Palaearctic species *Hercostomus* (*Gymnopternus*) *chalybeus* (Wiedemann). Historically, the placement of these species has been somewhat contentious (Van Duzee, 1921; Negrobov, 1980; Pollet, 1990); however, recent regional classifications (Chandler, 1998; Pollet et al., 2004) put them in *Gymnopternus* Loew on the basis of wing venation (i.e. M straight and subparallel to R4+5), and a cluster of fine hairs in front of the posterior thoracic spiracle, the latter of which is also present in *Dolichopus* Latreille.

Although *Ethiomyia* is similar to *Gymnopternus*, the phylogenetic analysis presented in Chapter 2 indicated that this genus is more closely related to *Dolichopus*. *Ethiomyia* and *Dolichopus* form a clade based on the distinctive dorsal surstylar lobe of the male genitalia, and by the possession of a pair of inner, medial acanthophorous spines on tergite 10 of the female terminalia. *Dolichopus* + *Ethiomyia*, in turn, form the sister group to *Gymnopternus* based on the cluster of hairs in front of the posterior spiracle. The monophyly of *Ethiomyia* is supported by the possession of an elongate apicoventral seta on the fore tibia of males, and the distinctive male cercus, which is characterized by long, fine marginal setae. The purpose of this chapter is to revise the genus *Ethiomyia* with redescriptions of all included species.

MATERIALS AND METHODS

This study is based on material housed in the collections of the Canadian National Collection of Insects, Ottawa, Ontario, Canada (CNC), the Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, Quebec, Canada (LEM) and the Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (ZMHB). Morphological terminology for adult structures mainly follows McAlpine (1981).

Terminology for male genitalic structures follows Cumming et al. (1995) and Sinclair (2000). Body length is measured from the base of the antenna to the tip of abdomen. Wing length is measured from the humeral crossvein to the wing apex. Relative lengths of each tarsomere are representative ratios expressed using the following formula: $t_1/t_2/t_3/t_4/t_5$, where t_1 refers to the basitarsus and t_5 refers to the fifth tarsomere.

Male and female terminalia were macerated in either 10% KOH, which was heated on a hot plate for about 10 minutes, or in 85% lactic acid, heated in a microwave oven. Each microwave heating interval comprised 30 seconds and was followed by a 1-2 minute cooling period during which macerated muscle tissue was removed with a fine probe.

Figures showing the male genitalia in lateral view are oriented as they appear on the intact specimen (rotated 180° and lateroflexed to the right), with the morphologically ventral surface up, dorsal surface down, anterior end facing right and posterior end facing left. Figures showing the male genitalia in ventral view are correspondingly oriented with the anterior end facing right and posterior end facing left. The following abbreviations are used in the figures: **apv lobe**: apicoventral epandrial lobe; **bv lobe**: basiventral epandrial lobe; **bv seta**: basiventral epandrial seta; **cerc**: cercus; **dsur**: dorsal lobe of surstylus; **ejap**: ejaculatory apodeme; **epand**: epandrium; **hy**: hypandrium; **hyap**: hypandrial apodeme; **pgon**: postgonite; **ph**: phallus; **S8**: sternite 8; **T8**: tergite 8; **T10**: tergite 10; **vsur**: ventral lobe of surstylus. Abbreviations used in the text include T: abdominal tergite, and S: abdominal sternite.

SYSTEMATICS

GENUS *ETHIROMYLA* BROOKS

Ethiromyia Brooks, 2004. Type species: *Hercostomus purpuratus* Van Duzee, 1925: 185 [Nearctic], by original designation.

Recognition. Species of *Ethiromyia* can be recognized by the following combination of characters: wing vein M straight and subparallel to R_{4+5} ; thoracic pleuron with a cluster of fine hairs in front of posterior spiracle; fore tibia of males with an elongate apicoventral seta; cercus of males whitish with black border and long, fine marginal setae; dorsal surstylus with preapical dorsal notch and keel-like projection; female terminalia with inner medial pair of acanthophorous spines on T10. *Ethiromyia* also lacks the dorsal setae on the hind basitarsus found in species of *Dolichopus* and the anterodorsal row of strong setae on the fore tibia present in most species of *Gymnopternus*.

Description. Head: Vertex not excavated, 1 pair of strong divergent ocellar setae, 1 pair of strong vertical setae, stronger than postverticals. Frons about 2-2.8x wider than high, sides weakly convergent anteriorly. Face broad in male, sides slightly convergent below or subparallel, broader in female with sides subparallel. Clypeus slightly produced to strongly bulging, especially in female, lower margin straight or slightly emarginate, ending well above lower eye margin. Palp ovoid, with weak setae on apical half of outer surface and a distinct apical seta. Proboscis large and projecting or moderate in size. Antennae inserted above middle of head; scape subconical, dorsally setose, with well-developed acute medioventral process; pedicel short, with nipple-like medial condyle; first flagellomere subtriangular to ovoid, about as long as wide; arista dorsal, 2-segmented, second segment weakly to strongly pubescent. Postocular setae uniseriate, lowermost seta sometimes stronger. One pair of postvertical setae, subequal to distinctly stronger than uppermost pair of postoculars.

Thorax: Acrostichals biserial; 6 dorsocentrals, fifth pair distinctly offset medially; postpronotum with 1 strong medioclinate seta and 2-3 weaker outer setae; 1 strong outer posthumeral, 1 weak inner posthumeral; 2 notopleurals; 1 presutural; 1 sutural; 2 supraalars; 1 postalar. Upper and lower part of propleuron with fine hairs; lower part of propleuron with 1 strong prothoracic seta; pleural surface in front of posterior spiracle with a cluster or row of fine hairs; metepisternum with a cluster of several fine hairs. Scutellum with 1 strong inner seta and 1 small outer seta on lateral margin, dorsum with sparse hairs, posterior margin with sparse short hairs or long dense hairs.

Legs: Pulvilli normal on all legs. Foreleg: Tibia of male with long, fine apicoventral seta. Midleg: Femur with 1 anterior preapical seta. Hindleg: Coxa with strong lateral seta near or slightly below middle; femur with 1 anterodorsal preapical seta; apex of tibia with weak to indistinct ridge-like process posterodorsally in male; basitarsus subequal to or slightly shorter than second tarsomere, without dorsal setae, with distinct basiventral seta, males with hook-like process posterobasally.

Wing (Fig. 46A-C): Brownish to grey. Costa of male with or without pterostigma near insertion of R_1 ; R_{2+3} relatively straight to weakly convex; R_{4+5} straight with posterior curve in apical section; distal section of M beyond crossvein dm-cu with barely discernable sinuous bend before middle, straight, or with slight convex curve in distal section similar to that of R_{4+5} , ending near wing apex; R_{4+5} and M subparallel; crossvein dm-cu subequal to or shorter than distal section of CuA_1 .

Abdomen: Subconical. T1-5 setose. Male: T6 bare; S2 unmodified; S3 unmodified or emarginate and mainly membranous posteromedially; S4 strongly emarginate or divided, membranous medially; S5 mainly to entirely membranous; S6 mainly membranous, sclerotized along anterior margin; segment 7 bare, forming well-developed peduncle; S8 subquadrate to subtriangular, setose. Hypopygium (Figs. 47A-C, 48A,B) large. Epandrium subtriangular in lateral view, about 1.5-2x longer than high, foramen positioned laterally, well-separated from base of cerci; basiventral epandrial lobe weakly developed, basiventral epandrial seta present; apicoventral epandrial lobe well-developed, subquadrate, rounded or flared apically, with 1 lateral and 2 apical setae. Surstylus 2-lobed. Ventral lobe more or less digitiform, with or without dorsal hump, with weak dorsal to dorsomedial preapical projection, apex with short, stout seta. Dorsal lobe larger than ventral lobe, with 1-2 strong dorsomedial setae and 1 preapical lateral seta, dorsal surface notched preapically with distinct to weakly developed keel-like projection across notch bearing a short seta (Fig. 47B). Postgonite with anteroventral portion weakly sclerotized, nearly membranous and bifurcate anteriorly; posterodorsal portion vestigial (Fig. 48A,B), or well-developed and digitiform (Fig. 47B). Proctiger brushes absent. Cercus (Figs. 47A, 48A,B) large, round to ovoid, pale with dark margin; apical and lateral margin jagged, sometimes with well-developed digitiform projections apicomediaally (Figs. 47A, 48A); lateral and/or apical margin with very long, fine setae. Hypandrium

elongate and slender, trough-like, free laterally with membranous connection to epandrium basally; hypandrial arms connected to hypandrium; hypandrial apodeme well-developed, with knob-like apex. Sperm pump cylindrical; ejaculatory apodeme rod-like; basal sclerite of sperm pump well-developed, thick and heavily sclerotized, broadly V-shaped in dorsal view. Phallus elongate and slender, apical portion with weak rounded projection (Figs. 47B, 48B), or finely serrate (Fig. 48A). Female (Fig. 47D,E): T6, T7, S6 and S7 undivided; T8 and S8 divided medially, tergite and sternite fused anterolaterally. Furca narrow and weakly sclerotized or absent. T10 divided medially into hemitergites each bearing 4-5 acanthoporous spines along outer margin and a single inner medial spine (Fig. 47D), spines pointed to blunt apically. Upper lobe of cercus with short apical seta.

KEY TO SPECIES OF *ETHIROMYIA*

1. Mid and hind tibiae pale with dark spots at insertion points of setae; male with wing margin concave between veins M and CuA₁ (Fig. 46C) cercus of male with weakly developed digitiform projections on apicodorsal margin (Fig. 48B).....
.....*violacea* (Van Duzee)
- Mid and hind tibiae without dark spots at insertion points of setae, hind tibia pale or brown; male with wing evenly convex between M and CuA₁ (Fig. 46A); cercus of male with well-developed digitiform projections on apicodorsal margin (Fig. 47A, 48A)2
2. Palp blackish-brown; antenna entirely black; fore leg with coxa dark, dorsal surface of femur usually brown; hind leg of male with long, fine posterior hairs on apical half of femur and basal part of tibia; hind tibia of male with four closely spaced, flattened posterodorsal setae on basal half; male wing with pterostigma near insertion of R₁ (Fig. 46A); male T2 and T3 velvety black laterally with fine hairs; male cercus with scythe-shaped apicoventral seta on first elongate digitiform projection, marginal setae about as long as width of cercus (Fig. 47A).....*purpurata* (Van Duzee)
- Palp pale yellow, darkened basally; antenna with scape and pedicel pale ventrally; fore leg with coxa mainly pale, infuscated basally on outer side, dorsal surface of femur

yellow; hind leg of male lacking fine posterior hairs on apical half of femur and basal part of tibia, tibia of male without four close set, flattened posterodorsal setae on basal half; male wing without pterostigma; male T2 and T3 not velvety black laterally, hairs unmodified; male cercus with spatulate apicoventral seta on first elongate digitiform projection, marginal hairs distinctly longer than width of cercus (Fig. 48A).....
*chalybea* (Wiedemann)

***Ethiomyia chalybea* (Wiedemann)**

(Fig. 48A)

Dolichopus chalybeus Wiedemann, 1817: 72

Dolichopus cinereomaculatus Roser, 1840: 56

Gymnopternus conformis Loew, 1857: 16

Gymnopternus chalybeus (Wiedemann): Loew 1857: 21

Hercostomus (*Gymnopternus*) *chalybeus* (Wiedemann): Lundbeck, 1912: 189; Chandler, 1998: 90

Hercostomus chalybeus (Wiedemann): Becker, 1917: 212; Pollet, 1990: 361

Ethiomyia chalybea (Wiedemann): Brooks (2004)

Description. Male: Body length = 3.6-4.4 mm, wing length = 3.8-4.6 mm. Head: Frons metallic violet-bronze or violet-blackish, lower and lateral margins often metallic bluish-green. Face and clypeus silvery-grey pollinose; face about 0.2x as wide as head; clypeus strongly bulging. Palp mainly yellow, brownish black near base, with black hair.

Proboscis large and projecting. Antenna: Scape and pedicel yellow ventrally, dark brown dorsally; first flagellomere blackish-brown, apex weakly pointed or rounded; arista dark brown, strongly pubescent. Postocular setae black. Ocellar tubercle with several hairs medially. Postvertical seta slightly stronger than upper postocular seta.

Thorax: Notum metallic greenish-black or bluish-black with violet reflections.

Pleuron dark metallic greenish-blue and bronze with whitish pollinosity. Scutellum black

with metallic violet, green and blue reflections, with long, dense hairs on posterior margin.

Legs: Fore coxa, femora, fore and mid tibiae mainly yellow, mid and hind coxae concolorous with thoracic pleuron, hind tibia more or less brownish, becoming darker towards apex. Foreleg: Coxa darkened basally on outer side; tibia with 2 strong anterodorsals in basal part, 1-2 weaker distal anterodorsals, 2 dorsals, 1-2 posteroventrals, distal seta often weaker or absent, 2 apicals in addition to long, fine apicoventral; basitarsus mainly yellow with brown apex, tarsomeres 2-5 brown, tarsomere ratio: 4.0/1.7/1.3/1.0/1.0. Midleg: Tibia with 3 anterodorsals, 2 dorsals, 2 anteroventrals, 5 apicals; basitarsus mainly yellow with brown apex, tarsomeres 2-5 brown, tarsomere ratio: 4.0/2.0/1.5/1.1/1.0. Hindleg: Coxa often yellow apically; femur brown apicodorsally; tibia with 4-6 anterodorsals, 1 preapical dorsal, 4-6 posterodorsals, 3-5 ventrals, 2 apicals, and dense, well-developed clothing hairs posteriorly; tarsus entirely blackish-brown, tarsomere ratio: 2.9/3.2/1.9/1.2/1.0.

Wing brown, darker on anterior half; pterostigma absent; wing margin evenly convex between veins M and CuA₁; calypter with black setae; halter pale yellow.

Abdomen: T1-5 dark bronze dorsally, metallic greenish-blue laterally with whitish pollinosity, with weak violet reflections; S5 with eversible membranous sac; T6, segment 7 and S8 dark brown. Hypopygium (Fig. 48A): Epandrium dark brown, abruptly narrowed in apical half, ventral margin (including basiventral and apicoventral epandrial lobes) pale yellow; basiventral epandrial lobe very weakly developed; apicoventral epandrial lobe flared apically. Surstylus pale yellow; ventral lobe slender, without dorsal hump; dorsal lobe with 2 strong, dark dorsomedial setae. Postgonite: posterodorsal portion vestigial. Cercus ovoid with well-developed digitiform projections apicomediaally, first elongate digitiform projection with apicoventral spatulate seta, marginal setae very long. Hypandrium amber, lacking dorsal process, tubular basally, open along right side exposing phallus. Phallus with a pair of serrate longitudinal bands apically.

Female: Body length = 4.0-4.7 mm, wing length = 4.1-4.6 mm. Identical to male except for the following: Head: Face and clypeus broader; face about 0.3x as wide as head, slightly darker; clypeus weakly pollinose, bronze, especially on upper part;

proboscis larger. Legs: fore tibia lacking long, fine apicoventral; posterior clothing hairs on hind tibia not as strongly developed.

Type material examined. 2 ♂♂, 1 ♀ Syntypes: GERMANY: Kiel (ZMHB, No. 2931).

Material examined. BELGIUM: Oost-Vlaanderern: 16 ♂♂ and 20 ♀♀ Heurne, Het Dal Nature Reserve, water trap, 1997, M. Pollet & P. Grootaert (LEM); AUSTRIA: Carinthia: 1 ♂ nr Drobollach am Faaker See, reedbed, 3.vii.1992, C.E. Dyte (LEM); 1 ♀ same date except nr Faaker See, woodland (LEM).

Distribution. Known throughout Europe (i.e. Britain, France, Belgium, The Netherlands, Denmark, Germany, Switzerland, Italy, Austria, Czech Republic, Slovakia, Poland, Romania, former Yugoslavia, Sweden, Finland) and western Russia (Negrobov, 1991).

***Ethiomyia purpurata* (Van Duzee)**

(Figs. 46A,B, 47A-E)

Hercostomus purpuratus Van Duzee, 1925: 185

Gymnopternus purpuratus (Van Duzee): Foote et al., 1965: 499; Pollet et al., 2004: 41

Ethiomyia purpurata (Van Duzee): Brooks (2004)

Description. Male: Body length = 4.2-5.0 mm, wing length = 3.7-4.3 mm. Head: Frons bronze to blackish-bronze with violet metallic reflections, lower and lateral margins usually metallic bluish-green. Face and clypeus silvery-grey pollinose, sometimes with weak blue-green reflections; face about 0.3x as wide as head; clypeus strongly bulging. Palp blackish-brown with black hair. Proboscis large and projecting. Antenna black; first flagellomere rounded or weakly pointed apically; arista with short pubescence. Postocular setae black. Ocellar tubercle with several hairs medially. Postvertical seta stronger than upper postocular seta.

Thorax: Notum metallic greenish-black with violet, blue and bronze reflections. Pleuron dark metallic greenish-blue with whitish pollinosity. Scutellum blackish with metallic violet, green and blue reflections, with fine, short hairs on posterior margin.

Legs: Coxae blackish-brown with metallic green tinge, concolorous with thoracic pleuron; femora and tibiae mainly yellow. Foreleg: Femur usually brown dorsally; tibia with 1-3 anterodorsals, distal anterodorsals sometimes weaker, 2 dorsals, 1-3 posteroventrals, 2 apicals in addition to long, fine apicoventral; basal two-thirds of basitarsus yellow, apical third black, tarsomeres 2-5 black, tarsomere ratio: 3.5/1.6/1.2/1.0/1.0. Midleg: Tibia with 3-5 anterodorsals, 2 dorsals, 1-3 anteroventrals, 5 apicals; basal two-thirds of basitarsus yellow, apical third black, tarsomeres 2-5 black, tarsomere ratio: 4.3/2.2/1.5/1.1/1.0. Hindleg: Apical half of femur and basal part of tibia with long, fine hairs posteriorly, hairs about as long as width of femur; tibia with 4-5 anterodorsals (distal 1-2 setae sometimes dorsal), 1 preapical dorsal, 4 close set, flattened posterodorsals on basal half, 3-6 weaker ventrals, 2 apicals, apex of tibia brown posteriorly; tarsus entirely blackish-brown, tarsomere ratio: 2.8/3.1/2.0/1.2/1.0.

Wing (Fig. 46A) evenly dark brown; pterostigma present near insertion of R_1 ; wing margin evenly convex between veins M and CuA_1 ; calypter with black setae; halter pale yellow.

Abdomen: T1-5 dark metallic greenish, lateral part of T2 and T3 velvety black with fine hairs, T4 also with fine hairs laterally; T6, segment 7 and S8 dark brown. Hypopygium (Fig. 47A-C): Epandrium mainly dark brown, ventral margin (including basiventral and apicoventral epandrial lobes) pale yellow, left basiventral epandrial lobe larger than right lobe (Fig 47C); apicoventral epandrial lobe subquadrate. Surstylus pale yellow; ventral lobe with dorsal hump; dorsal lobe with 1 strong, dark dorsomedial seta. Postgonite with posterodorsal portion pale, digitiform, bent ventrally. Cercus round with well-developed digitiform projections apicomediaally, first elongate digitiform projection with apicoventral scythe-shaped seta. Hypandrium amber with dorsal process near middle, tubular basally, open along right side exposing phallus. Phallus with weak rounded process in apical portion.

Female: Body length = 4.3-5.5 mm, wing length = 3.9-4.5 mm. Identical to male except for the following: Head: Face and clypeus darker, broader; face about 0.35x as wide as head, clypeus very strongly bulging. Proboscis slightly larger. Legs: fore tibia lacking long, fine apicoventral; hind femur and basal part of hind tibia lacking long, fine hairs posteriorly; hind tibia with three normally developed posterodorsals on basal half. Wing: Pterostigma absent. Abdomen: dark metallic green with violet, blue and bronze reflections, T2 and T3 without lateral velvety black patch, T2-4 without with fine hairs laterally.

Type material examined. Holotype ♂: CANADA: Manitoba: Stockton, 29.vii.1924, N. Criddle (CNC, No. 1413). Allotype ♀: same data as holotype.

Other material examined. CANADA: Ontario: 1 ♂ Swastika, 7.vii.1987, J.R. Vockeroth (CNC); Quebec: 1 ♂ Beachgrove (45°37'N, 76°8'W), 24.vi.1988, J.R. Vockeroth (CNC); Lac St-Francois Natural Wildlife Area: 18 ♂ ♂ and 6 ♀ ♀ Marais Fraser, 45°02.37'N, 74°27.73'W, *Carex* meadow, pan trap, 03.vi-11.vi.1999, F. Beaulieu (LEM); 7 ♂ ♂ and 3 ♀ ♀ same data except 26.v-03.vi.1999 (LEM); 1 ♀ same data except sweep net, 28.v.1999 (LEM); 4 ♂ ♂ and 3 ♀ ♀ same data except sweep net, 05.vi.1999 (LEM); 8 ♂ ♂ and 4 ♀ ♀ same data except 11.vi.-19.vi.1999 (LEM); 3 ♂ ♂ and 5 ♀ ♀ same data except 45°02.40'N, 74°28.03'W (LEM); 2 ♀ ♀ same data except 26.v-03.vi.1999 (LEM); 3 ♂ ♂ and 6 ♀ ♀ same data except 11.vi-19.vi.1999 (LEM); 5 ♂ ♂ and 12 ♀ ♀ NW of Aménagement Therrien, close to ruisseau Therrien, 45°00.39'N, 74°30.99'W, *Carex* meadow, pan trap, 03.vi-11.vi.1999, F. Beaulieu (LEM); 2 ♂ ♂ and 3 ♀ ♀ same data except 11.vi.-19.vi.1999 (LEM); 1 ♂ same data except 19.vi.-26.vi.1999 (LEM); 8 ♂ ♂ and 3 ♀ ♀ same data except sweep net, 05.vi.1999 (LEM); 1 ♂ same data except 45°00.17'N, 74°30.63'W (LEM); 8 ♂ ♂ and 1 ♀ same data except pan trap, 03.vi-11.vi.1999 (LEM); 1 ♂ same data except 11.vi-19.vi.1999 (LEM); 2 ♂ ♂ and 1 ♀ same data except 19.vi-26.vi.1999 (LEM).

Distribution. Known from Manitoba, Michigan, northern Ontario and southwestern Quebec.

Remarks. Beaulieu and Wheeler (2001) collected large numbers of this species (as “*Gymnopternus* n. sp. 1”) in lakeside sedge meadows in southwestern Quebec.

***Ethiomyia violacea* (Van Duzee)**

(Figs. 46C, 48B)

Proarchus violaceus Van Duzee, 1921: 123

Hercostomus (*Proarchus*) *violaceus* (Van Duzee): Leonard, 1928: 782

Hercostomus violaceus (Van Duzee): Steyskal, 1959: 5

Gymnopternus violaceus (Van Duzee): Robinson, 1964: 158; Foote et al., 1965: 500;
Pollet et al., 2004: 41

Ethiomyia violacea (Van Duzee): Brooks (2004)

Description. Male: Body length = 3.6-4.6 mm, wing length = 3.7-4.4 mm. Head: Frons bronze to blackish with violet and bluish-green metallic reflections. Face and clypeus silvery-grey pollinose; face about 0.2x as wide as head; clypeus weakly or strongly bulging. Palp mainly yellow, brown near base, with black hair. Proboscis medium-sized. Antenna: Scape and pedicel mainly yellow, brown dorsally; first flagellomere yellow basally, distal portion blackish-brown, apex rounded or weakly pointed; arista blackish-brown, strongly pubescent. Postocular setae black. Ocellar tubercle with several hairs medially. Postvertical seta stronger than or subequal to upper postocular seta.

Thorax: Notum metallic greenish-black to greenish-bronze with violet and bluish reflections. Pleuron dark metallic greenish-grey to greenish-bronze, with whitish pollinosity. Scutellum dark bronze or blackish with violet, green, and blue reflections, with fine, short hairs on posterior margin.

Legs: Fore and hind coxae mainly yellow, brown at base on outer side, mid coxa more or less concolorous with thoracic pleuron; femora and tibiae yellow, mid and hind

tibiae with dark spots at insertion points of setae. Foreleg: Tibia with 2-4 anterodorsals, distal 2 anterodorsals usually weaker if developed, 2 dorsals, 1-3 posteroventrals, 2 apicals in addition to long, fine apicoventral; basitarsus mainly yellow with brown apex, tarsomeres 2-5 brown, tarsomere ratio: 4.1/1.7/1.3/1.0/1.0. Midleg: femur with long, fine hairs basoventrally, hairs slightly shorter than width of femur; tibia with 3-4 anterodorsals, 2 dorsals, 2-3 anteroventrals, 1 ventral at apical third, 5 apicals; basitarsus mainly yellow with brown apex, tarsomeres 2-5 brown, tarsomere ratio: 4.0/2.0/1.5/1.1/1.0. Hindleg: Femur with well-developed dorsal clothing setae; tibia with 3-4 anterodorsals, 3-4 posterodorsals, 3-4 ventrals, 1 preapical dorsal, 2 apicals; basitarsus mainly yellow with brown apex, tarsomeres 2-5 brown, tarsomere ratio: 2.6/3.2/2.0/1.3/1.0.

Wing (Fig. 46C) grey; pterostigma absent; wing margin concave between M and CuA₁; calypter with black setae; halter pale yellow.

Abdomen: T1-5 dark metallic green with greyish pollen laterally, T1-3 metallic black or bronze dorsomedially; T6, segment 7 dark brown; S8 brown or metallic greenish-brown. Hypopygium (Fig. 48B): Epandrium dark brown, sometimes dark metallic green basally, ventral margin (including basiventral and apicoventral epandrial lobes) pale yellow-amber; basiventral epandrial lobe very weakly developed; apicoventral epandrial lobe rounded apically. Surstylus pale yellow; ventral lobe slender, without dorsal hump; dorsal lobe with 2 strong, dark dorsomedial setae. Postgonite: posterodorsal portion vestigial. Cercus ovoid with jagged margin, lacking well developed digitiform projections, marginal setae very long. Hypandrium pale amber, apex enlarged. Phallus with weak rounded preapical projection.

Female: Body length = 4.2 mm, wing length = 3.8-4.4 mm. Identical to male except for the following: Head: Face and clypeus broader; face about 0.3x as wide as head; clypeus strongly bulging. Proboscis slightly larger. Legs: Fore tibia lacking long, fine apicoventral. Wing margin not distinctly concave between M and CuA₁.

Type material. Holotype ♂: USA: New York: Erie County, Dayton, 5.vii.1920, M.C. Van Duzee (California Academy of Sciences, No. 3467) (not examined).

Material examined. CANADA: Ontario: 1 ♂ Ottawa, 8.viii.1993, J.R. Vockeroth (CNC); Quebec: 2 ♂ ♂ Rigaud, Chemin de la Mairie, Parc Lévy Macdonald, 6.viii.2000, sweep net, S.E. Brooks (LEM); 1 ♀ Old Chelsea, 24.vi.1956, J.R. Vockeroth (CNC); USA: North Carolina: 1 ♂ Highlands, 3800', 7.vi.1957, W.R.M. Mason (CNC); 1 ♂ same data except 10.vi.1957, J.R. Vockeroth (CNC); 1 ♂ same data except 16.vi.1957 (CNC); 1 ♀ same data except 20.vi.1957 (CNC); Tennessee: 1 ♂ Knoxville, Univ. Farm, 20.v.1957, J.R. Vockeroth (CNC); 1 ♂ Knoxville Co., 26.v.1957 (CNC); 1 ♀ same data except 30.v.1957 (CNC).

Distribution. Ontario, Michigan, New York, Quebec to Massachusetts, south to Ohio, Virginia, Tennessee, North Carolina and South Carolina (Pollet et al. 2004).

ACKNOWLEDGEMENTS

Thanks to Frédéric Beaulieu whose studies of the Diptera associated with sedge meadows of southern Quebec provided a large number of specimens of *E. purpurata*. Thanks to Jeff Cumming (CNC) for the loan of the type specimens of *E. purpurata* and specimens of *E. violacea*. Thanks to Joachim Ziegler (ZMHB) for the loan of the type specimens of *E. chalybea*. Additional specimens of *E. chalybea* were kindly provided by Marc Pollet and Peter Dyte. Thanks also to Marc Pollet for identifying specimens of *E. purpurata* from Lac St-Francois Natural Wildlife Area, Quebec. Funding was provided by an NSERC Discovery Grant to T.A. Wheeler.

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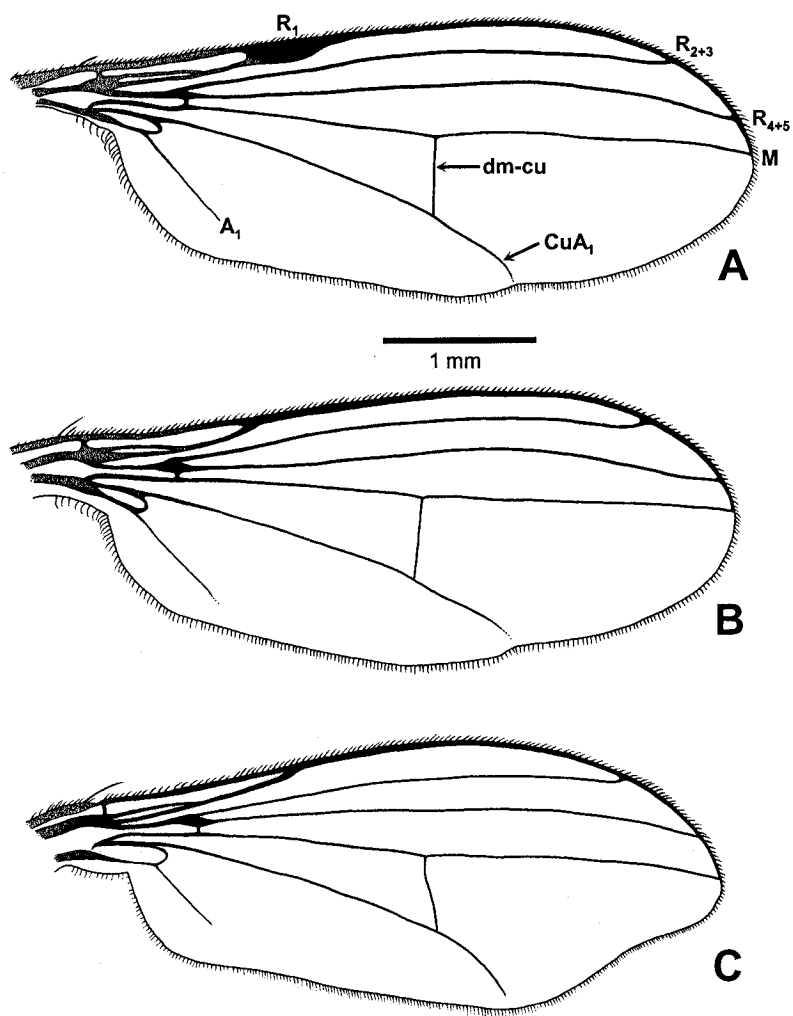


Figure 46. *Ethiomyia purpurata* and *E. violacea*: (A) *E. purpurata*, male wing. (B) *E. purpurata*, female wing. (C) *E. violacea*, male wing.

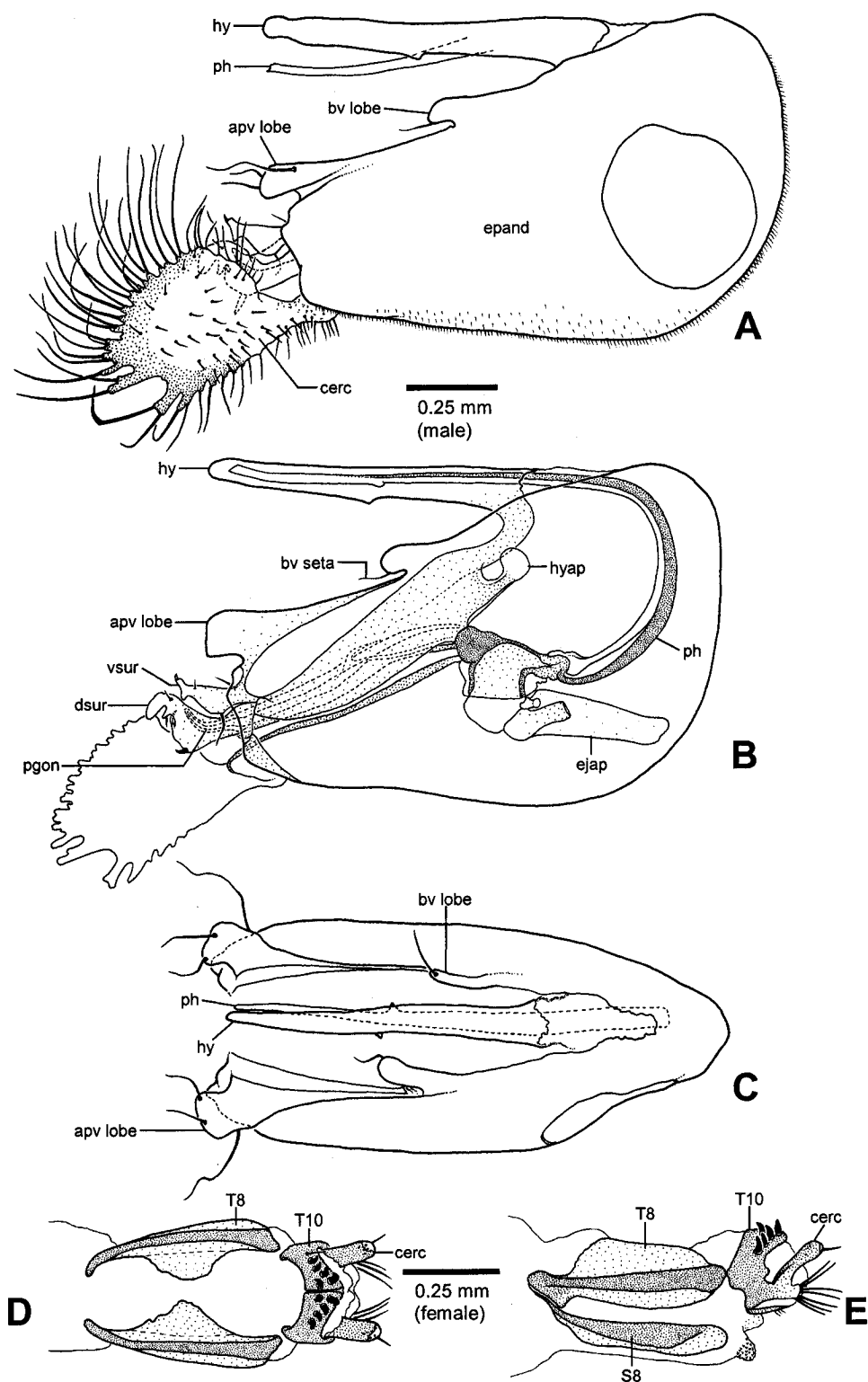


Figure 47. *Ethiomomyia purpurata*: (A) Male genitalia, left lateral view (external). (B) Male genitalia, left lateral view (internal). (C) Male genitalia, ventral view (postgonite, surstylus and cerci not shown). (D) Female genitalia, dorsal view. (E) Female genitalia, left lateral view.

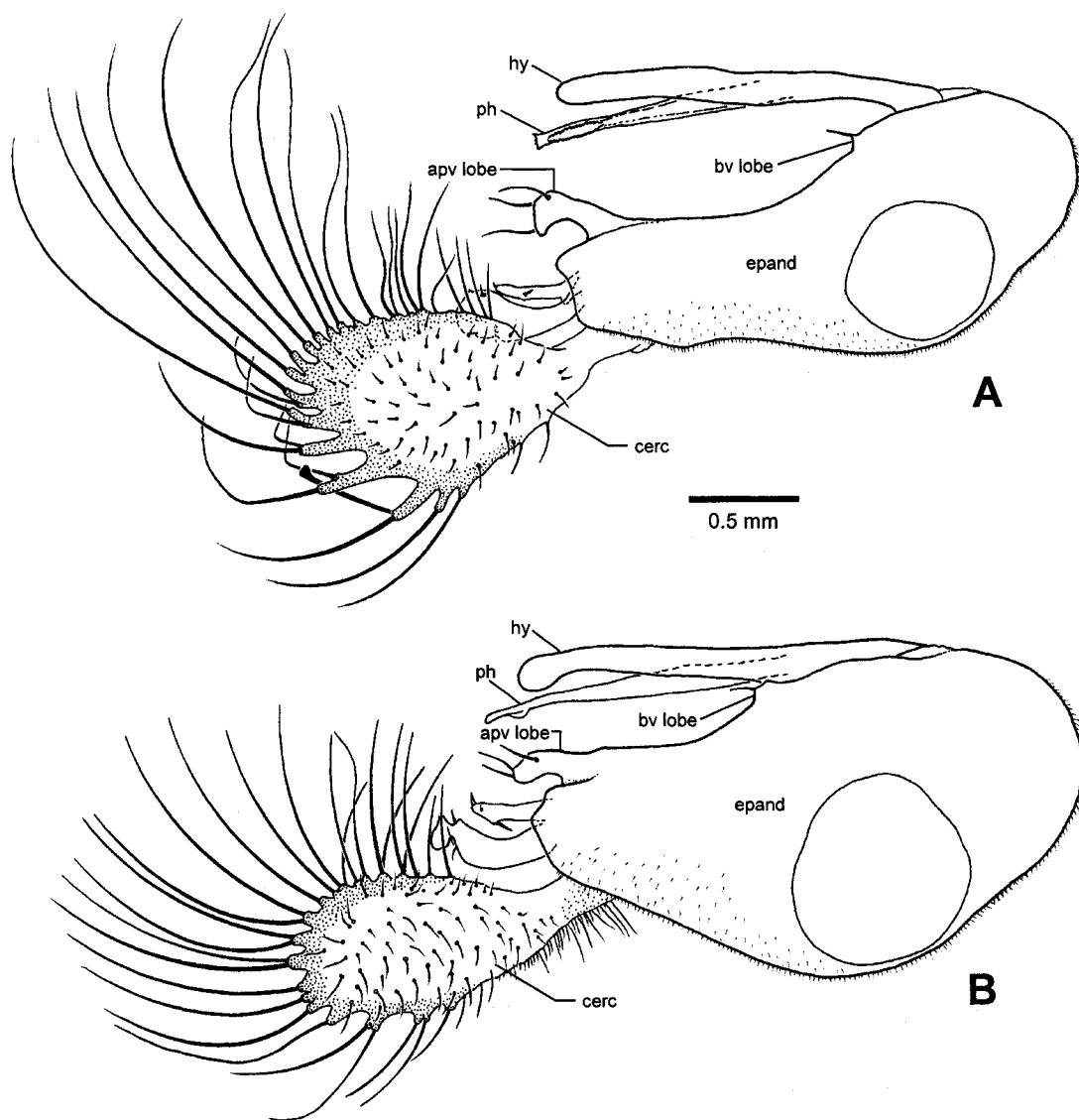


Figure 48. *Ethiromyia chalybea* and *E. violacea*: (A) *E. chalybea*, male genitalia, left lateral view. (B) *E. violacea*, male genitalia, left lateral view.

CHAPTER 5. GENERAL DISCUSSION AND CONCLUSION

This thesis has made an important contribution to the systematics of the Dolichopodinae, including the first ever phylogenetically-based hypothesis of generic relationships for the subfamily, and species level revisionary studies of both the *Tachytrechus alatus* species group and the new genus *Ethiomyia* Brooks.

The phylogenetic analysis presented in Chapter 2 has brought about a number of significant changes in the classification of the Dolichopodinae. The analysis indicated that the current world-based concept of the subfamily was paraphyletic. Accordingly, the limits of the Dolichopodinae were redefined and four genera were excluded from the subfamily (i.e. *Colobocerus* Parent, *Katangaia* Parent, *Pseudohercostomus* Stackelberg and *Vetimicrotes* Dyte). In addition, eleven dolichopodine genera were synonymized, i.e. *Halaiba* Parent (= *Argyrochlamys* Lamb), *Lichtwardtia* Enderlein (= *Dolichopus* Latreille), *Phalacrosona* Becker (= *Hercostomus* Loew), *Steleopyga* Grootaert and Meuffels (= *Hercostomus* Loew), *Proarchus* Aldrich (= *Pelastoneurus* Loew), *Sarcionus* Aldrich (= *Pelastoneurus* Loew), *Pterostylus* Mik (= *Poecilobothrus* Mik), *Ludovicus* Rondani (= *Sybistroma* Meigen), *Nodicornis* Rondani (= *Sybistroma* Meigen), *Gonioneurum* Becker (= *Tachytrechus* Stannius), *Syntomoneurum* Becker (= *Tachytrechus* Stannius), one new genus, *Ethiomyia*, was erected, eighty-one new generic combinations were made, and one new replacement name was proposed as a result of these changes in classification.

Although the phylogeny presented in Chapter 2 represents a significant step forward in our understanding dolichopodine relationships, it should be noted that this work is intended as a preliminary hypothesis to be tested in future studies by the incorporation of additional morphological characters, additional exemplar species, and other sources of data (e.g., molecular characters). In particular, additional studies are needed in order to resolve the basal relationships of the subfamily, and to determine the limits of certain genera that remain problematic (e.g., *Hercostomus*, *Paraclius* Loew, *Pelastoneurus* Loew).

Chapter 2 has also made a significant contribution to our knowledge of dolichopodine morphology, particularly that of the male and female genitalia. These

studies have resulted in the discovery of many new characters which proved to be extremely important in reconstructing the phylogeny of the subfamily and diagnosing the genera. In addition, these morphological studies have provided a basis for the interpretation of genitalic homology within the Dolichopodinae.

Higher level phylogenetic studies, like that of Chapter 2, provide important perspective for revisionary work at lower taxonomic levels by allowing the identification of monophyletic groups such as the *Tachytrechus alatus* species group and the newly established genus *Ethiromyia*, which were revised in Chapters 3 and 4 respectively. The work presented in these two chapters has verified the status of each species and provided keys to facilitate their identification. Similar revisionary work is needed for the majority of remaining dolichopodine genera.