The evolutionary biology of Conopidae (Diptera): A life history, molecular, morphological,
systematic, and taxonomic approach

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For my family.

Little fly,
Thy summer's play
My thoughtless hand
Has brushed away.

Am not I
A fly like thee?
Or art not thou
A man like me?

For I dance
And drink and sing,
Till some blind hand
Shall brush my wing.

If thought is life
And strength and breath,
And the want
Of thought is death,

Then am I
A happy fly,
If I live,
Or if I die.

William Blake (1757-1827)

Abstract

Conopidae is a fascinating family commonly referred to as thick-headed flies. Over 800 species, in over 50 genera and subgenera have been described, but little phylogenetic work has been completed. Past theories on life history, conopid-host interactions, mating strategies, family placement, phylogeny, and classification have been based on very little data and analysis. Based on field observation and collections analysis, evidence of hilltopping mating behaviour is confirmed for thirteen species of Conopidae in the vicinity of Ottawa, Ontario. This represents only the second ever record of this behaviour amongst species of Conopidae. DNA sequence data from ten gene regions is used in a phylogenetic analysis of ten species of Conopidae and representatives of seventeen other families of Diptera. Parsimony and Bayesian analyses are used to propose a phylogenetic hypothesis that places Conopidae within Schizophora as adelphotaxon to Lauxaniidae. Also, a comparison of the informative qualities of mitochondrial versus nuclear DNA sequence data and ribosomal versus protein coding DNA sequence data is included. Further DNA sequence data from five gene regions and over fifty species of Conopidae are combined with morphological data. A cladogram recovered via parsimony analysis confirms the monophyly of five subfamilies within Conopidae. Relationships between subfamilies are also determined with morphological autapomorphies proposed for all nodes in the cladogram. A phylogenetic analysis including only morphological data for all world genera of Conopidae is completed. The recovered

cladogram includes six monophyletic subfamilies, two monophyletic tribes within Myopinae, and eleven monophyletic tribes within Conopinae. This phylogenetic hypothesis is used as the basis of a new classification of the genera of Conopidae. *Chrysiatomyia* Smith, 1989 is placed as a junior synonym of *Callosiconops* Kröber, 1940a, **stat. rev.** A new genus, *Schedophysoconops* **gen. nov.**, and subgenus, *Asiconops* (*Aegloconops*) **subgen. nov.**, are described. The evolution of body structures within the family is discussed. Biogeographic patterns within subfamilies are noted. The first ever key to world genera of Conopidae is included.

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Preface

Chapters 1, 4, 5, and 6 have not been previously published. J. Gibson completed all data gathering, analysis, and writing for these chapters. Funds to pay for costs of obtaining DNA sequence data for Chapter 4 were supplied by the research budget of J. Skevington.

The contents of Chapter 2 were combined with other data and published previously. M. Mei supplied the initial data gathered in Italy, as well as original figures not included in Chapter 2. J. Skevington initially proposed the collaboration, conceptualized the analysis, and provided additional photographs and editorial input. A manuscript including combined Canadian and Italian data was written by J. Gibson and submitted for publication. Chapter 2 contains only the Canadian data as gathered and analyzed by J. Gibson. The original paper (Mei et al. 2008) was published under a Creative Commons Attribution 3.0 license, therefore, no permission is required to reprint portions of text or Table 2.1.

Chapter 3 was previously published in a slightly edited form, with S. Kelso and J. Skevington as junior co-authors. S. Kelso supplied some DNA sequences included in the analysis and developed most of the protocols employed. J. Skevington helped in conceiving of the experimental design and supplied funding to gather DNA sequence data. Most DNA sequence gathering and all analysis and

writing of Chapter 3 were completed by J. Gibson. All text, data tables, and figures are reprinted from *Molecular Phylogenetics and Evolution*, volume 56, Gibson, J.F., Skevington, J.H., and Kelso, S., Placement of Conopidae (Diptera) within Schizophora based on mtDNA and nrDNA gene regions, pp. 91-103, Copyright (2010), with permission from Elsevier.

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Mei, M., **Gibson, J.F.,** and Skevington, J.H. (2008) Observations on hilltopping in the Conopidae (Diptera). *Journal of Insect Science*. 10(27): 1-15, available online <insectscience.org/10.27>

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Gibson, J.F. 2011. Review of *Manual of Central American Diptera Volumes 1 and 2*.
The Canadian Field-Naturalist. Volume 125.

Gibson, J.F., Kelso, S., Jackson, M.D., Kits, J., Miranda, G.F.G., and Skevington, J.H.
(2011) Diptera-specific PCR-amplification primers of use in molecular
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104(5): 976-997.

Gibson, J.F., Skevington, J.H., and Camras, S. 2011. Conopidae (Diptera). In:
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Roig-Juñent, S. (eds.). La Sociedad Entomológica Argentina. In press.

Proposed taxonomic changes included in this thesis are not to be considered as
published according to the rules of the International Code of Zoological
Nomenclature.

1. Introduction to Conopidae

1.1. The use of Conopidae in biological research

Conopidae is a fascinating family commonly referred to as thick-headed flies. Species of Conopidae are found in every bioregion excluding Pacific islands and Antarctica. Adults feed on flowers, but the impact of their role as pollinators is suspected to be minimal (Maeta & Macfarlane, 1993). Larvae are obligatory parasitoids of other insects. Host records are only known for approximately 5% of described species. Most of those species for which host records are known are parasitoids of bees and wasps (Freeman, 1966; Smith, 1966). Members of one subfamily, Stylogastrinae, are suspected to oviposit on cockroaches and crickets. In a few documented cases, these hosts are flushed out of underbrush by advancing ant swarms (Aldrich, 1930; Woodley & Judd, 1998). For a summary of the research completed on conopid biology in the eighteenth and nineteenth centuries, see De Meijere (1904, 1912).

The largest economic impact of species of Conopidae is likely to be their role as parasitoids of honeybees, *Apis mellifera* Linnaeus, 1758 and other hymenopteran pollinators. Species in four genera, *Myopa*, *Physocephala*, *Pseudophysocephala*, and *Zodion*, parasitize honeybees (Freeman, 1966; Mei, 1999; Severin, 1937; Smith, 1966). Once again, complete host records for most species are unknown. Exploring evolutionary linkages between species attacking honeybees, or even between suspected host-specialist species and host-generalist species would require a classification of the family based on phylogenetic analysis. Furthermore, considering

that the Stylogastrinae represent a suspected wide divergence in host use from the rest of the family, the placement of this subfamily is of particular importance. Theories, including evidence from host records, have placed stylogastrines as sister to the remaining conopids (Hennig, 1966), as a completely separate family (Rohdendorf, 1964), or as nested within the remaining conopids (Smith & Peterson, 1987). A phylogenetic hypothesis is necessary for any interpretation of the evolution of host use within Conopidae.

Species of Conopidae have served as important components of an ongoing research project on host-parasitoid relationships. The ecology and behaviour of parasitoids and their bumblebee (*Bombus* spp.) hosts have been the focus of a series of papers by Schmid-Hempel and others in Switzerland (Allander & Schmid-Hempel, 2000; Baer & Schmid-Hempel, 1999; Durrer & Schmid-Hempel, 1995; König & Schmid-Hempel, 1995; Korner & Schmid-Hempel, 2003; Müller & Schmid-Hempel, 1993; Müller et al., 1996; Poulin, 1992; Schmid-Hempel, 2001; Schmid-Hempel & Heeb, 1991; Schmid-Hempel & Müller, 1991; Schmid-Hempel & Schmid-Hempel, 1989, 1996a, 1996b; Schmid-Hempel & Stauffer, 1998; Schmid-Hempel et al., 1990) and Otterstatter and others in Alberta, Canada (Otterstatter, 2004; Otterstatter et al., 2002). In most of the listed publications, the parasitoids included in the study are merely referred to as “conopid,” but two genera, *Physocephala* and *Sicus*, are mentioned specifically in a few cases. The lack of adequate keys to species and genera likely impedes the inclusion of more details about the conopids included in these studies. Also, in order for researchers to add a greater level of detail about the

evolutionary history of conopid-host interactions, a phylogeny of genera of Conopidae is required.

In addition to their ecologically important role as parasitoids, conopids are also interesting due to the prevalence of mimicry within the group (Nicholson, 1927). Many species appear to be mimics of bees and wasps (Godfray, 1993), perhaps even of the same species that serve as hosts to their young. It has been proposed that the mimicry within conopids is Batesian, but that the resemblance between host and parasite is often not close (Askew, 1971; Godfray, 1993). Without accurate host records or even useful keys to species, the nature and evolution of mimicry within Conopidae cannot be adequately tested.

Mimicry is demonstrated in two subfamilies (Conopinae and Dalmanniinae) and not in three others (Myopinae, Stylogastrinae, and Zodioninae). A series of studies (Waldbauer, 1988; Waldbauer & LaBerge, 1985; Waldbauer et al., 1977) have included conopids from two genera (*Physocephala* and *Physoconops*) in an ongoing study of asynchrony in Batesian mimics, their hymenopteran models, and insectivorous birds. One species, *Physoconops (Pachyconops) brachyrhynchus* (Macquart, 1843), was noted as having a different phenology from all other observed Batesian mimics, possibly due to its unique position as mimic and parasitoid. Unfortunately, the preferred host of this species is unknown. The role of conopids as valuable models to those studying the evolution of mimicry, would be enhanced if a robust phylogeny, including subfamilial and generic classification based on monophyly were available.

1.2. Previous systematic research on Conopidae

Important early taxonomic work on Conopidae was completed by Macquart (1834, 1835, 1840, 1843, 1846, 1851) in Europe; Aldrich (1905), Say (1823, 1829), Van Duzee (1927, 1934), and Williston (1882, 1883, 1885, 1888, 1892a, 1892b, 1893) in North America; and Brunetti (1912, 1923, 1925a, 1925b, 1925c, 1925d, 1929) in Africa and India. A number of works focusing on individual genera or restricted regions have been completed by Aldrich (1930); Banks (1916); Bohart (1938, 1941); Borges et al. (2008); Freeman (1966, 1968); Howell (1967); Kahaanpää (2007); Lopes (1937, 1938, 1971, 1972; Lopes & Monteiro, 1959); Maeta and Macfarlane (1993); Malloch (1919); Mei (1999, 2000; Mei & Stuke, 2008); Monteiro (1960); Nayar (1968); Newman (1841); Ôuchi (1939); Papavero (1970); Parsons (1940); Pearson (1974; Pearson & Camras, 1978); Rocha and Mello-Patiu (2009); Röder (1892a, 1892b); Smith (1959a, 1960); and Stuke (1996, 1997, 1999, 2000, 2002a, 2002b, 2003a, 2004a, 2004b, 2004c, 2005a, 2006a, 2006b, 2006c, 2007, 2008a, 2008b; Stuke & Barták, 2004; Stuke & Clements, 2005a, 2005b, 2008; Stuke & Kehlmaier, 2008; Stuke & Standfuss, 2007; Stuke et al., 2006a, 2006b, 2008). Schneider (2010) published a major revision of Australian species including 45 new species and five new genera.

Conopid fossils are limited to specimens from Green River Shale (Scudder, 1878) and Eocene Baltic amber (Meunier, 1899; Stuke, 2003b, 2005b). These fossil specimens were reviewed by Hennig (1966). Studies of immature stages and oviposition have been focused mainly on the unusual habits of the Stylogastrinae

(Kotrba, 1997; Rettenmeyer, 1961; Smith, 1967a; Smith & Cunningham-Van Someren, 1970, 1985).

Regional surveys and catalogues of Conopidae have been completed for China by Chen (1939); the New World by Curran (Curran, 1942); the former USSR by Zimina (1958, 1960, 1963, 1969, 1970, 1974, 1975) [all translated and summarized by Clements and Vincent (2001)]; the British Isles by Collin (1959) and Smith (1959b, 1969); Central Europe by Chvála (1961); the Neotropical region by Malloch (1933), Aczél (1950), and Papavero (1971); the Oriental region by Smith (1975); the Afrotropical region by Smith (1980); the Nearctic region by Parsons (1948) and Smith and Peterson (1987); the Palaearctic region by Chvála and Smith (1988); the Australasian region by Smith (1989) and Schneider (2010); and Central America by Skevington et al. (2010).

In addition to these papers, two authors represent the vast majority of the publications on Conopidae: Kröber (1913, 1914a, 1914b, 1914c, 1914d, 1914e, 1914f, 1914g, 1915a, 1915b, 1915c, 1915d, 1915e, 1915f, 1915g, 1915h, 1915i, 1916, 1919, 1925, 1927a, 1927b, 1928a, 1928b, 1928c, 1929a, 1929b, 1930, 1932, 1933, 1936a, 1936b, 1937, 1939a, 1939b, 1939c, 1939d, 1940a, 1940b) and Camras (1943, 1944, 1945a, 1945b, 1953a, 1953b, 1954, 1955a, 1955b, 1957a, 1957b, 1957c, 1957d, 1957e, 1960, 1961, 1962a, 1962b, 1963, 1965, 1966, 1967, 1976, 1979, 1981, 1989a, 1989b, 1992, 1994a, 1994b, 1996, 2000, 2001, 2004, 2007a, 2007b, 2007c; Camras & Chvála, 1984; Camras & Hurd, 1957; Camras & Parrillo, 1985, 1995). While both authors described many species from all regions of the

world over a long time-span, neither one attempted a phylogenetic analysis of the family.

Current catalogues offer a combined list of nearly 800 species of Conopidae, organized into four subfamilies and 56 genera. Zimina (1960, 1974) divided the subfamilies Conopinae and Myopinae into four tribes each based on species found in the former USSR. Subsequent workers have adopted this tribal classification with varying degrees of modification (Camras, 1965; Papavero, 1970; Smith, 1980; Smith & Peterson, 1987). The subfamily Stylogastrinae has been proposed as a separate family (Rohdendorf, 1964; Smith and Cunningham-Van Someren, 1985) based on its unusual biology, but this classification has been neither tested nor widely adopted. Likewise, Rondani (1856) elevated the genus *Zodion* to subfamily status based on the presence of a singly geniculate proboscis, yet few have acknowledged this ranking. Hennig's (1966) research on fossil specimens of *Palaeomyopa tertiaria* Meunier, 1912 includes a discussion of the monophyly of proposed subfamilies, the possible ancestral states for the family, and important morphological characters for future analysis. As such, it represents the only truly phylogenetic work done within the family to date.

1.3. Molecular and morphological methodology employed

1.3.1. DNA sequence-based phylogenetic analysis

Like morphological character states, DNA nucleotide sequence data can be used in a phylogenetic matrix analysis. Polymerase chain reaction (PCR) amplification followed by direct Sanger sequencing of PCR products (Sanger et al.,

1977) is currently the most common protocol for obtaining DNA sequence data for phylogenetic analysis. While early molecular phylogenetic studies included data from only small portions of single gene regions, there has been a trend of increasing number of both nucleotide characters and gene regions included in analysis. It is not conclusive in the present research which gene regions are most informative for answering phylogenetic questions at any given level. Studies comparing the phylogenetic information contained in different types of gene regions have been few (e.g., Almeida & Danforth, 2009; Baker et al, 2001) and have not yet focused strictly on Diptera.

DNA sequence data will be used in some of the phylogenetic analysis employed in this thesis. The successful amplification and sequencing of target gene regions depends on a number of factors including the gene region of choice and the relative quality of the specimen. Older specimens, or those prepared in a way likely to destroy DNA are not candidates for providing DNA sequence data using the current technology. For this reason, the older, pinned specimens included in the Chapter 5 analysis will be analyzed using only morphological data.

Even with carefully prepared specimens, obtaining informative DNA sequence data is sometimes difficult. Sequencing specimens from widely separate evolutionary lineages necessitates the use of universal PCR-amplification oligonucleotide primers (Palumbi, 1996). While these primers allow the amplification and sequencing of a target gene region for never-before-sequenced taxa, they introduce the possibility of producing non-specific PCR products. A new protocol for the isolation and purification of target PCR product from multiplex PCR

amplification products was developed in collaboration with Scott Kelso and Dr. Jeff Skevington of Agriculture and Agri-food Canada, Ottawa, Ontario. The results of a test of this new protocol are not included in this thesis (Gibson et al., 2010a). An alternative to purification is the development of taxon-specific PCR-amplification primers. In collaboration with Scott Kelso and Dr. Jeff Skevington, as well as Joel Kits, Morgan Jackson, and Gil Miranda of the University of Guelph, a review of nearly 400 existing Diptera-specific primers as well as the development of 94 new Diptera-specific primers was completed. The results of this research are not included in this thesis (Gibson et al., 2011). Many of the new primers developed were employed in producing DNA sequence data for Chapter 4.

1.3.2. Morphological phylogenetic analysis

The exemplar approach to phylogenetic analysis involves the use of individual specimens of chosen taxa as terminals to determine character states for phylogenetic analysis (Yeates, 1995). This method is chosen here over the groundplan approach, which determines character states from a theorized general condition of a broader taxon (e.g. genus) (Yeates, 1995). While the exemplar method is preferred, it does have some limitations. Of particular note is the necessity of both male and female specimens and intact specimens for analysis. For specimens that are missing a body part (e.g., both middle legs) or for which one gender is not available, some morphological characters must be coded as unknown. Also, for outgroup taxa, rather than including the supposed groundplan state for the

family they represent, character states are determined based on the species included in analysis.

Colour of body structures is often employed in identification keys and phylogenetic analyses of insects. Even highly distinctive colouration, however, can be highly variable within some species of Diptera (Costa et al., 2003; Holloway, 1993). Instances have been recorded where colouration is dependent on season and temperature (Costa et al., 2003; Martín-Vega & Baz, 2011). This is particularly emphasized in species with wide geographical ranges (Holloway, 1993). In Conopidae, especially, this has led to a number of species complexes that include two or three highly variable species and intermediate species described between them (e.g., Camras, 1953b). For this reason, colour-based morphological character states are used sparingly in this thesis. Only instances of non-variable colours (e.g., wing pattern) are used as the basis of phylogenetic comparison.

Size measurements of various anatomical structures are also commonly employed in identification keys and phylogenetic analyses of Diptera. While overall body length and absolute size of some structures are somewhat indicative of some genera of Conopidae, they are highly variable even within species. This may be due to the parasitoid nature of Conopidae. Past research has indicated that parasitoid body size is dependant on the size of the host (Kitthawee, 2000). To counteract the problem of variable absolute body measurements, only relative size comparisons between structures are used to determine morphological character states in this thesis.

The vast majority of previous authors have referred to the subfamily Stylogasterinae. Sabrosky (1999), however, notes that this is an alternate spelling of Kröber (1919) and that Stylogastrinae was the original spelling used by Williston (1885) in his description of the subfamily. Throughout this paper, the original spelling will be used.

1.4. Organization of thesis

The following chapters of this thesis each focus on an aspect of the evolutionary biology of Conopidae. The chapters are arranged in accordance with a deductive approach, moving from general topics to more specific examinations within Conopidae.

Chapter 2 focuses on the life history of Conopidae. This chapter includes data based on collections research and life history observations. Hilltopping behaviour is observed and recorded for species of Conopidae in the Ottawa area. Conclusions about the role of hilltopping as a mating strategy in the family are discussed.

Chapter 3 uses a molecular phylogenetic approach to investigate the relationship between Conopidae and other families of flies. Sequence data from ten gene regions are used as characters in parsimony and Bayesian analyses of relationships of flies in the group Schizophora.

Chapter 4 combines molecular and morphological data to construct a phylogenetic hypothesis for relationships between genera of Conopidae. Over 70 specimens representing 23 different genera and subgenera of Conopidae and seven

outgroup families are included for phylogenetic analysis. A dataset including sequence data from five gene regions and 113 morphological characters is used to draw conclusions about the monophyly of and relationships between subfamily groups within Conopidae.

In chapter 5, an expanded dataset of over 150 species representing all genera and subgenera is included in a morphological phylogenetic analysis. The resulting phylogenetic hypothesis is used as a basis for a revised classification of Conopidae. A dichotomous identification key to the world genera of Conopidae is included. Chapter 6 summarizes the conclusions of chapters 2 through 5, as well as states the overall conclusions of the thesis.

2. Hilltopping behaviour in species of Conopidae in the Ottawa area

2.1. Introduction

Hilltopping in insects, as initially defined by Shields (1967), is the behaviour of males aggregating on a peak to wait for the females that fly there in order to mate. In a paper dealing with some Conopidae from South Africa, Smith (1967b) reported an observation made by Stuckenberg on hilltopping behaviour in a species of *Pleurocerinella* Brunetti, 1923. Stuckenberg described a little swarm of these flies, consisting of males and females he had found clustering tightly together on a leaf “on the flat summit of a mountain”, and suggested that this behaviour could have had a sexual function. Gathering of Conopidae at a particular landmark, though not on a hilltop, has been reported also by Kröber, in a short note apparently unnoticed by later researchers (Kröber, 1927a). Hundreds of *Leopoldius coronatus* (Rondani, 1857) of both sexes were observed consecutively for a few days in Lautembach, a site near Gernsbach (Schwarzwald, Germany), in a forest path bend reached by the sun in the late afternoon. The *L. coronatus* were flying together along a small ditch filled with ferns and brambles but otherwise devoid of flowers, “[a place where I could have never expected to find conopids]” (Kröber, 1927a). Though matings were apparently not observed, a sexual function of the gathering seems the most likely.

The above mentioned observations, both relevant to species of the subfamily Conopinae, seem to be the only published evidence of hilltopping and swarming behaviour in this family of flies. Despite this, the phenomenon has been recognized

for some time. Label data on specimens in collections clearly indicate that some entomologists have noticed and collected these insects on hilltops for decades. Skevington (2008) suggests that hilltop collecting may be an effective way to survey many groups of insects, particularly parasitoids such as Conopidae, Pipunculidae, and Tachinidae.

In the present research, the phenomenon is elaborated upon and the first evidence of hilltopping in species belonging to the subfamilies Myopinae and Dalmanniinae is presented and discussed. Field observations and museum specimen examinations were conducted. These data are worthy of mention, considering the very poor knowledge we have of the life history and biology of these elusive Diptera. Furthermore, the present research, by adding new observational data on hilltopping and mating behaviour in parasitoid Diptera, will be of interest to those studying insect mating systems, parasitoid-host interactions, and hilltopping specifically.

2.2. Materials and methods

2.2.1. Mount Rigaud observational data

Mount Rigaud is a well-defined hill south of the Ottawa River in southwestern Quebec, Canada (45°27'59" N, 74°19'35" W). The hill is in a 5440 ha forested area that is dominated by *Acer saccharum* and *Fagus grandifolia*. This area of Quebec has a mosaic of farmland and forest but the location of the hilltop in a large tract of accessible forest makes it one of the most entomologically diverse hilltops in eastern North America (Skevington, 2008). The summit of Mount Rigaud is rocky and

largely open, with two thickets of stunted *Quercus rubra* (maximum height about 5 m) and shorter thickets of *Amelanchier humilis*, *Prunus pennsylvanica*, and *Prunus virginiana*. A viewing stand and large cross have been built on the summit, but the vegetation is still intact apart from these structures. This site was visited in the months of May to July 2008. Behaviour of individual flies was observed directly and captured specimens were collected with a hand net and deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes.

2.2.2. Data from insect collections

All data from Conopidae collected within 120 km of Ottawa, ON, Canada and represented in the CNC are summarized. Ottawa was chosen as a focal point because three hilltops in the vicinity have received annual collecting attention since 1961. The hilltops involved are King Mountain, QC (49°29'20" N, 75°51'45" W), Duncan Lake vicinity, Masham, QC (45°40'53" N, 76°3'1" W) and Mount Rigaud, QC.

2.3. Results

2.3.1. Ottawa area collection records

Nineteen species of Conopidae have been collected in the Ottawa area (Table 2.1). Three of these are regularly found on hilltops and are rarely found away from hilltop sites: *Myopa clausa* Loew, 1866, *Physocephala marginata* (Say, 1823), and *Physocephala sagittaria* (Say, 1823). A further four species have been collected regularly on hilltops, in addition to non-hilltops: *Dalmannia nigriceps* Loew, 1866, *Myopa vesiculosa* Say, 1823, *Zodion fulvifrons* Say, 1823 and *Zodion intermedium* Banks, 1916. Six species have been collected on hilltops, but more evidence is

needed to confirm hilltopping as a mating strategy for these species: *Dalmannia vitiosa* Coquillett, 1892, *Myopa virginica* Banks, 1916, *Physocephala furcillata* (Williston, 1882), *Physocephala texana* (Williston, 1882), *Thecophora occidentalis* (Walker, 1849) and *Thecophora nigripes* (Camras, 1945b). The remaining six species have no records of males collected on hilltops and are likely not hilltoppers: *Myopa vicaria* Walker, 1849, *Thecophora abbreviata* (Loew, 1866), *Thecophora longicornis* (Say, 1823), *Thecophora propinqua* (Adams, 1903), *Zodion abitus* Adams, 1903, and *Zodion americanum* Wiedemann, 1830.

The earliest specimens collected were a male *Zodion fulvifrons* on 13.v.1987 and a male *Physocephala texana* on 13.v.2008. The latest specimen taken was a male *Zodion americanum* on 25.ix.1985. The peak of the diversity on Rigaud is from late May to the end of June. Only two species seem to be common later in the season: *Physocephala furcillata* and *P. sagittaria* typically occur in July and August.

2.3.2. Observations on Mount Rigaud

Conopids were found at Mt. Rigaud on most visits. Perch site preference was noted for only a few of the species that occur at Mt. Rigaud. *Physocephala marginata* individuals are restricted to perching on a single *Prunus virginiana* bush, on a small area of exposed leaves 1.0 m above the ground. This shrub is at the very summit of the hill between the viewing platform and a patch of *Quercus rubra*. The site is in full sun for most of the day and is one of the most protected spots (i.e., lowest wind) on the summit. Specimens collected are generally replaced within five minutes by another specimen. *Myopa clausa* males seem to use a larger variety of perching sites

and are typically closer to the ground. They are often on the *Amelanchier* leaves, and appear to readily use sites in both direct sun and dappled light. Individuals of *Dalmannia nigriceps* have been collected at Mt. Rigaud on *Quercus* by Monty Wood. During a visit to Rigaud in June, 2008 it was found that the largest *Quercus* had been pruned of nearly all branches and that males of *Dalmannia nigriceps* could now be found perching on leaves of a nearby *Prunus virginiana* shrub at a height of 1.5m.

2.4. Discussion

Hilltopping is considered to be a strategy that facilitates mate-finding in insect species that are either rare and widely dispersed or dependent on sparsely distributed resources (Alcock, 1987; Skevington, 2008; Thornhill & Alcock, 1983). Many species of Conopidae apparently have very sparse populations and are very rarely seen, and more research may show that all but the most common conopids are engaged at least to some extent in hilltopping activity.

Of the nineteen conopid species found in the Ottawa area, only two might be considered common (Table 2.1). The CNC contains 59 specimens of *Physocephala furcillata* from over 30 sites in the region. Interestingly, only five specimens of this species have been taken on local hilltops, suggesting that it is either not a hilltopper or it may only use hilltopping as a mating strategy in rare instances, perhaps when population densities are low. *Zodion intermedium* follows a similar pattern, although another possible explanation for this species is given below. Although commonly encountered on hilltops, *Myopa clausa*, *Physocephala marginata*, and *Physocephala sagittaria* have rarely been collected away from hilltops. The species *Dalmannia*

nigriceps, *Myopa vesiculosa*, *Zodion fulvifrons*, and *Zodion intermedium* have been collected on hilltops at some point in the past, but not exclusively so. Also, it is almost entirely males of these species that have been collected on hilltops. These specimens may represent instances of facultative hilltopping in years of low population density (Skevington, 2008).

On the hilltops, males aggregate at locations that are species-specific and are occupied year after year with great consistency (e.g., Alcock & Kemp, 2006; Skevington, 2008; Wood, 1987, 1996). Species of *Myopa* on Mount Rigaud were found to choose perches close to the ground. The males have been almost invariably found at their specific “mating stations” (Chapman, 1954; Wood, 1987) during the period of the study. Similarly, *Physocephala marginata* is very specific in its site choice and is rarely encountered away from a single bush. *Dalmannia nigriceps*, on the other hand, may represent an instance of aggregation location shifting due to human interference.

Amongst truly hilltopping insects, the females are rarely encountered on hilltops, probably because they frequent the summit singly and only for the time necessary to select a mate. As a consequence, copulations are rarely observed (e.g., Alcock, 1987; Alcock & Kemp, 2006; Chapman, 1954; Dodge & Seago, 1954; Hansen, 2003; Wood, 1987). The present study is no exception, with females of eight species never observed on hilltops.

From the present research, hilltopping appears to be an important mating strategy in Conopidae. More research is required to understand why some species

hilltop and other species do not. It may be that non-hilltoppers are more likely to attack colonial Hymenoptera. Remaining near such a colony thus is more likely to ensure mating success than hilltopping. Species of conopids that have rare or less predictably distributed hosts may be more prone to using hilltopping as a mating strategy. For example, among the European species of *Dalmannia* Robineau-Desvoidy, *D. punctata* (Fabricius, 1794) is known to mate near the colonies of their host bee (Knerer, 1973), and has not been found on hilltops.

Zodion fulvifrons and *Zodion intermedium* have many variant forms and ranges covering the entire southern half of the Nearctic region (Camras and Hurd, 1957). The present data indicates that both species are often, but not exclusively collected on hilltops in the Ottawa area (Table 2.1). These two species may represent a species complex. Further study may help to unravel the taxonomy of these taxa by showing that some of these forms hilltop while others do not. Research on the systematics and ecology of conopids will certainly benefit from future efforts that focus on hilltop collecting and observation.

Thirteen species have been collected on the summit of Mt. Rigaud (Table 2.1). This partly emphasizes the significance of hilltops but also suggests that many more species from other regions will be found hilltopping if the effort is made to document them. It also illustrates how important hilltops are when conducting a survey of parasitoid flies in a region. Furthermore, a loss of hilltop habitats to human development will likely endanger many rare insect species.

3. Placement of Conopidae (Diptera) within Schizophora based on mtDNA and nrDNA gene regions

3.1. Introduction

Conopidae are typically organised into four subfamilies: Conopinae, Dalmanniinae, Myopinae, and Stylogastrinae (e.g., Chvála & Smith, 1988; Smith, 1989). The subfamily Stylogastrinae has been proposed as a separate family (Rohdendorf, 1964; Smith & Cunningham-Van Someren, 1985) based on its unusual biology and distinct morphology. Within the subfamily Myopinae, the tribe Zotionini has been proposed as a separate subfamily based on its singly geniculate proboscis (Hendel, 1936; Rondani, 1856). These proposed changes to the classification of Conopidae have been neither widely accepted nor tested phylogenetically.

Early classifications placed Conopidae within Syrphoidea based on adult morphological similarities (reviewed in De Meijere, 1904). The presence of a ptilinum in Conopidae, however, refutes this hypothesis, as two independent origins of this structure seem unlikely. The ptilinum is a complex facial structure that helps with eclosion from the puparium (Hennig, 1973). A single lineage with a synapomorphic ptilinum ("Schizophora") is a more likely explanation (McAlpine, 1989). The question of how Conopidae is related to the remaining schizophoran families, however, has been the source of some debate.

Enderlein (1936) proposed Conopidae as sister to the remaining schizophoran flies ("Muscaria"). Hennig (1958, 1966, 1971) supported this

conclusion but noted a lack of unequivocal synapomorphies for “Muscaria”. A recent hypothesis based on morphological analysis (Korneyev, 2000; McAlpine, 1989) is that the sister group to Conopidae is within one of two schizophoran superfamilies: Tephritoidea or Diopsoidea (Fig. 3.1). Two recent studies (Han & Ro, 2005; Han et al, 2002) include representatives of Conopidae in molecular phylogenetic analyses of Tephritoidea. Both of these studies place Conopidae+Diopsidae as sister to remaining schizophoran exemplars (Fig. 3.1). Thus, at least two competing hypotheses are present for the placement of Conopidae within Schizophora. Determining support for one of these hypotheses, or an alternate hypothesis, is necessary for future phylogenetic work within schizophoran groups. Whatever the placement of Conopidae may be it will help to establish a ground plan for characters within Schizophora. In Hennig’s (1971) approximation, the placement of Conopidae, represented one of the two most pressing issues in Schizophoran systematics, the other being the uncertain monophyly of the two schizophoran subgroupings, Acalyptratae and Calyptratae.

A review of dipteran phylogenetics (Yeates & Wiegmann, 1999) emphasizes the need for superfamily-level relationships within Schizophora and Acalyptratae to be clarified through the use of new approaches. In both previous molecular phylogenetic studies including Conopidae specimens (Han & Ro, 2005; Han et al, 2002), the authors admit a lack of sufficient ingroup and outgroup sampling and conclude that the sequencing of further genes, including nuclear protein-coding genes, is necessary for future dipteran molecular phylogenetic studies. Other researchers (Collins & Wiegmann, 2002a, 2002b; Kutty et al, 2008; Moulton & Wiegmann, 2004, 2007; Petersen et al, 2007;

Wiegmann et al, 2000; Winterton et al, 2007) have utilized DNA sequences as characters in phylogenetic analyses of Diptera at the family or superfamily level. It should be noted, however, that each of these studies focused on a single family or superfamily ingroup and were not intended as comprehensive analyses of dipteran, schizophoran, or acalyptrate relationships as a whole. There has been a trend of both increasing number of nucleotide characters and increasing percentage of phylogenetically-informative characters. There exists, however, a lack of overlap in genes of choice that significantly hampers the future possibility of data combination. The nuclear ribosomal gene, 28S, appears to be the only gene approaching universal usage in dipteran phylogenetic studies.

Two previous studies (Petersen et al, 2007; Winterton et al, 2007) compared the phylogenetic information contributed by the genes used in their studies using partitioned Bremer support (PBS) values. Cameron et al (2007) used complete mitochondrial genomes of a number of Diptera to assess the relative informative value of all mitochondrial gene sequences. There is, however, no consensus as to which genes, either mitochondrial or nuclear, provide the highest phylogenetic signal at a given level of divergence within the Diptera. Especially lacking has been the determination of which gene(s) have evolved on a timescale that comprise sufficient levels of phylogenetically informative changes to adequately resolve the radiation of Schizophora. While comparisons of the phylogenetic utility of mitochondrial versus nuclear gene sequence characters (e.g., Baker et al, 2001; Light & Reed, 2009; Lin & Danforth, 2004) and ribosomal versus protein-coding gene sequence characters (Almeida & Danforth, 2009;

Danforth et al, 2005; Mueller, 2006) have been completed for other animal groups, such a comparison using dipteran examples is necessary.

The primary purposes of this chapter are to test the hypothesis of a monophyletic Conopidae and to test past hypotheses for the placement of Conopidae within Schizophora. To this end, a selection of taxa representing all five proposed conopid subfamilies are presently examined using molecular phylogenetic techniques. In addition, exemplar specimens of seventeen dipteran families representing eight schizophoran lineages and three non-schizophoran lineages (*sensu* Woodley et al, 2009) are included to determine the sister group to Conopidae (Table 3.1). The determination of this sister group will facilitate future morphological and molecular research on the phylogenetic relationships within Conopidae as well as within Schizophora and Acalyptratae.

Another purpose of this chapter is to determine the comparative utility of currently-used and newly-developed mitochondrial and nuclear gene sequences as molecular characters for phylogenetic studies of dipteran families and of Conopidae in particular. To this end, DNA sequences from a total of eleven genes, including mitochondrial genes, nuclear genes, ribosomal genes, and protein-coding genes are examined: 12S ribosomal DNA (12S), cytochrome c oxidase subunit I (COI), cytochrome b (CytB), 28S ribosomal DNA (28S), the carbamoyl phosphate synthetase region of CAD (CAD), elongation factor-1 α (EF-1 α), *white*, *wingless*, alanine-tRNA synthetase (AATS), triose phosphate isomerase (TPI), and phosphogluconate dehydrogenase (PGD).

3.2. Materials and methods

3.2.1. Taxon sampling

Exemplars of ten species of Conopidae, representing all five putative subfamilies of Conopidae, (Conopinae, Dalmanniinae, Myopinae, Stylogastrinae, and Zodioninae) are included in the present analysis (Table 3.1). Also included are eighteen specimens from seventeen other dipteran families. These families serve as representatives of ten superfamilies. *Heterophlebus versabilis* (Collin, 1933) (Brachystomatidae) is used to root all trees.

3.2.2. DNA extraction and amplification

Total genomic DNA was extracted from whole specimens using a DNeasy® Tissue kit (Qiagen Inc., Santa Clara, CA, USA). Following extraction, specimens were critical-point dried and deposited as vouchers in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC).

For genes amplified using *Taq* polymerase (Table 3.2), DNA amplifications were carried out in 25µL reactions with 17µL ddH₂O, 2.5µL 10X PCR buffer, 2.5µL 25mM MgCl₂, 0.5µL of each 10µM primer, 0.5µL 10µM dNTPs, 0.5 µL *Taq* DNA polymerase (Promega Corp., Madison, WI, USA), and 1 µL genomic DNA template. For genes amplified using ExTaq polymerase, DNA amplifications were carried out in 25µL reactions with 16.75µL ddH₂O, 2.5µL 10X ExTaq PCR buffer (containing 20mM MgCl₂), 0.625µL 25mM MgCl₂, 1µL of each 10µM primer, 2µL 10µM dNTPs, 0.125 µL ExTaq HS DNA polymerase (Takara Bio USA, Madison, WI, USA), and 1 µL

genomic DNA template. Amplification cycles were performed on an Eppendorf ep Gradient S Mastercycler (Eppendorf AG, Hamburg, Germany). For amplification cycle details for each primer pair, please see Gibson et al. (2010) supplementary material.

3.2.3. DNA sequencing and editing

Amplification products and negative controls were visualized on 1% agarose electrophoresis gels and purified for sequencing using either a QIAquick Gel Extraction kit® (Qiagen Inc., Santa Clara, CA, USA) or an ExoSAP-IT® protocol (USB Corp., Cleveland, OH, USA). Sequencing of purified products was performed at the Agriculture & Agri-Food Canada, Eastern Cereal and Oilseed Research Centre Core Sequencing Facility (Ottawa, ON, Canada). Sequencing reactions were carried out in a volume of 10µL and used an ABI BigDye® Terminator v3.1 Cycle Sequencing kit (PE Applied Biosystems, Foster City, CA, USA). Sequencing reactions were purified using the ABI ethanol/EDTA/sodium acetate precipitation protocol and analysed on an ABI 3130xl Genetic Analyzer (PE Applied Biosystems, Foster City, CA, USA). All sequence chromatograms were edited and contigs formed using Sequencher 4.7 (Gene Codes Corp., Ann Arbor, MI, USA).

3.2.4. Sequence alignment

3.2.4.1. Ribosomal genes

ClustalX (Thompson et al., 1997) with default settings was used to produce an alignment for 12S. 28S was aligned by hand according to the secondary structure model proposed by Kjer et al. (Kjer et al., 1994) for *Aedes albopictus* (Skuse, 1894)

and by Hancock et al. (1988) for *Drosophila melanogaster* Meigen, 1830. The region amplified corresponds to almost the entire length of the 28S gene. Expansion segments that matched the location of those listed by Kjer et al. (1994) and Hancock et al. (1988) were identified for the 28S matrix. While ten of these expansion segments could be aligned across all taxa, the three largest segments (D2, D8, and D10 – 946 base pairs (bp) in total) could not be unambiguously aligned and were excised from the matrix.

3.2.4.2. Protein-coding genes

The remaining genes are protein-coding and were aligned manually according to translated amino acid codons with the following notes. For CAD, the region amplified corresponds to the entire carbamoyl phosphate synthetase region (CPS) of the CAD gene (Moulton & Wiegmann, 2004). Three introns were identified, occupying positions 871-1041, 1147-1245, and 4042-4112 in the present alignment. They were excluded from analysis. For PGD, one intron corresponding to position 538-610 in the present alignment was identified and excised from the matrix prior to analysis. For TPI, a 50 bp intron located at position 179-229 of the present matrix was identified for only one taxon, *Heterophlebus versabilis* (Brachystomatidae). It was excluded from the analysis. The *white* sequence amplified corresponds with the 3' end of exon 3 (Bennett & Frommer, 1997). The final ~150 bp of all sequences were hypervariable and unalignable. This segment corresponds to the 5' end of intron 3 and was excluded from analysis.

3.2.5. Parsimony analyses

Parsimony analyses were conducted using PAUP* 4.0 (Swofford, 2003). All characters were treated as unordered. An heuristic search with tree bisection-reconnection (TBR) branch swapping in a random stepwise addition of taxa was repeated 100 times. Two weighting schemes, the first with equal weighting and the second with the third codon position (nt3) weighted to zero, were explored for the combined data set. Likewise, gaps were treated as either missing or as a fifth state for the combined dataset. For all individual genes and concatenation subsets, nt3 were weighted to zero and gaps were treated as a fifth state. Node support for individual genes and all concatenations was determined by jackknife resampling with 36% of characters excluded and 100 random replicates. PBS values for the combined dataset (nt3 weighted to zero, gaps as fifth state) were calculated for each gene partition using TreeRot v3 (Sorenson & Franzosa, 2007) and PAUP* 4.0 (Swofford, 2003) using an heuristic search and 100 random replicates. Topological congruence between the most parsimonious tree(s) of concatenated subsets and the most parsimonious tree of the total evidence dataset was calculated with the Congruent Topological Information (CTI) statistic of Almeida and Danforth (2009). This statistic gives the proportion of nodes in the most parsimonious total evidence tree recovered by the most parsimonious tree(s) of a given subset.

3.2.6. Bayesian analysis

Models of evolution were determined based on the Akaike Information Criterion (AIC) for each gene partition separately using ModelTest 3.7 (Posada &

Crandall, 1998). Bayesian analyses on the total evidence dataset were conducted using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) with a Markov Chain Monte Carlo (MCMC) method. The dataset was partitioned into ten genes and parameter estimation was unlinked for each gene partition. Four chains (three hot, one cold) were run simultaneously for 20,000,000 generations. Trees were sampled every 1000 generations and each simulation was run twice. The MCMC chains achieved stationarity (standard deviation of split frequencies <0.01; all parameter estimates asymptotic) at 316,000 generations. Following the discard of the first 316 samples as burn-in, 19,685 samples were used for each simulation to generate a majority-rule consensus tree, posterior probabilities for each node, and branch length estimates.

3.3. Results

3.3.1. wingless

The *wingless* gene has been used successfully in past phylogenetic analyses of schizophoran flies (e.g., Baker et al., 2001; Kotrba & Balke, 2006; Marshall et al., 2009). A pair of primers used in an analysis of Vespoidea (Hymenoptera) (Pilgrim et al., 2008) was chosen to amplify the gene for the present taxa (Table 3.2). In total, ~130bp at the 5' terminus and ~200bp at the 3' terminus were alignable for all taxa. The central 800bp of sequence was unalignable across all taxa. Some individual taxa included multiple ~100bp introns. Furthermore, a BLAST search of the recovered *wingless* sequences revealed similarities to widely disparate taxa from Orthoptera to Lepidoptera to Hymenoptera for most sequences. Also, four sequences revealed a

similarity to the *wnt-4* gene. This result speaks to the established orthologous nature of the *wingless* gene. With up to five different orthologs likely present in the dipteran genome (Sidow, 1992), homology cannot be established with any confidence and all data from *wingless* were excluded from further analysis.

3.3.2. Individual gene sequence characteristics and parsimony analyses

Gene segments were successfully amplified and sequenced for between 20 (PGD) and 28 (12S and 28S) taxa for each gene (Tables 3.1 and 3.3). The lengths of the sequences included in analyses range from 374bp (12S) to 3824bp (CAD) (Table 3.3). The percentages of characters that are constant range from 30.4% (PGD) to 69.9% (28S). The percentages of characters that are phylogenetically informative range from 17.4% (28S) to 62.9% (PGD). Base frequencies reveal an A/T bias in all genes, ranging from 52% (*white*) to 76.9% (12S). Base frequencies are heterogeneous across all taxa for each of the eight protein-coding genes ($\chi^2 > 88.8$, $p < 0.05$). Base frequencies are homogeneous across all taxa for each of the two ribosomal genes ($\chi^2 < 55$, $p > 0.05$). The shape parameter of the gamma distribution (α), as calculated by ModelTest 3.7, ranges from 0.233 (COI) to 0.858 (CAD).

Parsimony analysis recovered between one (28S, AATS, *white*) and 56 (EF-1 α) most parsimonious trees for each gene (all trees not shown). Lengths of shortest trees range from 213 (EF-1 α) to 3158 (28S) (Table 3.3). Consistency Index (CI) values for most parsimonious trees range from 0.414 (COI) to 0.563 (EF-1 α). Retention Index (RI) values for most parsimonious trees range from 0.369 (COI) to 0.581 (EF-1 α). Also

included in Table 3.3 are PBS values and jackknife support (JKS) values for each gene and for each node concordant with a node in the most parsimonious total evidence tree (Figure 3.2: nt3 weighted to zero; gaps coded as fifth base).

3.3.3. Concatenated sequence subset characteristics and parsimony analyses

Concatenated subsets were analysed for mitochondrial DNA (mtDNA - COI, cytB, and 12S), nuclear DNA (nrDNA - 28S, AATS, CAD, EF1a, PGD, TPI, and *white*), ribosomal DNA (rDNA - 12S and 28S), and protein-coding DNA (PCG - COI, cytB, AATS, CAD, EF1a, PGD, TPI, and *white*). For each subset analyzed all taxa were included and between 2587 (mtDNA) and 10211 (nrDNA) base pairs were included in analysis (Table 3.3). The percentage of characters that are constant range from 47% (PCG) to 66.8% (rDNA). The percentage of characters that are phylogenetically informative range from 20% (rDNA) to 45.4% (PCG). Base frequencies reveal an A/T bias in all subsets, ranging from 56.3% (nrDNA) to 64.2% (mtDNA). Base frequencies are heterogeneous across all taxa for mtDNA, nrDNA, and PCG ($\chi^2 > 645$, $p < 0.01$). Base frequencies are homogeneous across all taxa for rDNA ($\chi^2 = 52.2$, $p = 0.995$). The shape parameter of the gamma distribution (alpha), as calculated by ModelTest 3.7, ranges from 0.524 (rDNA) to 0.557 (mtDNA).

Parsimony analysis recovered either one (mtDNA, rDNA, PCG) or three (nrDNA) most parsimonious trees (all trees not shown). Lengths of shortest trees range from 2436 (mtDNA) to 7713 (nrDNA) (Table 3.3). Consistency Index (CI) values for most parsimonious trees range from 0.408 (mtDNA) to 0.485 (nrDNA). Retention Index (RI) values for most parsimonious trees range from 0.334 (mtDNA) to 0.394 (nrDNA). Also

included in Table 3.3 are PBS and JKS values for each subset and for each node concordant with a node in the most parsimonious total evidence tree (Figure 3.2: nt3 weighted to zero; gaps coded as fifth base).

3.3.4. Total evidence parsimony analysis

The complete dataset with all ten genes included comprises 28 taxa and 12798 characters (Table 3.3). Of these characters, 6753 (52.8%) are constant and 4861 (38.0%) are phylogenetically informative. Nucleotide frequencies (A=29.4%, C=18.5%, G=23.5%, and T=28.6%) reveal an A/T bias common to insect genomes. Base frequencies are heterogeneous across all taxa ($\chi^2=140.891$, d.f.=81, $p<0.000$). With gaps coded as a fifth base and nt3 weighted to zero, a single most parsimonious tree was found with a length of 10,204 (CI=0.464, RI=0.373) (Figure 3.2). This tree is well supported with JKS values above 50% for all but two nodes and values of 100% for ten nodes. Total Bremer support (TBS) values are likewise high (>5) for all nodes but one. Conopidae is recovered as monophyletic (Figure 3.2; node 9) with high support values (TBS=19; JKS=95). Three pairs of congeners within Conopidae (*Dalmannia* node 2; *Zodion* node 5; *Stylogaster* node 8) as well as each of the other two conopid subfamilies (Conopinae node 1; Myopinae node 4) are all recovered as monophyletic with high levels of support (TBS>30; JKS=100). Schizophora, likewise, is recovered as monophyletic (node 21) with high support values (TBS=20; JKS=99). Schizophora excluding Conopidae is recovered as monophyletic (node 20) with weak support values (TBS=9; JKS=65). Two representatives of Lauxaniidae are recovered as monophyletic (node 12) with high support values (TBS=60; JKS=100).

Acalyptratae is recovered as paraphyletic with respect to the sole representative of Calyptratae (Muscidae: *Spilogona* sp.). Of superfamilies proposed by McAlpine (1989) for which multiple exemplars are included, only Syrphoidea (node 22) is recovered as monophyletic (TBS=10; JKS=83).

A plot of uncorrected pairwise divergence at nt1 and nt2 versus uncorrected pairwise divergence at nt3 for the entire dataset (not shown) shows a plateau in sequence divergence in nt3 corresponding to approximately 6% sequence divergence in nt1 and nt2. This plateau corresponds to the divergence within subfamilies of Conopidae and suggests saturation of substitutions in nt3 beyond this level.

Parsimony analysis with gaps coded as missing recovered two most parsimonious trees (treelength=9,262, CI=0.460, RI=0.372), but with reduced JKS values at all nodes. Analysis with equal weights for all characters and gaps coded as a fifth base recovered a single most parsimonious tree (treelength=27,194, CI=0.388, RI=0.317), also with JKS values reduced for most nodes. Analysis with equal weights for all characters and gaps coded as missing recovered a single most parsimonious tree (treelength=26,213, CI=0.385, RI=0.316), also with JKS values reduced for most nodes (Table 3.3). Topologies for these alternate analyses (not shown) differed from the tree shown in Figure 3.2. All key clades (i.e., Conopidae, Conopinae, *Dalmannia*, Myopinae, *Zodion*, *Stylogaster*, Lauxaniidae, Schizophora) were recovered as monophyletic in each alternate analysis.

3.3.5. *Subset congruence analysis*

Most parsimonious trees of concatenated subsets based on gene type (mtDNA, nrDNA, rDNA, and PCG) recovered varying degrees of congruence with the total evidence most parsimonious tree (Figure 3.4). mtDNA recovered 32% of nodes overall, but this was divided between 78% of nodes within Conopidae and just a single node (6%) outside of Conopidae. nrDNA recovered 64% of nodes overall, 67% of nodes within Conopidae, and 63% of nodes outside of Conopidae. rDNA recovered 64% of nodes overall, 67% of nodes within Conopidae, and 63% of nodes outside of Conopidae. PCG recovered 52% of nodes overall, 78% of nodes within Conopidae, and only 38% of nodes outside of Conopidae.

3.3.6. *Bayesian analysis*

The tree recovered by Bayesian analysis differs from that of the parsimony analysis and has 100 percent posterior probabilities (PP) at 20 of 25 nodes (Figure 3.3). Conopidae are recovered as monophyletic (PP=100). Congeners within Conopidae as well as each of the other two conopid subfamilies are all recovered as monophyletic, all with 100 percent posterior probabilities. Lauxaniidae and Schizophora are both recovered as monophyletic (PP=100). Schizophora excluding Conopidae is not recovered as monophyletic. Instead, Conopidae+Lauxaniidae is recovered (PP=100). Acalyptratae is recovered as paraphyletic with respect to the sole representative of Calyptratae (Muscidae: *Spilogona* sp.). None of the superfamilies proposed by McAlpine (1989) for which multiple exemplars are included are recovered as monophyletic.

3.4. Discussion

3.4.1. Total evidence and the preferred trees

Recovery and strong support for the monophyly of previously defined taxonomic groups has been suggested as a measure of the strength of a dataset (Wild & Maddison, 2008; Winterton et al., 2007; Yoder et al., 2001), and this method is employed here. Specifically, recovery of congeneric and confamilial nodes with high support values is taken as evidence of a well-resolved tree. The parsimony tree based on the total evidence dataset, with nt3 weighted to zero and gaps coded as a fifth base (Figure 3.2) recovers and strongly supports genera within Conopidae (*Dalmannia*, *Zodion*, and *Stylogaster*) and a family within Schizophora (Lauxaniidae). The Bayesian analysis tree based on the total evidence dataset, with model parameters for each gene estimated individually (Figure 3.3) recovers all of the same nodes with high support. No individual gene, data subset, or alternate analysis recovers these key nodes with the same level of support (Table 3.3). This result supports previous research (e.g., Cameron et al., 2007; Mitchell et al., 2000) indicating that combined molecular datasets will produce more accurate and better-supported trees than individual gene trees. As such, all genes analyzed are included in the final total evidence analysis.

3.4.2. Phylogeny of Schizophora

The monophyly of Schizophora has been established by a number of morphological analyses (Cumming et al., 1995; Griffiths, 1972; McAlpine, 1989) and synapomorphies for the group have been proposed, including the presence of the

ptilinum and complete rotation of the male genital capsule within the puparium. Our data supports monophyly of Schizophora with high TBS, JKS, and PP values (Figs. 3.2 and 3.3).

Schizophora has been historically divided into two subgroupings, Calyptratae and Acalyptratae. While Calyptratae have a number of generally-accepted synapomorphies (McAlpine, 1989), the monophyly of Acalyptratae has been a source of controversy. Morphological analyses (Griffiths, 1972; McAlpine, 1989) suggest little or no support for a monophyletic Acalyptratae. Some molecular analyses (Cameron et al., 2007; Collins & Wiegmann, 2002b; Han & Ro, 2005; Han et al., 2002) have recovered Acalyptratae as paraphyletic with respect to Calyptratae. Other studies (Junqueira et al., 2004; Moulton & Wiegmann, 2004) have recovered Acalyptratae as monophyletic. The focus of all of these studies, however, was on resolving family-level or lower relationships and not the relationships of Acalyptratae overall. As such, they did not include exemplars from across all acalyptrate superfamilies. Considering the broad family-level diversity of Acalyptratae, these studies should not be considered comprehensive molecular analyses of acalyptrate phylogeny (Woodley et al., 2009). The present study, including eleven of 65 acalyptrate families and seven of ten acalyptrate superfamilies (*sensu* McAlpine, 1989), represents the largest single sampling of acalyptrate diversity to date, but is still far from comprehensive. Further sampling from still more acalyptrate families will be necessary to resolve the question of acalyptrate monophyly.

Enderlein (1936) first proposed a sister-group relationship between “Archischiza” (Conopidae) and “Muscaria” (the remaining Schizophora). Hennig (1958) elaborated on Enderlein’s classification. In his opinion, autapomorphies of Conopidae include a parasitoid lifestyle, peculiar posterior spiracles in the larva, a specialized proboscis, and the development of the female fifth sternite into a theca. Hennig is not clear as to the placement of Stylogastrinae as the females of this subfamily do not possess a theca. Hennig could propose only two vague synapomorphies for Muscaria: a relatively longer anal cell and relatively longer femora of the ptilinal suture. In addition, the number of synapomorphic characters of the Conopidae that actually represent plesiomorphies of the Schizophora was not speculated. Subsequent research placed Conopidae as near to Tephritoidea (Korneyev, 2000) or Diopsidae (Han & Ro, 2005), although placement of the Conopidae was not the goal of these studies.

The sister group relationship between Conopidae and Diopsidae as proposed by Han et al. (2002) and Han and Ro (2005) cannot be directly tested with the data presented here. Rejection of this proposed relationship is possible based on the inclusion of two other members of Diopsoidea (Psilidae: *Chyliza scrobiculata* and Strongylophthalmyiidae: *Strongylophthalmyia angustipennis*). These taxa cluster together and are well-removed from Conopidae in both parsimony and Bayesian analyses (Figs. 3.2 and 3.3). Likewise, no members of Tephritoidea are recovered as possible sister to Conopidae.

The present data are equivocal on the nearest sister group to Conopidae. The preferred parsimony tree (Fig. 3.2) supports the original conclusions of Enderlein and Hennig, with Conopidae as sister to the remaining Schizophora ("Muscaria"). Support for the "Muscaria" clade, however, is weak. This clade is not recovered with high support in any other parsimony analysis. Bayesian analysis recovers a sister group relationship between Conopidae and Lauxaniidae with high support (PP=100). This is a novel hypothesis for the placement of the Conopidae. The topology of the preferred parsimony tree, while not including a Conopidae+Lauxaniidae clade, does entertain the possibility of such a relationship. If three of the most weakly supported nodes (13, 14, and 20) were to be collapsed, a polytomy would be formed that would include Lauxaniidae as one of four possible sister clades to Conopidae. The present study is the first molecular analysis, and the only one of any kind besides McAlpine (1989) and Wiegmann et al. (2011), to include representatives of both Lauxaniidae and Conopidae. McAlpine's (1989) hypothesis proposes the closest superfamilies to Lauxanioidea as Sciomyzoidea, Carnoidea, and Opomyzoidea (Fig. 3.1), none of which are included in the present study. The recent FLYTREE analysis (Wiegmann et al., 2011) includes morphological and molecular data from over 150 fly families and places Conopidae within Sciomyzoidea, thus supporting the results of this chapter. Further sampling of these groups will help to further elucidate the relationships within this branch of Schizophora.

3.4.3. Monophyly of Conopidae

Working only with Neotropical species, Rohdendorf (1964) proposed *Stylogaster* as a separate family. Smith and Cunningham-Van Someren's (1985) research, including Nearctic, Oriental, Afrotropical, and Australasian species, agreed with the family status of Stylogastridae. Non-aculeate host biology and unique larval structure are cited as support for separate family status. It is noted, however, that complete data on these features for all Conopidae (s.s.), especially Dalmanniinae, is lacking. Hennig's (1966) analysis of the fossil specimens of Conopidae concluded that, based on their likely age of divergence, Stylogastridae and Conopidae (s.s.) are as valid as family classifications as many other recognised Acalyptrate families. Smith and Peterson (1987) considered similarities between *Stylogaster* and Dalmanniinae strong enough to warrant the maintenance of Stylogastrinae as a subfamily within the Conopidae. All of these past studies have suggested a sister group relationship between *Stylogaster* (either as family or subfamily) and the remaining Conopidae.

In the present analysis, Conopidae (including *Stylogaster*) are recovered as monophyletic (Figs. 3.2 and 3.3), with high TBS, JKS, and PP values. It is also noted that all alternate analyses and data subsets recover the Conopidae as monophyletic. Each of the five proposed subfamilies within Conopidae are recovered as monophyletic with high PBS, JKS, and PP values in all analyses. *Stylogaster* could clearly be elevated to family status as a monophyletic sister to Conopidae (s.s.) However, I do not support the proliferation of family group names within

Schizophora and suggest maintaining *Stylogaster* as a subfamily within Conopidae. This classification maintains a clear link between these lineages and highlights the relationship between *Stylogaster* and other conopids. Relationships between conopid subfamilies show weak support in the preferred parsimony tree, but high PP values in the Bayesian tree. These relationships vary in alternate analyses (not shown). A revision of classification within Conopidae awaits a larger analysis including representatives of as many genera as possible.

3.4.4. Mitochondrial DNA vs. nuclear DNA

Past research has drawn direct comparisons between the phylogenetic utility of mitochondrial and nuclear DNA sequence data (Baker et al., 2001; Light & Reed, 2009; Lin & Danforth, 2004). In these studies, mtDNA and nrDNA were compared based on levels of support for nodes on total evidence trees, CI values, and degree of heterogeneity in among-site rate variation (“alpha”). Specifically, recovery of congruent nodes with large support values, large CI values, and large “alpha” values are considered signs of an informative gene or gene subset. The general conclusion has been that mtDNA is of less phylogenetic value than nrDNA for determining family-level relationships. At deep nodes it provides little or contradictory information and is suited only to shallow (i.e., species- and genus-level) analysis.

Our data subset of seven nrDNA genes recovers all key nodes (i.e., nodes 2, 5, 8, 12) with high PBS and JKS values (Table 3.3). The data subset of three mtDNA genes offers weak support for the monophyly of *Zodion* (node 5). Likewise, the nrDNA dataset produces a higher Consistency Index (CI) than the mtDNA.

Furthermore, the lowest CI of any of the nuclear genes (TPI) is higher than the highest CI of the mitochondrial genes (cytB). Both mtDNA and nrDNA exhibit heterogeneous base composition across taxa ($\chi^2 > 273$, $p < 0.01$ and $\chi^2 > 646$, $p < 0.01$ respectively). Unexpectedly, the mtDNA dataset has a larger mean “alpha” value (0.557) than does the nrDNA dataset (0.538). This contradictory result can be explained by a closer examination of the mitochondrial genes. One gene, COI, has an exceptionally low “alpha” value. The other two mtDNA genes perform at average or above average levels in this and other measures, with the exception of support for nodes outside of Conopidae. Calculated CTI values (Fig. 3.4) confirm these results, with mtDNA recovering more congruent nodes within Conopidae and nrDNA recovering more congruent nodes overall and outside of Conopidae. Our data suggests that the mitochondrial genes tested are of lesser value for family-level and higher problems, yet may be quite useful within a more closely related taxon set (i.e., genus and species level).

3.4.5. Ribosomal DNA vs. protein-coding DNA

Previous attempts to compare the phylogenetic utility of ribosomal genes to that of protein-coding genes (Almeida & Danforth, 2009; Cameron et al., 2007; Danforth et al., 2005; Mueller, 2006) found that there was little difference in the value of the two sets of genes. Ease of alignment (coding genes) and presence of universal primers (rDNA) were found to be the main means of preferring one set of genes to the other.

Our data subset of two rDNA genes recovers all key nodes with high PBS and JKS values (Table 3.3). The data subset of eight PCG offers contradictory Bremer support for the monophyly of *Zodion*. At the deepest nodes (i.e., 23 and 25), only the rDNA subset provides any support. The rDNA dataset produces a most parsimonious tree with a nearly equal CI to that of the PCG dataset. The PCG dataset has a mean “alpha” value (0.549), higher than that of the rDNA dataset (0.524), but with a much wider range of values within the included genes (0.253-0.858). These values suggest that neither dataset subset is clearly superior. Calculated CTI values (Fig. 3.4) confirm these results, with PCG recovering slightly more congruent nodes within Conopidae and rDNA recovering more congruent nodes overall and outside of Conopidae.

Other values to be noted are the proportion of constant and informative sites and the degree of heterogeneity of base frequencies among taxa. The rDNA dataset includes nearly 70% constant characters and only 20% of characters phylogenetically informative. This is in stark contrast to the PCG dataset (47% and 45%, respectively). One gene seems to explain this discrepancy. The 28S ribosomal DNA sequence provides a large proportion of the Bremer support at nearly every node yet includes only 17% informative characters. Likewise, combined and individually, the ribosomal genes exhibit homogeneous base frequencies among taxa. This would suggest that 28S and 12S are of equal value to protein-coding genes for dipteran phylogenetic research. Further analysis will reveal the regions

that are most phylogenetically informative and the regions that are identically conserved across diverse dipteran lineages.

3.4.6. Conclusions

Analysis of the current dataset allows a number of phylogenetic conclusions to be drawn. The monophyly of Schizophora, Conopidae (including *Stylogaster*), and each of the five hypothesised subfamilies of Conopidae are strongly supported. Paraphyly of Acalyptratae with respect to Calyptratae is supported, although sampling of more calyptrate families and of the remaining acalyptrate superfamilies is necessary. A sister-group relationship between Conopidae and the remaining Schizophora ("Muscaria" *sensu* Enderlein, 1936) is supported in parsimony analyses. Bayesian analysis suggests that Conopidae+Lauxaniidae is sister to the remaining Schizophora. Closer examination of both analyses reveals that this latter relationship, though surprising, is supported by our data. Lauxaniidae has not yet been offered as a possible sister to Conopidae, nor has it been directly tested in any molecular analysis to date. Future sampling of still more acalyptrate families will be necessary to shed more light on schizophoran relationships. Relationships between subfamilies and genera of Conopidae, likewise, will require further examination with greater sampling of genera.

With regard to comparisons of gene sequences based on phylogenetic information, the nuclear genes tested provide more value, but the mitochondrial genes tested are still useful, especially when investigating more recent divergences. The two most commonly sequenced genes in dipteran molecular phylogenetics are

COI and 28S. Of these, COI appears to be a poor choice in terms of phylogenetic information provided outside of species and genus-level relationships. The other popular gene, 28S appears to be highly useful for the study of schizophoran relationships, but either the entire gene must be sequenced or further refinement to target only variable subsections of the gene is necessary. In general, the greatest resolution can be provided by including sequence data from all four gene categories: mtDNA, nrDNA, rDNA, and PCG.

4. Phylogenetic analysis of relationships between genera of Conopidae based on molecular and morphological data

4.1. Introduction

Current catalogues (Camras, 1965; Chvála & Smith, 1988; Papavero, 1971; Smith, 1975, 1980, 1989) offer a combined list of nearly 800 species of Conopidae, organized into four (or five) subfamilies and 56 genera and subgenera. While placement of genera within subfamilies is generally agreed upon between catalogues, the status of the subfamilies Zodioninae and Stylogastrinae is uncertain. A phylogenetic test of the present classification within Conopidae is necessary.

In addition to numerous diagnoses and keys to subfamilies and tribes of Conopidae, a few authors have provided more detailed analyses of morphological character states and their potential use in phylogenetic analysis. Hennig's (1966) review of the fossil specimens of *Palaeomyopa tertiaria* Meunier, 1912 includes a discussion of the monophyly of proposed subfamilies, relationships between those subfamilies, the possible ancestral states for the family, and important morphological characters for future analysis. Griffiths (1972) and McAlpine (1989) each discussed potentially apomorphic characters of Conopidae as part of phylogenetic analyses of all Schizophora. Steyskal (1957) discusses five species of Conopidae in four genera in his analysis of male terminalia of Acalyptratae. Steffek (1977) illustrates and discusses the male terminalia of 28 species of Conopidae in nine genera, however, a phylogenetic analysis is not included. Kotrba (1997) describes, in detail, the internal and external features of the female terminalia, but

only for select species of *Stylogaster*. Schneider (2010) includes some discussion of phylogenetically informative morphological characters amongst Australian species, but does not include analysis of these characters.

The most comprehensive phylogenetic analyses based on morphological characters (Griffiths, 1972; Korneyev, 2000; McAlpine, 1989) have all placed Conopidae near or within the superfamily Tephritoidea. Enderlein (1936) and Hennig (1958) both propose Conopidae [“Archischiza”] as the sister to the remaining Schizophora [“Muscaria”]. A phylogenetic analysis based on DNA sequence data from ten gene regions (Chapter 3), supports the phylogeny of Hennig, but also suggests a close relationship between Conopidae and Lauxaniidae. The recent FLYTREE analysis (Wiegmann et al., 2011) includes morphological and molecular data from over 150 fly families and places Conopidae within Sciomyzoidea. Because of this uncertainty of the adelphotaxon to Conopidae, any phylogenetic analysis of relationships within Conopidae must include outgroup taxa from a variety of other schizophoran groups as well as aschizan groups to ensure proper character polarity.

Song and Bucheli (2010) analyze the phylogenetic utility of genitalic versus non-genitalic characters in phylogenetic analyses across different insect orders. They conclude that genitalic characters are phylogenetically informative despite being sexually selected. The composite nature of genitalia provides a number of characters of equal value to non-genitalia regardless of the hierarchical level at which the phylogenetic question is being asked.

A number of studies (e.g., Almeida and Danforth, 2009; Cameron et al., 2007; Light & Reed, 2009; Lin & Danforth, 2004) investigate the informative qualities of DNA sequence data from different gene regions. The general conclusion is that mitochondrial DNA gene regions (mtDNA) are useful for determining relationships among recent radiations, while nuclear DNA gene regions (nrDNA) are more useful for determining relationships at deeper evolutionary timescales. Chapter 3 confirms these findings and suggests that DNA sequence data from four categories (mtDNA, nrDNA, ribosomal DNA (rDNA), and protein coding genes (PCG)) are necessary for maximum resolution in phylogenetic analysis. Of potential nuclear protein coding gene regions, Chapter 3 indicates that alanyl-tRNA-synthetase (AATS) has the highest level of resolution and support for clades within Conopidae.

The primary purpose of this chapter is to test phylogenetic support for the present subfamily classification of Conopidae (Table 4.1). Also, relationships between subfamily clades will be explored. Molecular and morphological data will be used to generate a phylogenetic hypothesis for taxa including members of all proposed subfamilies. In addition, morphological character states will be evaluated to determine their evolution within Conopidae.

4.2. Materials and methods

4.2.1. Taxon sampling

A total of 64 specimens representing 59 species of Conopidae are included. These specimens represent 20 different genera and all five putative subfamilies of Conopidae (Conopinae, Dalmanniinae, Myopinae, Stylogastrinae, and Zotioninae)

(Table 4.1). Representatives of two different subgenera of the genus *Physoconops* and three different subgenera of the genus *Conops* are included. To serve as outgroup taxa, seven species from seven other dipteran families, including three families of Aschiza and four families of Schizophora, are included. *Conicera* (*Conicera*) *dauci* (Phoridae) and *Lonchoptera tristis* (Lonchopteridae) are used to root all trees.

4.2.2. DNA extraction and amplification

Total genomic DNA was extracted from whole specimens using a DNeasy® Tissue kit (Qiagen Inc., Santa Clara, CA, USA). To provide additional genomic template, most specimens were extracted a second time using another DNeasy® Tissue kit. Following extraction, specimens were critical-point dried or dried in ethyl acetate and deposited as vouchers in the Canadian National Collection of Insects, Arachnids, and Nematodes (CNC).

Five gene regions were chosen for DNA sequence analysis: 12S ribosomal DNA (12S); cytochrome oxidase *c* subunit I (COI); cytochrome *b* (CytB); 28S ribosomal DNA (28S); and AATS. These include mtDNA gene regions (12S, COI, and CytB), nrDNA gene regions (28S and AATS), rDNA gene regions (12S and 28S), and PCG gene regions (COI, CytB, and AATS). For gene regions amplified using *Taq* polymerase (Table 4.2), DNA amplifications were carried out in 25µL reactions with 16µL ddH₂O, 2.5µL 10X PCR buffer, 2.5µL 25mM MgCl₂, 0.5µL of each 10µM primer, 0.5µL 10µM dNTPs, 0.5 µL *Taq* DNA polymerase (Promega Corp., Madison, WI, USA), and 2 µL genomic DNA template. For gene regions amplified using ExTaq

polymerase, DNA amplifications were carried out in 25 μ L reactions with 15.75 μ L ddH₂O, 2.5 μ L 10X ExTaq PCR buffer (containing 20mM MgCl₂), 0.625 μ L 25mM MgCl₂, 1 μ L of each 10 μ M primer, 2 μ L 10 μ M dNTPs, 0.125 μ L ExTaq HS DNA polymerase (Takara Bio USA, Madison, WI, USA), and 2 μ L genomic DNA template. For full gene maps depicting location and direction of all primers, please refer to Gibson et al., 2011.

Amplification cycles were performed on an Eppendorf ep Gradient S Mastercycler (Eppendorf AG, Hamburg, Germany). Amplification conditions for 12S were as follows: initial denaturation at 94°C for three minutes; 35 amplification cycles (94°C for one minute, 54°C for one minute, 72°C for ninety seconds); final extension at 72°C for five minutes. Amplification conditions for 28S were as follows: initial denaturation at 94°C for three minutes; 35 amplification cycles (94°C for one minute, 52-61°C (annealing temperature dependent on primer pair used) for ninety seconds, 72°C for ninety seconds); final extension at 72°C for five minutes. Amplification conditions for AATS were as follows: initial denaturation at 94°C for three minutes; 40 amplification cycles (94°C for one minute, 50°C for one minute, 72°C for ninety seconds); final extension at 72°C for five minutes. Amplification conditions for COI were as follows: initial denaturation at 94°C for three minutes; 40 amplification cycles (94°C for one minute, 45°C for one minute, 72°C for ninety seconds); final extension at 72°C for five minutes. Amplification conditions for CytB were as follows: initial denaturation at 94°C for three minutes; 35 amplification

cycles (94°C for one minute, 50°C for one minute, 72°C for ninety seconds); final extension at 72°C for five minutes.

Individual legs of some specimens (as noted in Table 4.1) were processed, amplified, and sequenced for COI by the International Barcode of Life facility at the Biodiversity Institute of Ontario (University of Guelph, Guelph, ON).

4.2.3. DNA sequencing and editing

Amplification products and negative controls were visualized on 1% agarose electrophoresis gels and purified for sequencing using either an ExoSAP-IT® protocol (USB Corp., Cleveland, OH, USA) or an E-Gel iBase Power System, an E-Gel Safe Imager™ Real-Time Transilluminator, and E-Gel CloneWell 0.8% SYBR Safe™ agarose cassettes (Invitrogen™, Carlsbad, CA, USA) according to the protocol described in Gibson et al. (2010a). Sequencing of purified products was performed at the Agriculture & Agri-Food Canada, Eastern Cereal and Oilseed Research Centre Core Sequencing Facility (Ottawa, ON, Canada). Sequencing reactions were carried out in a volume of 10µL and used an ABI BigDye® Terminator v3.1 Cycle Sequencing kit (PE Applied Biosystems, Foster City, CA, USA). Sequencing reactions were purified using the ABI ethanol/EDTA/sodium acetate precipitation protocol and analysed on an ABI 3130xl Genetic Analyzer (PE Applied Biosystems, Foster City, CA, USA). All sequence chromatograms were edited and contigs formed using Sequencher 4.7 (Gene Codes Corp., Ann Arbor, MI, USA).

4.2.4. Sequence alignment

ClustalX (Thompson et al., 1997) with default settings was used to produce an alignment for 12S sequences. Sequences for 28S were aligned by hand according to the secondary structure model proposed by Kjer et al. (1994) for *Aedes albopictus* (Skuse, 1894) and by Hancock et al. (1988) for *Drosophila melanogaster* Meigen, 1830. The region amplified corresponds to almost the entire length of the 28S gene region. Expansion segments that match the location of those listed by Kjer et al. (1994) and Hancock et al. (1988) were identified for the 28S alignment. The remaining genes are protein-coding and were aligned manually according to translated amino acid codons. A single Glycine is inserted at position 364 in the AATS gene region in seven taxa. No other introns were detected.

4.2.5. Morphological analysis

In addition to specimens from which DNA was extracted for molecular analysis, other, conspecific specimens were examined to determine morphological character states. These specimens were obtained from and have been deposited at the following institutions: Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, ON, Canada (CNC); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); Field Museum of Natural History, Chicago, IL, USA (FMNH); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Natal Museum, Pietermaritzburg, South Africa (NMSA); R.M. Bohart Museum of Entomology, University of California-Davis, Davis, CA, USA (UCDC); National

Museum of Natural History, Washington D.C., USA (USNM); personal collection of Dr. Milan Chvála, Charles University, Prague, Czech Republic.

Male and female terminalia were removed, cleared in lactic acid, temporarily mounted in glycerol, and observed. Following observation, terminalia were stored in terminalia tubes and attached to original specimen pins.

Morphological terminology, including that of male and female terminalia, follows that of Cumming and Wood (2009). Many of the characters included here have been discussed and used in previous morphological and taxonomic research. Notes on the original reference, initial definition, and present informative qualities of certain characters, especially the male terminalia, are discussed here and in section 4.4. Any novel terminology is fully described. The plesiomorphic state of each character, as determined by outgroup analysis, is included as state “0”. All non-binary characters are analyzed as unordered.

Head

1. Ptilinum: (0) absent; (1) present. A ptilinum is present in all included taxa except Syrphidae, Phoridae, and Lonchopteridae.
2. Central ocellus: (0) present; (1) absent. The central ocellus is absent in Pyrgotidae and all examined specimens of Conopinae except members of *Atrichoparia*, *Camrasiconops*, *Physoconops*, *Pleurocerina*, and *Smartiomyia*.
3. Lateral ocelli: (0) present; (1) absent. Lateral ocelli are absent in Pyrgotidae and all examined members of *Conops*, *Euconops*, *Leopoldius*, and *Physocephala*.

4. Ocellar tubercle: (0) present; (1) absent. The ocellar tubercle is completely absent in Pyrgotidae and all examined members of *Conops* (except *C. flavipes* and *C. vesicularis*), *Euconops*, and *Physocephala*.
5. Vertex: (0) divided; (1) complete. The vertex is divided by a large, triangular ocellar tubercle in most examined taxa. In Pyrgotidae and all examined members of Conopinae, the vertex is complete and surrounds the ocellar tubercle, if present.
6. Length of vertex: (0) restricted to less than half of the depth of the frons; (1) expanded. The vertex is expanded no farther than the midpoint of the frons in most examined taxa. In all examined members of *Stylogaster* (except *S. biannulata* and *S. stylata*), the vertex extends deep into the frons and in some specimens meets the ptilinal suture.
7. Texture of frons: (0) almost entirely smooth; (1) with extensive lateral grooves. In all examined members of *Atrichoparia*, *Camrasiconops*, *Conops* (*Asiconops*), *Heteroconops*, *Pleurocerina*, and *Smartiomyia*, the frons has extensive lateral grooves. All other examined taxa have the frons entirely smooth, or with only minor rugosity.
8. Posterior margin of compound eye: (0) round; (1) with triangular, shiny notch. All examined members of *Conops* (*Asiconops*), *Physocephala*, and *Physoconops* have a triangular, shiny notch in the posterior margin of the compound eye.

9. Fronto-orbital bristles: (0) present; (1) absent. Bristles on the frons or orbital region are absent in Psilidae, Pyrgotidae, Syrphidae and all examined members of Conopidae (except *Stylogaster biannulata*, *S. breviventris*, *S. decorata*, *S. inca*, *S. neglecta*, *S. rectinervis*, and *S. stylata*).
10. Frontal setae: (0) absent or dense; (1) confined to two convergent medial rows. In all examined members of *Parazodion* and *Zodion* there are two distinct, convergent rows of dark setae on the frons.
11. Ocellar bristles: (0) present; (1) absent. Ocellar bristles are absent in Pyrgotidae, Syrphidae, all examined members of *Dalmannia* and Conopinae, and some species of *Stylogaster* (*S. biannulata*, *S. frauci*, *S. pauliani*, *S. stylata*, *S. westwoodi*, and *S. sp.*).
12. Postocellar bristles: (0) present; (1) absent. Postocellar bristles are absent in Pyrgotidae, Syrphidae, and all examined members of *Dalmannia* and Conopinae.
13. Gena: (0) very small; (1) expanded to be at least one-third of the total height of the head. The gena are absent, very small, or only slightly developed in most examined specimens. In all examined members of *Myopa*, the gena are expanded and are over one-third of the total head height.
14. Compound eye: (0) ommatidia uniform across width; (1) ommatidia larger anteriorly. In all examined members of *Stylogaster*, the ommatidia are distinctly larger anteriorly.

15. Facial fovea: (0) absent; (1) present. A concave facial fovea beneath the antennal bases is present in all specimens examined except for Phoridae, Syrphidae, Lonchopteridae, and *Stylogaster*.
16. Lunule: (0) not developed; (1) expanded, visible between antennal bases and ptilinum. The lunule is developed and projecting forward over the base of the antennae in all examined members of Conopinae except *Atrichoparia*, *Camrasiconops*, *Euconops*, *Heteroconops*, *Pleurocerina*, and *Smartiomyia*.
17. Facial carina: (0) absent; (1) present. A facial carina, if only weakly developed, is present in Lauxaniidae, Strongylophthalmyiidae, Psilidae, Pyrgotidae, and all examined members of Conopidae.
18. Prominent facial carina: (0) absent; (1) present. In all examined members of *Stylogaster* the facial carina is strongly developed and projects beyond the facial ridge.
19. Facial ridge: (0) absent; (1) present. A facial ridge, extending from the antennal bases to the subcranial cavity is present in all examined taxa except Lonchopteridae, Phoridae, and Syrphidae.
20. Pointed facial ridge: (0) absent; (1) present. The facial ridge meets the subcranial cavity at a pointed 90° angle in all examined members of *Atrichoparia*, *Heteroconops*, *Microconops*, and *Smartiomyia*.
21. Scape: (0) quadrate; (1) elongate. The scape is at least twice as long as wide in *Pseudoconops antennatus* and all examined members of Conopinae.

22. Pedicel: (0) quadrate; (1) elongate. The pedicel is quadrate in all outgroup taxa, except Pyrgotidae. In all examined members of Conopidae, the pedicel is elongate, with the length at least one and one half times the width at the base.
23. Transverse dorsal ridge on pedicel: (0) absent; (1) present. A prominent transverse dorsal ridge is present near the base of the pedicel in all examined members of *Camrasiconops* and *Pleurocerina*.
24. Pedicel: (0) narrow; (1) broad. In Lonchopteridae and all examined members of *Dalmannia*, the width of the pedicel is at least twice the width of the scape.
25. First flagellomere: (0) normal; (1) elongate. In Lauxaniidae, Phoridae, *Stylogaster inca*, *S. neglecta*, and all examined members of *Heteroconops* and *Smartiomyia*, the first flagellomere is at least twice as long as the combined length of the scape and pedicel.
26. Location of arista: (0) dorsal; (1) apical. The arista is located either mid-dorsally or dorsobasally in most examined taxa. In all examined members of Conopinae, the arista is located at the apex of the first flagellomere.
27. Arista: (0) filiform; (1) thickened. All outgroup taxa have a filiform arista. All examined members of Conopidae have a thickened arista.
28. Stylate arista: (0) absent or normal; (1) reduced and retracted into first flagellomere. In all examined members of *Heteroconops* and *Smartiomyia*, the arista is barely as long as wide and is partly retracted within the first flagellomere.

29. Second aristomere: (0) as wide as other segments; (1) expanded ventrally. The second aristomere is greatly expanded ventrally in all examined members of Conopinae.
30. Anterior margin of subcranial cavity: (0) broad, straight or rounded; (1) pointed anteriorly. The anterior margin of the subcranial cavity projects forward to reach a narrow point where it meets the facial carina in all examined members of *Stylogaster* and Conopinae.
31. Setae on maxillary palpi: (0) present; (1) absent. Setae on the maxillary palpi are absent in all examined members of *Atrichoparia*, *Conops* (except *C. flavipes* and *C. vesicularis*), *Heteroconops*, *Physocephala*, *Physoconops*, *Pleurocerina*, *Smartiomyia*, and *Stylogaster*.
32. Maxillary palpus: (0) elongate; (1) absent or length less than half of the width of prementum. The maxillary palpi are reduced or completely absent in all examined members of *Stylogaster* and Conopinae.
33. Prementum: (0) unmodified; (1) fused. The prementum is present as two separate lobes in all outgroup taxa. The prementum is fused into a tube-like structure in all examined members of Conopidae. Previous authors have referred to the fused prementum and the labella together as a singular “haustellum” (e.g., Griffiths, 1972; Schneider, 2010) or “proboscis” (e.g., Hennig, 1966; Skevington et al., 2010) without reference to the component structures.

34. Prementum: (0) short; (1) elongate. The prementum has a length greater than the width of the head in all examined members of Conopidae (except *Myopa occulta* and members of *Heteroconops* and *Leopoldius*). See note in character 33.
35. Labellum: (0) folded back and at least as long as prementum; (1) not folded and less than half of the length of the prementum. The labellum is folded back along the prementum and is at least the same length as the prementum in all outgroup taxa and most members of Conopidae. In all examined members of *Parazodion*, *Zodion*, and Conopinae, the labellum is less than one half of the length of the prementum and projects forward from the apex of the prementum. See note in character 33.
36. Shape of labella: (0) broad, separate; (1) filiform, fused. The labella are broad and separate in all outgroup taxa, as well as all examined members of *Parazodion*, *Zodion*, and Conopinae. In all other examined members of Conopidae, the labella are filiform and fused for at least a portion of their length. See note in character 33.

Thorax (including legs)

37. Basisternum shape: (0) broad; (1) reduced to short, narrow single sclerite; (2) reduced to narrow sclerite divided posteriorly [unordered]. The basisternum is broad in all outgroup taxa as well as in all examined members of Conopinae, *Dalmannia*, *Sicus*, and *Stylogaster*. It is reduced to a narrow, single sclerite in all examined members of *Myopa*, *Pseudoconops*, and

Thecophora. In all examined members of *Parazodion* and *Zodion* the basisternum is reduced into a narrow, elongate sclerite that is divided posteriorly.

38. Posterolateral extensions of the basisternum: (0) absent; (1) present. Posterolateral extensions on the basisternum are lacking in all outgroup taxa. They are present in all examined members of Conopidae.
39. Setae on posterolateral extensions of the basisternum: (0) absent; (1) present. The posterolateral extensions of the basisternum are elongate, narrow, and with setae in all examined members of Conopidae (except Conopinae, *Sicus*, and *Stylogaster*).
40. Protibial apical spurs: (0) absent; (1) present. Protibial apical spurs are present in all examined members of *Stylogaster*.
41. Shape of metafemur: (0) parallel or spindle-shaped; (1) distinctly broadened basally. The hind femur has a distinct shape in all examined members of *Physocephala*.
42. Double row of spines on ventral surface of femora: (0) absent; (1) present. A distinct double row of black spines on the ventral surface of all femora is present in all examined members of *Myopa*, *Pseudoconops*, and *Thecophora*.
43. Apical shiny patch on metatibia: (0) absent; (1) present. A defined, shiny patch near the apex of the metatibia is present in all examined members of Conopinae, *Parazodion*, and *Zodion*.

44. Prominent row of setae on mesofemur: (0) absent; (1) present. There is a distinct row of setae on the posterior surface of the mesofemur in all examined members of Conopidae (except *Physocephala*).
45. Male pro- and mesocoxa: (0) bare or with sparse setae; (1) with dense patch of long, pale setae. Males of *Stylogaster biannulata*, and *S. stylata* have a patch of long, pale setae on the pro- and mesocoxa.
46. Metacoxa: (0) normal; (1) with diagonal, pale marking. *Stylogaster breviventris* and *S. rectinervis* have a diagonal, pale marking on the metacoxa.
47. Ventral half of proepisternum: (0) with setae and/or bristles; (1) bare. Setae and bristles are absent on the ventral half of the proepisternum of all examined members of *Physocephala* and *Euconops*.
48. Dorsal half of proepisternum: (0) bare; (1) with patch of setae. A patch of setae is present on the dorsal half of the proepisternum in all examined members of *Thecophora* and *Pseudoconops*.
49. Postpronotal bristles: (0) present; (1) absent. Postpronotal bristles are absent in Psilidae, Pyrgotidae, Strongylophthalmyiidae, Syrphidae, and all members of Conopidae (except *Stylogaster biannulata*, *S. frauci*, *S. pauliani*, *S. stylata*, *S. westwoodi*, and *S. sp.*).
50. Supra-alar bristles: (0) 0 or 1; (1) 2. There are two supra-alar bristles in *Stylogaster decorata*, *S. inca*, and *S. neglecta*.
51. Bristles on anepimeron: (0) absent; (1) present. The anepimeron is bare or with only small setae in most examined taxa. Defined bristles on the

anepimeron are present in Strongylophthalmyiidae, Pyrgotidae, and all examined members of *Stylogaster*.

52. Bristles on anepisternum: (0) absent; (1) present. Bristles on the anepisternum are present only in Strongylophthalmyiidae, Pyrgotidae, and Lauxaniidae.
53. Katepisternum: (0) bare; (1) with bristles and/or setae. The katepisternum is bare in Lonchopteridae, Phoridae, Syrphidae, and all examined members of *Stylogaster*. In all other examined taxa the katepisternum has at least one seta or bristle.
54. Scutellum: (0) developed, with bristles; (1) reduced, lacking bristles. In all examined members of *Conops* (except *C. flavipes* and *C. vesicularis*), *Physocephala*, and *Physoconops*, the scutellum is reduced and lacking bristles.
55. Scutellar bristles: (0) zero, one, or two pairs; (1) more than two pairs. In Psilidae and all examined members of *Parazodion* and *Zodion* there are more than two pairs of distinct bristles on the scutellum.

Wing

56. Wing pattern: (0) at least partly opaque or darkened; (1) completely hyaline. In Phoridae, Strongylophthalmyiidae, Syrphidae and all examined members of *Atrichoparia*, *Camrasiconops*, *Heteroconops*, *Microconops*, and *Smartiomyia* the wings are completely hyaline.
57. Wing pattern: (0) hyaline or pattern variable; (1) wing distinctly darker anteriorly. In all examined members of *Physoconops*, *Physocephala*, and

Pleurocerina the wing anterior to vein CuA₁ is partly or entirely darkened, whereas as the wing posterior to vein CuA₁ is hyaline.

58. M vein: (0) parallel to vein R₄₊₅; (1) deflected towards vein R₄₊₅. The M vein is parallel to vein R₄₊₅ in all outgroup taxa. In all examined members of Conopidae, the M vein is deflected toward, or joins, vein R₄₊₅.
59. Petiole of vein R₄₊₅+M: (0) absent or short; (1) elongate. Vein M is curved such that it meets vein R₄₊₅ at a 90° angle and the petiole formed from their union is greater than the length of cross-vein dm-cu in *Atrichoparia* sp. A and all examined members of *Heteroconops* and *Smartiomyia*.
60. Sc vein: (0) incomplete, or ends at a point before four-tenths of the length of the costa; (1) ends at or beyond a point four-tenths of the length of the costa. Vein Sc is either incomplete or ends before a point four-tenths of the length of the costa in all outgroup taxa as well as all examined members of *Stylogaster*. Vein Sc ends at or beyond a point four-tenths of the length of the costa in all other examined members of Conopidae.
61. R₁ vein: (0) ends at or before a point six-tenths of the length of the costa; (1) ends beyond a point six-tenths of the length of the costa. Vein R₁ ends beyond a point six-tenths of the length of the costa in all examined members of Conopinae, *Parazodion*, *Sicus*, and *Zodion*.
62. Veins Sc and R₁: (0) separate for their entire length; (1) fused before reaching costa. Veins Sc and R₁ are separate for their entire length for all examined taxa except all members of *Myopa*, *Thecophora*, and *Pseudoconops*.

63. Vein R_{2+3} : (0) ends beyond endpoint of vein R_1 ; (1) ends at or near endpoint of vein R_1 . Vein R_{2+3} meets the costa at a point at least two tenths of the length of the costa beyond the end point of vein R_1 in all examined taxa except members of Conopinae, *Parazodion*, *Sicus*, and *Zodion*.
64. Crossvein sc-r: (0) absent; (1) present. A crossvein between veins Sc and R_1 is present in all examined members of Conopinae, *Parazodion*, *Stylogaster*, and *Zodion*.
65. Vein CuA_2+A_1 : (0) absent or shorter than crossvein dm-cu; (1) longer than crossvein dm-cu. The vein formed by the union of veins CuA_2 and A_1 is absent or shorter than crossvein dm-cu in Lonchopteridae, Phoridae, Syrphidae, and all examined members of Conopinae (except members of *Atrichoparia*, *Heteroconops*, and *Smartiomyia*). In the remaining examined taxa, vein CuA_2+A_1 is longer than crossvein dm-cu.
66. Vein CuA_2 : (0) straight; (1) curved. Vein CuA_2 is curved along its length in Syrphidae as well as all examined members of Conopinae, *Parazodion*, and *Zodion*.
67. Vena spuria: (0) absent; (1) present. A spurious vein bisecting crossvein r-m is present in Pyrgotidae, Syrphidae, and all examined members of Conopinae.
68. Width of alula: (0) absent or narrow; (1) broad. The alula is broad in most examined taxa. It is absent or reduced to being less than one fourth of the width of the wing in Lonchopteridae, Phoridae, and all members of *Stylogaster*.

Female abdomen

69. Sternites 2 and 3: (0) present; (1) absent. Abdominal sternites 2 and 3 are absent in all examined members of *Stylogaster*.
70. Tergite 5 and sternite 5: (0) separate; (1) fused. Abdominal tergite 5 and sternite 5 are fused in all examined members of Conopinae, *Parazodion*, and *Zodion* (Figs. 4.1, 4.4).
71. Tergite 6 and sternite 6: (0) at least partially separate; (1) fused. In all examined members of *Stylogaster*, abdominal tergite 6 and sternite 6 are completely fused and ring-like (Fig. 4.2).
72. Tergite 7 and sternite 7: (0) separate; (1) fused. Abdominal tergite 7 and sternite 7 are fused and ring-like in Lauxaniidae, Psilidae, Pyrgotidae, Strongylophthalmyiidae, and all examined members of Conopidae (Figs. 4.1-4.5).
73. Sternite 6: (0) unmodified; (1) with rows of spicules. Rows of spicules cover the surface of sternite 6 in all examined members of Conopidae (except *Dalmannia*, *Parazodion*, and *Stylogaster*) (Figs. 4.1, 4.5).
74. Sternite 5: (0) unmodified; (1) with rows of spicules. In all examined members of Conopidae (except *Dalmannia* and *Stylogaster*), sternite 5 has rows of spicules and may or may not be expanded ventrally into a genital plate (Figs. 4.1, 4.4, 4.5). The ventral extension of the fifth abdominal sternite females of most species of Conopidae has been referred to as the theca by most previous authors. As this terminology can lead to confusion with an

analogous structure present in other Insecta, the example of Schneider (2010) is followed and the term theca is replaced with ventral genital plate.

75. Spicules confined to tip of ventral genital plate: (0) absent; (1) present. There are only a few rows of spicules at the apex of the ventral genital plate in all examined members of *Heteroconops* and *Smartiomyia*. See note in Character 74.
76. Segment 7: (0) absent or parallel to tergite 6; (1) deflected ventrally at 90° to segment 6. Segment 7 projects posteriorly from segment 6 in all outgroup taxa as well as all examined members of *Dalmannia* and *Stylogaster*. In all other examined members of Conopidae, segment 7 meets segment 6 at a 90° angle (Figs. 4.1-4.5).
77. Segment 7: (0) absent or broad; (1) compressed laterally along entire length; (2) compressed laterally only in posterior half [unordered]. Segment 7 is compressed laterally, forming a sharp, narrow point in all examined members of *Dalmannia*. In all examined members of *Parazodion*, segment 7 is broad and bulbous at the base and laterally compressed apically (Figs. 4.1-4.5).
78. Epiproct: (0) present; (1) absent. The epiproct is absent in Pyrgotidae as well as all examined members of Conopidae (Figs. 4.1-4.5).
79. Cerci: (0) quadrate, rounded, narrow, or absent; (1) elongate, broad, flattened. The cerci are elongate, broad, flattened, and cupped in all examined members of Conopinae, *Sicus*, and *Zodion* (Fig. 4.1).

80. Hypoproct: (0) broad and short, membranous and internal, or absent; (1) sclerotized and elongate beyond cerci. The hypoproct is sclerotized and elongate well beyond the cerci in all examined members of *Stylogaster* (Fig. 4.2).
81. Two square lobes on sternite 8: (0) absent; (1) present. Sternite 8 is present as two well-sclerotized lobes in all examined members of Conopidae (except *Stylogaster*) (Figs. 4.1-4.5).
82. Lateral lobes on sternite 8: (0) absent; (1) present. Elongate lateral lobes are present on sternite 8 in all examined members of *Stylogaster* (except *decorata* and *neglecta*) (Fig. 4.2).
83. Sclerotized posteroventral hooks on syntergite 8+9: (0) absent; (1) present. In all examined members of Conopidae (except *Stylogaster*), the posteroventral surfaces of syntergite 8+9 are developed into a pair of sharp, sclerotized hooks (Figs. 4.1, 4.3, 4.4, 4.5).

Male abdomen

84. Sternites 2-4: (0) partly or entirely membranous; (1) broad, sclerotized plates. In *Conops flavipes* and *C. vesicularis*, sternites 2 through 4 are present as broad, sclerotized plates.
85. Tergites 3 and 4: (0) narrow and/or tapering; (1) broad and parallel-sided. In *Conops flavipes*, *C. vesicularis*, and *Leopoldius*, tergites 3 and 4 are as broad as the thorax and parallel-sided.

86. Tergites 2 and 3: (0) broad, rectangular; (1) petiolate. In all examined members of *Physocephala* and *Physoconops*, tergite 2 is extremely narrow and is longer than any other tergite. Also in these taxa, tergite 3 is distinctly narrowed anteriorly.
87. Sternite 5: (0) unmodified; (1) broad, with setae or spicules. Sternite 5 is wider and broader than all preceding sternites and has thick setae or spicules on the posterior margin in all examined members of Conopidae (except *Stylogaster* and *Dalmannia*) (Figs. 4.1, 4.4, 4.5).
88. Syntergosternite 7+8: (0) absent; (1) present. Tergite 7 and sternite 8 are fused into a single pre-genital sclerite in all examined members of Lauxaniidae, Pyrgotidae, Strongylophthalmyiidae, and Conopidae (Figs. 4.1-4.5). Although he labelled it the “protandrium”, Steyskal (1957) notes the presence of a developed sclerite between tergite 5 and the terminalia bearing the sixth and seventh spiracles in five species of Conopidae. Griffiths (1972) and McAlpine (1989) consider this pregenital sclerite to be composed of sternites 7 and 8, with tergites 7 and 8 absent. Griffiths (1972) considered the pregenital sclerite to be missing in *Stylogaster*. Smith and Peterson (1987) suggest that the pregenital sclerite is formed from tergites 6, 7, and 8 with sternites 6 and 7 variable.
89. Broad, hemispherical syntergosternite 7+8: (0) absent; (1) present. Syntergosternite 7+8 is absent altogether or present as a narrow band in all outgroup taxa as well as *Dalmannia* and some members of *Stylogaster* (S.

biannulata, *S. breviventris*, *S. decorata*, *S. inca*, *S. neglecta*, *S. rectinervis*, and *S. stylata*) (Figs. 4.2-4.3). In all other examined members of Conopidae, syntergosternite 7+8 is present as a large, dorsal sclerite (Figs. 4.1, 4.4, 4.5). See note in character 88.

90. Sternite 8: (0) absent; (1) present. The posterior portion of syntergosternite 7+8, here described as sternite 8, is present as a clearly differentiated portion of the sclerite in all examined members of Conopidae (except *Dalmannia* and *Stylogaster*) (Figs. 4.1, 4.4, 4.5). Steyskal (1957) notes the presence of a clearly demarcated “tergite 8” for *Physocephala furcillata* (Williston, 1882), *Myopa vesiculosa*, *M. virginica* Banks, 1916, and *Zodion intermedium*. He notes that it is lacking in *Dalmannia nigriceps*. Schneider (2010) notes the presence of sternite 8 at the posterior margin of syntergosternite 7+8 [“protandrium”] of many Australian Conopidae.
91. Elongate cerci: (0) absent; (1) present. The cerci are elongate to a length of at least three times their width in Pyrgotidae, Strongylophthalmyiidae, and all examined members of *Stylogaster* (Fig. 4.2). While referred to as cerci by most authors (e.g., Steffeck, 1977) they are also referred to as “para-anal plates” (Steyskal, 1957) or “parapodial plates” (Cole, 1927).
92. Cercal attachment: (0) broad; (1) narrow, sclerotised stalk. The sclerotized portion of the cercal attachment is a narrow stalk in all examined members of Conopinae, *Parazodion*, and *Zodion* (Figs. 4.1, 4.4).

93. Epandrium: (0) two separate lobes beyond cerci; (1) fused beyond cerci. The epandrium is fused into a single plate beyond the cerci in all examined members of Conopinae (Fig. 4.1).
94. Anterior surstyli: (0) absent; (1) present. Anterior surstyli are present either as a pad of dense spinules or as an elongate lobe in all examined members of *Myopa*, *Parazodion*, *Sicus*, *Thecophora*, and *Zodion* (Figs. 4.4, 4.5). Steyskal (1957) notes the absence of anterior and posterior surstyli in *Dalmannia nigriceps* and *Physocephala furcillata* and the presence of anterior and posterior surstyli in *Myopa vesiculosa*, *M. virginica*, and *Zodion intermedium*.
95. Posterior surstyli: (0) single lobed; (1) bi- or tri-lobed; (2) absent [unordered]. Posterior surstyli are bi- or tri-lobed in all examined members of *Stylogaster*. In Lonchopteridae and all examined members of Conopinae and *Dalmannia*, posterior surstyli are absent. In all other examined taxa, posterior surstyli are present as single lobes. (Figs. 4.2, 4.4, 4.5). See note in character 94.
96. Tergite 6: (0) broad plate; (1) narrow, bare strip, fused with syntergosternite 7+8; (2) broad, internal hemispherical plate [unordered]. In all examined members of *Stylogaster*, tergite 6 is present as a broad, internal, ventral, hemispherical plate (Fig. 4.2). In all other examined members of Conopidae, tergite 6 is a narrow, bare strip, located on the ventral surface and fused laterally with syntergosternite 7+8 (Figs. 4.1, 4.3-4.5). Steyskal (1957) notes

a narrow, ventral sclerite that he terms “sternite 6” anterior to the terminalia in *Physocephala furcillata*. See note in character 88.

97. Hypoproct: (0) absent; (1) present. The hypoproct is present as two fleshy, setose lobes in all examined members of *Parazodion* and *Zodion* (Fig. 4.4). Steyskal (1957) notes the presence of the “tenth sternite” in *Zodion intermedium*, and Howell (1967) refers to the “phallobase” in *Zodion obliquefasciatum* (Macquart, 1846), but these are considered here to be homologous to the hypoproct.
98. Anterior hypandrial arms: (0) absent; (1) two, separate; (2) one [unordered]. The hypandrium forms a ring anteriorly with no arms in all outgroup taxa, as well as *Atrichoparia* sp. B and all examined members of *Dalmannia* and *Stylogaster* (Figs. 4.2-4.3). Two anterior hypandrial arms are present in all examined members of *Myopa*, *Parazodion*, *Sicus*, *Thecophora*, and *Zodion* (Figs. 4.4-4.5). There is a single anterior hypandrial arm in all examined members of Conopinae, except *Atrichoparia* sp. B (Fig. 4.1). An anterior Y-shape to the hypandrium is noted by Steyskal (1957) in *Physocephala furcillata*. He also notes a U-shaped hypandrium in *Dalmannia nigriceps*, two “stout, converging rods” arms in *Myopa vesiculosa* and *M. virginica*, and two “slender parallel apodemes” in *Zodion intermedium*.
99. Anterior hypandrial plate: (0) absent; (1) present. A setose, broad plate on the anterior portion of the hypandrium is present in all members of *Thecophora* (Fig. 4.5). Cole (1927) noted a peculiar shape to the hypandrium

["basal part of the double apodeme"] in *Thecophora modesta* and *T. abbreviata* (Loew, 1866).

100. Hypandrial dorsal bridge: (0) absent or weakly sclerotized; (1) complete and heavily sclerotized. The dorsal bridge of the hypandrium is heavily sclerotized and forms a nearly complete tube around the phallus in all examined members of Conopinae (Fig. 4.1). Steyskal (1957) notes that the hypandrium of *Physocephala furcillata* forms a sheath for the phallapodeme ["aedeagal apodeme"].
101. Lobes on subepandrial sclerite: (0) absent; (1) present. Two lobes are present on the subepandrial sclerite of *Pleurocerina brevis* and *P. vespiformis*.
102. Medial spine on epandrium: (0) absent; (1) present. A medial spine is present at the fusion point of the lobes of the epandrium in all examined members of *Australoconops* and *Microconops*.
103. Posterior hump on epandrium: (0) absent; (1) present. A posterior hump where the cerci attach to the epandrium is present in all examined members of Conopinae (except *Atrichoparia*, *Camrasiconops*, *Heteroconops*, *Pleurocerina*, and *Smartiomyia*) (Fig. 4.1).
104. Phallus: (0) present as single, combined structure; (1) present as at least two, distinct, sclerotized segments. The phallus is divided into a distinct basiphallus and distiphallus, in some cases also with a sclerotized acrophallus, in Pyrgotidae, Strongylophthalmyiidae, and all examined members of *Stylogaster*. In all other examined taxa, the phallus is evident as

only a single, unified segment (Figs. 4.1-4.5). In the past, this structure has been referred to as the “aedeagus” (e.g., Steffeck, 1977). Steyskal (1957) describes the phallus of *Physocephala furcillata* as “short and spherical”. He describes the phallus of *Myopa vesiculosa* and *M. virginica* as “fusiform and tapering.”

105. Phallus leaf-shaped: (0) absent; (1) present. In all examined members of *Zodion* and *Parazodion*, the sclerotized rods of the phallus are fused into one and are contained in a leaf-shaped membranous structure (Fig. 4.4). Steyskal (1957) first notes this peculiar shape to the phallus in *Zodion intermedium*. See note in character 104.
106. Phallus coiled and setose: (0) absent; (1) present. In all examined members of *Dalmannia*, the phallus is coiled and includes two rows of setae along its length (Fig. 4.3). Steyskal (1957) notes the long, setose condition of the phallus in *Dalmannia nigriceps*. See note in character 104.
107. Phallapodeme: (0) cylindrical rod; (1) broadened into wide, thin lobe. In all examined members of *Stylogaster*, the anterior end of the phallapodeme is broadened into a wide thin lobe (Fig. 4.2). Most previous authors (e.g., Griffiths, 1972; Steffeck, 1977; Steyskal, 1957) have referred to this structure as the “aedeagal apodeme.”
108. Ejaculatory apodeme: (0) unsclerotized, or small, sclerotized spine; (1) broadened into a wide, thin lobe. In all examined members of *Stylogaster*, the ejaculatory apodeme is broadened into a wide, thin lobe (Fig. 4.2).

109. Sperm pump: (0) unsclerotized, or weakly sclerotized sphere with short sperm duct; (1) sclerotized sphere with two lateral lobes and a long sperm duct. In all examined members of *Stylogaster*, the sperm pump is well-sclerotized, has two sclerotized lateral lobes, and has a sperm duct which extends well beyond the anterior margin of the epandrium (Fig. 4.2).
110. Pregonites: (0) present; (1) absent. In all outgroup taxa, (except Pyrgotidae), as well as all examined members of *Stylogaster*, well-developed pregonites are present (Fig. 4.2). In all other examined taxa, they are absent.
111. Postgonites: (0) absent; (1) present. Postgonites are present as sclerotized structures arising from the hypandrium, posterior to the phallus in Psilidae, Strongylophthalmyiidae, and all examined members of Conopidae (except *Stylogaster*) (Figs. 4.1, 4.3-4.5). Cole (1927) notes and illustrates prominent “interior forceps” in *Thecophora modesta* and *T. abbreviata*. Steyskal (1957) notes the presence of a “stout anterobasal process” in *Myopa vesiculosa*, *M. virginica*, and a “short linguiform apodeme” in *Zodion intermedium*, but does not note their presence or absence in *Dalmannia nigriceps* and *Physocephala furcillata*.

Morpho-molecular characters

112. Single Glycine inserted at position 364 of AATS: (0) absent; (1) present. A single Glycine insertion is present in AATS in Psilidae and all examined members of *Australoconops*, *Microconops*, and *Smartiomyia*.

113. Repeated sequence in D2 of 28S: (0) absent; (1) present. In all examined members of *Pseudoconops* and *Thecophora* there is a repeated 47bp segment in the D2 region of 28S.

4.2.6. Parsimony analyses

A combined total evidence data matrix, including sequence data from all five gene regions and the morphological data was analyzed. In addition, various subsets of data were examined individually. These subsets are: molecular characters only (allDNA), mitochondrial gene regions (mtDNA: 12S, COI, CytB), nuclear gene regions (nrDNA: 28S, AATS), ribosomal DNA (rDNA: 12S, 28S), protein-coding gene regions (PCG: COI, CytB, AATS), and morphological characters only (morph).

Parsimony analyses were conducted using PAUP* 4.0 (Swofford, 2003). All characters are treated as unordered. An heuristic search with tree bisection-reconnection (TBR) branch swapping in a random stepwise addition of taxa was repeated 100 times. For the total evidence matrix, two weighting schemes, one with equal weighting and the other with the third codon position (nt3) weighted to zero were explored. Likewise, gaps were treated as either missing or as a fifth state. Node support for the most parsimonious tree of the total evidence matrix as well as the most parsimonious trees for each alternate subset and analysis were determined by jackknife resampling with 36% of characters excluded and 100 random replicates. An exclusion of 36% of characters is based on the value $(1/e)$ as recommended by Farris et al. (Farris et al., 1996). Partitioned Bremer support (PBS) (Baker & DeSalle, 1997; Baker et al., 1998; Bremer, 1988, 1994) values for the total

evidence dataset (nt3 weighted to zero, gaps as fifth state) were calculated for each partition (five gene regions plus morphological characters) using TreeRot v3 (Sorenson and Franzosa, 2007) and PAUP* 4.0 (Swofford, 2003) using an heuristic search and 100 random replicates.

4.2.7. Bayesian analysis

Bayesian analyses on the allDNA dataset (nt3 excluded) were conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) with a Markov Chain Monte Carlo (MCMC) method as submitted remotely to the Cornell Computational Biology Service Unit computing cluster (Ithaca, NY, USA). The dataset was partitioned into five genes and parameter estimation is unlinked for each gene partition. Four chains (three hot, one cold) were run simultaneously for 20,000,000 generations. Trees were sampled every 1000 generations and each simulation was run twice. The MCMC chains achieved stationarity (standard deviation of split frequencies <0.005; all parameter estimates asymptotic) at 3,120,000 generations. Following the discard of the first 3120 samples as burn-in, 16,881 samples were used for each simulation to generate a majority-rule consensus tree, posterior probabilities for each node, and branch length estimates. The consensus tree was viewed in TreeView X ver. 0.5 (Page, 1996).

4.3. Results

4.3.1. Individual gene sequence results

Gene region segments are successfully amplified and sequenced for all taxa for COI and 28S. For 12S, 70 of 71 taxa (99%) are successfully amplified and

sequenced. For CytB, 65 of 71 taxa (92%) are successfully amplified and sequenced. For AATS, 68 of 71 taxa (96%) are successfully amplified and sequenced (Table 4.1). The length of each gene region as aligned and analyzed is as follows: 28S-4752bp; 12S-368bp; COI-657bp; CytB-600bp; AATS-447bp.

4.3.2. Concatenated DNA sequence parsimony analysis

The combined data matrix of all five gene regions (allDNA) contains 6824 characters as aligned and analyzed. A total of 4055 (59.4%) characters are constant and 2227 (32.6%) characters are parsimony informative. Base frequencies (A-31.3%; C-16.2%; G-20%; T-32.3%) reveal an A/T bias. Base frequencies are heterogeneous across all taxa ($\chi^2=278.9$, $df=210$, $p<0.01$). Parsimony analysis (with nt3 weighted to zero and gaps counted as a fifth base) recovers one shortest tree (not shown) with a length of 12,770, a consistency index (CI) of 0.372, and a retention index (RI) of 0.635. Jackknife support (JKS) values for each node congruent with the total evidence tree (Fig. 4.6) are given in Table 4.3.

The mtDNA combined data matrix contains 1625 characters as aligned and analyzed. A total of 653 (40.2%) characters are constant and 871 (53.6%) characters are parsimony informative. Base frequencies (A-31.4%; C-16.5%; G-14.8%; T-37.3%) reveal an A/T bias. Base frequencies are heterogeneous across all taxa ($\chi^2=686.6$, $df=210$, $p<0.001$). Parsimony analysis (with nt3 weighted to zero and gaps counted as a fifth base) recovers one shortest tree (not shown; length 3717; CI - 0.265; RI - 0.571). Table 4.3 provides JKS values for each node congruent with the total evidence tree (Fig. 4.6).

The nrDNA combined data matrix contains 5199 characters as aligned and analyzed. A total of 2712 (52.2%) characters are constant and 1701 (32.7%) characters are parsimony informative. Base frequencies (A-31.4%; C-16.1%; G-22%; T-30.5%) reveal an A/T bias. Base frequencies are homogeneous across all taxa ($\chi^2=83.7$; $df=210$; $p=1.00$). Parsimony analysis (with nt3 weighted to zero and gaps counted as a fifth base) recovers two shortest trees (not shown; length 8957; CI - 0.420; RI - 0.667). Table 4.3 provides JKS values for each node congruent with the total evidence tree (Fig. 4.6).

The rDNA combined data matrix contains 5120 characters as aligned and analyzed. A total of 2611 (51%) characters are constant and 1696 (33.1%) characters are parsimony informative. Base frequencies (A-32%; C-15.6%; G-21.2%; T-31.2%) reveal an A/T bias. Base frequencies are homogeneous across all taxa ($\chi^2=98.1$; $df=210$; $p=1.00$). Parsimony analysis (with nt3 weighted to zero and gaps counted as a fifth base) recovers fourteen shortest trees (not shown; length 10,139; CI - 0.404; RI - 0.649). Table 4.3 provides JKS values for each node congruent with the total evidence tree (Fig. 4.6).

The PCG combined data matrix contains 1704 characters as aligned and analyzed. A total of 744 (43.7%) characters are constant and 883 (51.8%) characters are parsimony informative. Base frequencies (A-25.5%; C-19.5%; G-21.5%; T-33.5%) reveal an A/T bias. Base frequencies are homogeneous across all taxa ($\chi^2=169.7$; $df=210$; $p=0.98$). Parsimony analysis (with nt3 weighted to zero and gaps counted as a fifth base) recovers 94 shortest trees (not shown; length 2534; CI -

0.259; RI - 0.604). Table 4.3 provides JKS values for each node congruent with the total evidence tree (Fig. 4.6).

A plot of uncorrected pairwise divergence at codon positions one and two (nt1 and nt2) versus uncorrected pairwise divergence at nt3 for the PCG subset (not shown) shows a plateau in sequence divergence in nt3 corresponding to approximately 6% sequence divergence in nt1 and nt2. This plateau corresponds to the divergence between genera of Conopidae and suggests saturation of substitutions in nt3 beyond this level.

4.3.3. Concatenated gene sequence Bayesian analysis

The phylogram generated by Bayesian analysis of the allDNA data subset (not shown) differs from that of the parsimony analysis (Fig. 4.6) and has 100% posterior probabilities (PP) at 70% of nodes. A clade including all members of Schizophora is recovered with 97% PP. A clade including all members of Conopidae is recovered with 100% PP. A clade including all members of Conopinae is recovered with 100% PP. A clade including all members of *Zodion* and *Parazodion* is recovered with 99% PP. A clade including all members of *Dalmannia* is recovered with 100% PP. A clade including all members of Myopinae (excluding *Sicus* and *Zodion*) is recovered with 100% PP. A clade including all members of *Stylogaster* is recovered with 100% PP. While a clade including all members of Conopidae (excluding *Stylogaster*) is recovered with 95% PP, other relationships between subfamilies are not resolved. Members of *Dalmannia*, *Sicus*, and (*Zodion*+*Parazodion*) are in an unresolved polytomy. This polytomy also has very little branch length between it and the clade

containing members of Myopinae (excluding *Zodion* and *Sicus*) suggesting a lack of resolution of inter-subfamily relationships.

4.3.4. Morphological character analysis

A total of 113 characters are included in the analysis. Characters included from each body region are as follows: head – 36 characters (31.9%); thorax, including legs – 19 characters (16.8%); wing – 13 characters (11.5%); female abdomen, including terminalia – 15 characters (13.3%); male abdomen, including terminalia – 28 characters (24.8%); morpho-molecular – 2 characters (1.8%). No characters are constant and all are parsimony informative. Parsimony analysis (all characters equally weighted) recovers four shortest trees (not shown; length 193; CI – 0.611; RI – 0.951). Table 4.3 provides JKS values for each node congruent with the total evidence tree (Fig. 4.11).

4.3.5. Total evidence parsimony analysis

The combined total evidence data matrix contains 6937 characters as aligned and analyzed. A total of 3355 (48.4%) characters are constant and 2692 (38.8%) characters are parsimony informative. Parsimony analysis (with nt3 weighted to zero and gaps counted as a fifth base) recovers one shortest tree (Fig. 4.11; length 12,985; CI – 0.375; RI – 0.655). PBS values for each data subset, as well as JKS values for the total evidence analysis, are given in Table 4.3. Partitioned Bremer support analysis indicates that the morphological character dataset provides 6.6% of overall Bremer support versus 93.4% for the DNA sequence dataset. The mtDNA data subset provides 27.3% of overall Bremer support versus 66.1% for the nrDNA

dataset. The rDNA data subset provides 69.5% of overall Bremer support versus 23.9% for the PCG data subset.

The most parsimonious tree (Fig. 4.6) is well supported with 59 of 68 nodes (87%) having a JKS value greater than 64% (i.e., $1-1/e$). A clade including all members of Schizophora is recovered as monophyletic with strong support (JKS – 100; total Bremer support (TBS) – 47; morphological autapomorphies (MAA) – 1:1, 17:1, 19:1, 72:1). A clade including all members of Conopidae is recovered with strong support (JKS – 99; TBS – 32; MAA – 27:1, 33:1, 38:1, 58:1; other morphological apomorphies and reversals (MA) – 22:1, 78:1). Each of the proposed subfamilies of Conopidae is recovered as monophyletic with strong support.

The clade including all members of Conopinae is recovered with strong support (JKS – 100; TBS – 88; MAA – 5:1, 26:1, 29:1, 93:1, 100:1; MA – 11:1, 12:1, 21:1, 30:1, 32:1, 67:1, 95:2). The clade including all members of *Zodion*, plus members of *Parazodion*, is recovered with strong support (JKS – 100; TBS – 111; MAA – 10:1, 37:2, 55:1, 97:1, 105:1; MA – 39:1, 98:1). The clade including all members of Myopinae, minus *Sicus* and *Zodion*, is recovered with strong support (JKS – 100; TBS, 34; MAA – 37:1, 42:1, 62:1; MA – 39:1, 98:1). The clade including all members of Dalmanniinae, minus *Parazodion*, is recovered with strong support (JKS – 100; TBS – 154; MAA – 77:1, 106:1; MA – 11:1, 12:1, 24:1, 39:1, 95:2). The clade including all members of Stylogastrinae is recovered with strong support (JKS – 100; TBS – 172; MAA – 14:1, 18:1, 40:1, 69:1, 71:1, 80:1, 95:1, 96:2, 107:1, 108:1, 109:1; MA – 30:1, 31:1, 32:1, 51:1, 64:1, 68:0, 91:1, 104:1).

Relationships between subfamilies of Conopidae are also determined. A clade including all members of Conopinae plus members of *Zodion* and *Parazodion* is recovered with strong support (JKS – 95; TBS – 13; MAA – 35:1, 43:1, 70:1, 92:1; MA – 64:1, 66:1). Conopinae, plus *Zodion*, *Parazodion*, and the single specimen of *Sicus*, is recovered with moderate support (JKS – 79; TBS – 7; MAA – 61:1, 63:1). Conopidae, excluding members of *Dalmannia* and *Stylogaster* is recovered with strong support (JKS – 99; TBS – 18; MAA – 74:1, 76:1, 87:1, 90:1; MA – 89:1). Conopidae, excluding members of *Stylogaster*, is recovered with strong support (JKS – 98; TBS – 13; MAA – 60:1, 81:1, 83:1, 96:1; MA – 15:1, 53:1, 110:1, 111:1).

Parsimony analysis with nt3 weighted to zero and gaps coded as missing recovered three most parsimonious trees (treelength=10309, CI=0.349, RI=0.653), but with lower CI and RI scores and reduced JKS values at most nodes. Analysis with equal weights for all characters and gaps coded as missing recovered two most parsimonious trees (treelength=18542, CI=0.259, RI=0.553), but with lower CI and RI scores and reduced JKS values at most nodes. Analysis with equal weights for all characters and gaps coded as a fifth base recovered one most parsimonious tree (treelength=21261, CI=0.286, RI=0.565), but with lower CI and RI scores and reduced JKS values at most nodes (Table 4.3). Topologies for these alternate analyses (not shown) differed from the tree shown in Fig. 4.6.

4.4. Discussion

4.4.1. Monophyly and character states of *Schizophora*

While determining groundplan morphological states for *Schizophora* is not

the focus of the present research, apomorphies for Schizophora are determined here in order to properly interpret character states in Conopidae. In the present analysis, Schizophora is recovered as monophyletic with strong support by the total evidence parsimony analysis and all alternate analyses. Morphological autapomorphies for the clade include: presence of a ptilinum, facial carina, and facial ridge; and fusion of female abdominal tergite and sternite 7.

Frey (1921) suggests that an elongate cell cup [“Analzelle sehr lang”] is characteristic of Conopidae. Hennig (1958) considers this state to be plesiomorphic to the Schizophora, yet is uncertain of what the groundplan state is for Conopidae. Other authors (Griffiths, 1972; Schneider, 2010; Speight, 1969) state that an elongate cell cup is present only in some Conopidae and is secondarily convergent with Syrphidae. As an alternate means to assess this character in the present research, the length of vein CuA_2+A_1 is compared to the length of crossvein dm-cu (character 65). When measured thusly, a long vein CuA_2+A_1 (equivalent to a short cell cup) is found to be an autapomorphy of Schizophora. Modifications to this character include a secondary reversion to a short vein CuA_2+A_1 (or long cell cup) in some members of Conopinae and an extreme lengthening of vein CuA_2+A_1 (or shortening of cell cup) in *Stylogaster*.

4.4.2. Monophyly and character states of Conopidae

The family Conopidae is recovered as monophyletic with strong support by the total evidence parsimony analysis and all alternate analyses. Morphological autapomorphies for the family include: a thickened arista; a prementum that is fused

into a tube; the presence of posterolateral extensions of the basisternum; and vein M deflected towards or joining vein R_{4+5} . Two additional synapomorphies of Conopidae are an elongate pedicel and the absence of an epiproct in the female, but these character states are also seen in Pyrgotidae. An elongate prementum is also an autapomorphy of Conopidae, but has been secondarily reduced in *Myopa occulta*, *Heteroconops* sp., and *Leopoldius coronatus*. Filiform, fused labella is an autapomorphy of Conopidae that has been reversed to a broad, separate state in members of Conopinae, *Zodion*, and *Parazodion*. A prominent row of bristles on the posterior surface of the mesofemur is also an autapomorphy of Conopidae, but has been secondarily lost in members of *Physocephala*.

An open cell r_{4+5} ["R₅"] is the plesiomorphic state for Conopidae, according to Hendel (1936) and Hennig (1966), and the petiolate state has derived convergently in Conopinae and Stylogasteridae. McAlpine (1989) considers the absence of a pterostigma and the convergence of veins M and R_{4+5} to be apomorphies of Conopidae with respect to the rest of the Acalypttratae. In the present analysis, the deflection of vein M towards vein R_{4+5} (58) is an autapomorphy of Conopidae. Whether this deflection results in a petiolate state varies within some groups. All examined members of *Dalmannia*, *Pseudoconops*, *Sicus*, and *Thecophora* have the veins separate. Species of the genera *Myopa* and *Zodion* can be found with a small petiole, with vein M meeting vein R_{4+5} at the costa, or with the veins separate. This variability even within some genera suggests that the petiolate state may be autapomorphic for Conopidae, with sporadic loss in some lineages and isolated taxa.

Hennig (1966) notes characteristic changes in the overall shape of the wings in some groups. This overall change may explain the evolution of the petiolate state. In all examined members of *Dalmannia*, *Sicus*, *Thecophora*, *Pseudoconops*, as well as in some species of *Myopa* and *Zodion*, there is a short and broad overall shape to the wing. This foreshortening has led to the loss of the petiolate state. In all remaining examined members of Conopidae, the wing retains its longer, narrower shape as well as the petiolate state. In certain members of Conopinae, vein M has been displaced even further, meeting vein R_{4+5} at a 90° angle and resulting in an extremely long petiole (59).

Based on its presence in Syrphidae, crossvein sc-r (or “Sc forked at its tip”) is considered by some authors a plesiomorphy of Conopidae (Hendel, 1936; Hennig, 1966; McAlpine, 1989; Schneider, 2010). This crossvein is absent in *Toxomerus marginatus*, the syrphid included here. It is present only in some Syrphidae and is likely associated with a reduction in the pterostigma (Vockeroth & Thompson, 1987). The most parsimonious interpretation of the character based on the present data is that crossvein sc-r has arisen independently in Conopinae+Zodioninae and Stylogastrinae (64).

Speight (1969) is the first to note the posterolateral extensions of the basisternum as an autapomorphy of Conopidae. This is used as a key diagnostic character by most subsequent authors (e.g., Griffiths, 1972, McAlpine, 1989, Schneider, 2010). Likewise, the fused, tube-like prementum [“proboscis” or “haustellum”] is used as a diagnostic character of Conopidae by Latreille (1802) and

every subsequent author. Griffiths (1972) and McAlpine (1989) both list an elongate pedicel as an apomorphy of Conopidae. In the present analysis, all of these character states are confirmed as apomorphies of Conopidae (38, 33, 22).

Griffiths (1972) suggests that the sclerotization of the posterior of the hypandrium, forming it into a sheath is an apomorphy of Conopidae. In the present analysis, this character state is an autapomorphy of Conopinae (100).

McAlpine (1989) lists fused female cerci as an apomorphy of Conopidae. The present analysis finds elongate, broad, and flattened cerci (79) to be an autapomorphy of (Conopinae+Zodioninae)+*Sicus* that has been secondarily lost in *Parazodion*.

Although with varying interpretations of the sclerites involved (see note in the description of character 88), past authors (Griffiths, 1972; McAlpine, 1989; Skevington et al., 2010; Steyskal, 1957) note the presence of a male abdominal syntergosternite 7+8 but suggest that this character state is apomorphic to Conopidae. The present analysis suggests that this character is autapomorphic to Schizophora with secondary loss in Psilidae.

Griffiths (1972) and McAlpine (1989) both suggest that the fusion of male abdominal tergite 6 laterally with syntergosternite 7+8 is an apomorphy of Conopidae. Griffiths (1972) also lists the absence of postgonites as an apomorphy of Conopidae. Based on his illustrations, however, Griffiths' "postgonites" are re-interpreted as pregonites. The present analysis finds that both of these character states are autapomorphies of (((Conopinae+Zodioninae)+*Sicus*)+Myopinae)

+Dalmanniinae (96, 110).

4.4.3. Monophyly and character states of clades within Conopidae

The subfamily Conopinae is recovered as monophyletic with strong support by the total evidence parsimony analysis and all alternate analyses. Membership, based on the current taxon sampling, includes: *Atrichoparia*, *Australoconops*, *Camrasiconops*, *Conops* (*Asiconops*, *Conops*, and *Smithiconops*), *Euconops*, *Heteroconops*, *Leopoldius*, *Microconops*, *Physocephala*, *Physoconops* (*Pachyconops* and *Physoconops*), *Pleurocerina*, and *Smartiomyia*. Morphological autapomorphies for the subfamily include: a reduced or absent ocellar tubercle; an apical, stylate arista; a ventrally expanded second aristomere; an epandrium fused beyond the cerci; and a heavily sclerotized dorsal bridge of the hypandrium forming a nearly complete tube around the phallus. Another likely autapomorphy for the subfamily is a single anterior arm on the hypandrium, which has been secondarily lost in *Atrichoparia* sp. B. Other synapomorphies that define Conopinae, but are also observed in other groups, include: an absence of ocellar and postocellar bristles; an elongate scape; a pointed anterior margin of the subcranial cavity; a reduced or absent maxillary palpus; a vena spuria; and the absence of posterior surstyli.

Nearly every previous author has noted the elongate antennae with stylate, apical aristae and the presence of vena spuria as characteristic of Conopinae. Schneider (2010) further suggests that the vena spuria are more prevalent in larger conopines and may be related to either adding strength to the wing or increasing mimetic similarity to Hymenoptera. The present analysis confirms both of these

characters (26, 67) as apomorphies of Conopinae.

According to Hennig (1966; see also Hendel, 1936), the plesiomorphic condition for the insertion of veins Sc, R₁, and R₂₊₃ is to be observed in *Stylogaster*. In this genus, the insertion of the three veins is equidistant along the costa. Hennig further asserts that in Conopinae, the insertion of R₂₊₃ is deflected proximally so as to be near or at the insertion of R₁. In Myopinae (including *Dalmannia* but excluding *Zodion* in Hennig's analysis), it is the insertion of R₁ instead that is deflected proximally so as to insert at or near the insertion of Sc.

The present analysis supports Hennig's hypothesis with some revision. The plesiomorphic state is observed in *Stylogaster* for a suite of characters related to the insertion of veins into the costa. The Sc vein is extended distally in all Conopidae excluding *Stylogaster* (60). The R₁ vein is also extended distally and ends near the insertion of vein R₂₊₃ in members of Conopinae, *Parazodion*, *Sicus*, and *Zodion* (61, 63). Conversely, vein R₁ is deflected proximally and fuses with vein Sc in *Myopa*, *Thecophora*, and *Pseudoconops* (62).

Speight (1969) claims that the shape of the basisternum in Conopinae is distinct from the shape that is common to the rest of the family. In the present interpretation, the overall shape of the basisternum in Conopinae does not differ significantly from that of the outgroup taxa and most other Conopidae. It is the members of Myopinae (excluding *Sicus* and *Zodion*) and Zodioninae (including *Parazodion*) that have autapomorphic states for this character (37).

Congeneric and conspecific taxa within Conopinae are recovered as

monophyletic with strong support, except for *Conops* in which the three subgenera are individually monophyletic, but are not recovered together. Also, two specimens of *Microconops ornatus* are recovered as paraphyletic with respect to *Microconops tasmaniensis*. This indicates a possible synonymy of these nearly identical species. Six particularly poorly supported nodes and one only moderately supported node (nodes 8, 13, 14, 22, 23, 25, 26; Fig. 4.6 and Table 4.3) are recovered within Conopinae. If all of these nodes were to be collapsed, Conopinae would be represented by a polytomy of eight, separate monophyletic clades, including two monotypic clades (*Euconops* and *Conops* (*Smithiconops*)). As alternate analyses offer conflicting topologies for this clade, the octotomy likely represents the best phylogenetic hypothesis for this clade based on the present data. The lack of resolution reflects undersampling in this clade. The current dataset represents only fifteen genera and subgenera of over 50 proposed for the subfamily. More taxa and more characters targeted at resolving conopine relationships are needed to resolve relationships within this subfamily.

The absence of ocelli has often been described as characteristic of Conopinae (e.g., Hendel, 1936; Skevington et al., 2010; Smith & Peterson, 1987). Some authors (Hennig, 1966; De Meijere, 1904) note that while three ocelli may be the groundplan state for Conopidae, the central and lateral ocelli may have been lost independently by groups within Conopinae. The current research supports the latter theory. In the present analysis, the central ocellus, the lateral ocelli, and the ocellar tubercle have been lost independently by separate lineages within Conopinae (2, 3, 4).

Likewise, Hennig (1966) suggests that a developed lunule is a shared derived character of the Conopinae. The present analysis finds that a well-developed lunule is not present in all members of Conopinae (16). It is indeterminate as to when and how many times this character has arisen within Conopinae.

A number of additional character states vary between conopine taxa. In addition to the ones previously mentioned, these character states include: texture of the frons; posterior margin of the compound eye; shape of the facial ridge where it meets the subcranial cavity; presence of a transverse dorsal ridge on the pedicel; elongate first flagellomere; reduced stylate arista; absence of maxillary palpus; elongate prementum; shape of the metafemur; absence of prominent row of setae on mesofemur; bare ventral half of proepisternum; reduced scutellum; wing pattern; elongate petiole of vein $R_{4+5}+M$; length of vein CuA_2+A_1 ; number of rows of spicules on the ventral genital plate; size and shape of male abdominal sternites 2-4 and tergites 2-4; presence of anterior arms on the hypandrium; presence of lobes on the subepandrial sclerite; presence of a medial spine on the epandrium; presence of a posterior hump on the epandrium; and presence of a single glycine inserted at position 364 of AATS. Further investigation with more conopine taxa will be necessary to hypothesize on the evolutionary history of these characters within Conopinae.

The subfamily Zodioninae is recovered as monophyletic with strong support by the total evidence parsimony analysis and all alternate analyses. Membership, based on the current taxon sampling, includes *Parazodion* and *Zodion*. Morphological

autapomorphies for the subfamily include: two medial rows of convergent setae on the frons; a basisternum that is narrow, yet divided posteriorly; more than two pairs of scutellar bristles; a developed, fleshy hypoproct in the male; and a leaf-shaped phallus with a single central, sclerotized rod. Other synapomorphies that define Zodioninae, but are also observed in other groups include: elongate, narrow posterolateral extensions of the basisternum; and the presence of two, separate, anterior arms on the hypandrium.

The genus *Parazodion* is recovered as nested within the genus *Zodion*. This is contrary to its traditional placement within Dalmanniinae. This previous placement is based almost exclusively on the condition of the female terminalia. While previous authors (e.g., Camras, 1953a; Kröber, 1927a; Skevington et al., 2010) refer to the female terminalia in both *Parazodion* and *Dalmannia* as an “ovipositor”, closer examination reveals superficially similar, yet distinct modifications of segment 7 (77). Likewise, abdominal sternite 5 in *Parazodion* is fused with tergite 5 and features rows of spicules. These are both derived character states absent in *Dalmannia* (70, 74).

Steyskal (1957) suggests that the male terminalia of *Zodion* is so different from that of other Myopinae that it could serve as the basis for subfamily designation. Steffek (1977) confirms that the dual anterior arms on the hypandrium and the unique shape of the phallus separate Zodioninae from the Myopinae. While dual hypandrial anterior hypandrial arms are also observed in Myopinae, both of these character states are confirmed by the present analysis as

apomorphies of Zodioninae (98, 105).

A clade including Conopinae+Zodioninae is recovered as monophyletic with strong support by the total evidence parsimony analysis and most alternate analyses. Morphological autapomorphies for the clade include: a reduced labellum that is not folded back along the prementum; a shiny, apical patch on the metafemur; a fusion of female abdominal sternite 5 and tergite 5; and a narrow, stalk-like attachment between the cerci and epandrium. Other synapomorphies that define Conopinae+Zodioninae, but are also observed in other groups include: the presence of crossvein sc-r and a curved vein CuA₂.

Frey (1921) notes that members of Conopinae and Zodioninae share an elongate prementum ["bulbus"], but not an enlargement of the labella. Hennig (1966) considers the elongate labella to be an apomorphy of most Myopinae (including *Dalmannia* and *Sicus* in his analysis) with *Zodion* an adelphotaxon retaining the plesiomorphic short labella. Hennig also asserts that the elongate labella found in *Stylogaster* is the product of secondary convergence.

In the present research, the length of the labella is compared to that of the prementum (35) and is found to be equal in all outgroup taxa as well as all members of Conopidae except Conopinae, *Zodion*, and *Parazodion*. The short labella, projecting forward from the apex of the prementum is, therefore, an autoapomorphy of Conopinae+Zodioninae. Likewise, the broad, unfused labella (36) are an autapomorphic reversal of the fused, filiform state found in all other Conopidae.

A clade including (Conopinae+Zodioninae)+*Sicus* is recovered with moderate

support by the total evidence parsimony analysis. Morphological autapomorphies for the clade include: a terminus of vein R_1 at a point beyond six-tenths of the length of the costa; and a terminus of vein R_{2+3} very near to the terminus of vein R_1 . The taxonomic status of *Sicus* with regards to other subfamilies of Conopidae cannot be determined based on a single included taxon. Further sampling of *Sicus* and related genera will be necessary to ascertain its status.

Zimina (1958, 1960) proposes Sicini as a separate tribe within Myopinae based on the shape of the basisternum [“whole plate of the prosternum”]; the absence of fusion or a crossvein between veins Sc and R_1 ; an elongate cell cup; and long red bristles on the mesonotum. In the present analysis, the shape of the basisternum and the wing vein characters in *Sicus* are all in a state plesiomorphic to the Conopidae (37, 62, 64, 65). The final character may be a species-specific autapomorphy. There are, therefore, no apomorphies to define a separate *Sicus* clade.

The subfamily Myopinae is recovered as monophyletic with strong support by the total evidence parsimony analysis and most alternate analyses. Membership, based on the current taxon sampling, includes: *Myopa*, *Pseudoconops*, and *Thecophora*. Morphological autapomorphies for the subfamily include: a reduced, short, narrow basisternum; a double row of spines on the ventral surface of the femora; and veins Sc and R_1 fused before reaching the costa. Other synapomorphies that define Myopinae, but are also observed in other groups include: elongate, narrow posterolateral extensions of the basisternum; and two, separate anterior

arms on the hypandrium.

Kröber (1939a) states that the arista reduced to two segments is characteristic of Myopinae (including *Sicus* and *Zodion* in his analysis). In Hennig's (1966) opinion, members of Myopinae (including *Dalmannia*, *Sicus*, and *Zodion* in his analysis) share a derived character of a reduced antenna overall. In the present analysis, no Conopidae were found with fewer than three aristomeres. Also, in every character state relating to antennae (21-29), Myopinae (excluding *Dalmannia* and *Zodion*) are found exclusively in the plesiomorphic state.

Hennig (1966) suggests (see also Kröber 1939a) that the groundplan for Myopinae (including *Dalmannia*, *Sicus*, and *Zodion* in his analysis) includes deep, defined facial foveae with a weak, but present, medial carina. Also synapomorphic for the group is an expansion of the gena leading to an "inflated" look to the head. In the present analysis, Myopinae is found to have foveae and a medial carina (15, 17) that are in the state apomorphic to Schizophora. The expansion of the gena (13) is autapomorphic to members of the genus *Myopa*.

A clade including ((Conopinae+Zodioninae)+*Sicus*)+Myopinae is recovered with strong support by the total evidence parsimony analysis and most alternate analyses. Morphological autapomorphies for the clade include: female abdominal sternite 5 with rows of spicules, and often a prominent ventral genital plate; female segment 7 deflected ventrally to meet tergite six at a 90° angle; male abdominal sternite 5 wide and broad with a posterior row of spicules or thick setae; and male abdominal sternite 8 present as a clearly delineated portion of syntergosternite 7+8.

Other synapomorphies that define the clade, but are also observed in other groups include: syntergosternite 7+8 present as a broad, hemispherical sclerite. Rows of spicules on female abdominal sternite 6 is also likely autapomorphic for the clade, but has been lost in *Parazodion*. The presence of anterior surstyli is also a likely autapomorphy of the clade, but has been secondarily lost in Conopinae.

Steyskal (1957) notes the presence of a clearly delineated male abdominal sternite 8 in representatives of Conopinae, Myopinae, and Zodioninae, but not Dalmanniinae. Griffiths (1972) asserts that this is a misidentification and that sternite 8 is absent. In the present analysis, the presence of sternite 8 is an autapomorphy of ((Conopinae+Zodioninae)+*Sicus*)+ Myopinae (90).

Past authors (Griffiths, 1972; McAlpine, 1989) suggest that a ventral flexion of the female postabdomen is a characteristic of Conopidae (excluding Stylogastrinae). In the present analysis, this character is determined by the angle formed between female abdominal segments 6 and 7 (76). While members of *Dalmannia* do display a ventral curvature of the entire abdomen, the angle between tergite 6 and segment 7 is in the plesiomorphic state. The full deflection of segment 7 to a 90° angle is an autapomorphy of ((Conopinae+Zodioninae)+*Sicus*)+ Myopinae.

The subfamily Dalmanniinae, including only the genus *Dalmannia*, is recovered with strong support by the total evidence parsimony analysis and all alternate analyses. Morphological autapomorphies for the subfamily include: female abdominal segment 7 compressed laterally along its entire length; and the phallus coiled and setose along its entire length. Other synapomorphies that define

Dalmanniinae, but are also observed in other groups include: absence of ocellar and postocellar bristles; a broadened pedicel; elongate, narrow posterolateral extensions of the basisternum; and absence of posterior surstyli.

Many authors (e.g., Schneider, 2010; Skevington et al., 2010; Speight, 1969) describe males of *Dalmannia* as having only five abdominal segments before the terminalia. Steyskal (1957) notes a narrow sixth sclerite or “protandrium” before the terminalia in *Dalmannia nigriceps*. In the present analysis, the presence of syntergosternite 7+8 in the males is an autapomorphy of Schizophora (88), but its narrow state (89) is an apomorphy derived independently in *Dalmannia* and New World *Stylogaster*.

Most authors (e.g., Steffeck, 1977; Zimina, 1960) suggest an elongate phallus and “ovipositor” as characteristic of Dalmanniinae. The present analysis recovers both of these character states as autapomorphies of Dalmanniinae (77, 106).

Zimina (1960) proposes the union of veins Sc and R₁ at the costa, without a crossvein or fusion, and a short cell cup as characteristics of Dalmanniinae. Steffeck (1977) also includes the U-shaped hypandrium as characteristic of Dalmanniinae. According to the present analysis, in all four of these characters, Dalmanniinae displays the state plesiomorphic to Conopidae (62, 64, 65, 98).

A clade including (((Conopinae+Zodioninae)+*Sicus*)+Myopinae)+Dalmanniinae is recovered with strong support by the total evidence parsimony analysis and all alternate analyses. Morphological autapomorphies for the clade include: vein Sc ending beyond a point four-tenths of the length of the costa; female

abdominal sternite 8 divided into two, sclerotized lobes; presence of sclerotized posteroventral hooks on female syntergite 8+9; and male abdominal tergite 6 narrow, bare, and fused with syntergosternite 7+8. Other synapomorphies that define the clade, but are also observed in other groups include: presence of facial foveae; katepisternum with bristles and/or setae; absence of pregonites; and presence of postgonites.

Based on the assumption that *Parazodion*, *Paramyopa*, and *Dalmannia* represent a clade within Myopinae, Hennig (1966) concludes that the ventral genital plate on female abdominal sternite 5 is a synapomorphy of Conopidae (excluding *Stylogaster*) and that it is secondarily absent in *Dalmannia*+*Parazodion*+*Paramyopa*. In the present analysis, the expanded ventral genital plate is found to be quite variable even within subfamilies. Individual genera may have greatly elongated or nearly absent ventral genital plates. Instead of using this character, the presence of rows of spicules on female abdominal sternite 5 is found to be an autapomorphy of ((Conopinae+ Zodioninae)+*Sicus*)+Myopinae (74).

The subfamily Stylogastrinae, including only the genus *Stylogaster*, is recovered as monophyletic with strong support by the total evidence analysis and all alternate analyses. Morphological autapomorphies for the subfamily include: compound eye with ommatidia larger anteriorly; facial carina strongly developed; presence of protibial apical spurs; absence of female abdominal sternites 2 and 3; fusion of female abdominal tergite and sternite 6 into a ring; a sclerotized and elongate hypoproct in the female; bi- or tri-lobed posterior surstyli; a broad, internal

and hemispherical abdominal tergite 6 in the male; both the phallapodeme and ejaculatory apodeme broadened into a wide, thin lobe; and the sperm pump modified into a sclerotized sphere with two lateral lobes and a long sperm duct. Other synapomorphies that define Stylogastrinae, but are also observed in other groups include: an anteriorly pointed margin to the subcranial cavity; absence of maxillary palpi; presence of bristles on the anepimeron; presence of crossvein sc-r; a narrow alula; elongate male cerci; and a phallus with two, distinct, sclerotized segments. Elongate, lateral lobes on female abdominal sternite 8 are also likely to be an autapomorphy of Stylogastrinae and have been subsequently lost in *Stylogaster decorata* and *S. neglecta*.

Williston (1885) and Speight (1969) both note the presence of apical tibial spurs as characteristic of Stylogastrinae. Hennig (1966) concludes that the fused female abdominal tergite and sternite 6 is an apomorphy of Stylogastrinae. Steffeck (1977) suggests that elongate male cerci and a greatly enlarged ejaculatory apodeme are autapomorphies of *Stylogaster*. Kotrba (1997) suggests the presence of lobes on female sternite 8 as characteristic of *Stylogaster*. In the present research, all of the aforementioned character states are confirmed as apomorphies of Stylogastrinae (40, 71, 91, 107, 82).

Hennig (1966) suggests that an elongate first flagellomere is another apomorphy of Stylogastrinae. In the present analysis, this character state is observed in only two species of *Stylogaster*. Although these species do form a well-supported, monophyletic clade, this character state cannot be considered an

apomorphy of Stylogastrinae (25).

4.4.4. Other morphological characters considered

Griffiths (1972) states that the elongate phallus [“aedeagus”] of *Dalmannia* and *Stylogaster* represents the plesiomorphic state of all Conopidae, with secondary reduction evident in some members of the family. This state represents an autapomorphy of the “Tephritoinea” to which he feels Conopidae belongs. Hennig (1966) and Schneider (2010) both state that correlation between phallic length and the shape of female terminalia is likely strong and is related to host choice and not necessarily common ancestry. Steffek (1977) and Schneider (2010) both note that phallic structures are often highly plastic, even within closely related Diptera, and that the similarity between some Conopidae and other groups should not be used as evidence of common ancestry. The present analysis supports the findings of Steffek (1977) and Schneider (2010). Character states of the phallus are limited to apomorphies of *Stylogaster* (104), *Zodion+Parazodion* (105), and *Dalmannia* (106), with no means to determine the plesiomorphic state of the phallus of Conopidae *sensu lato*.

Previous authors suggest that spermathecae number is characteristic for each subfamily. Griffiths (1972) lists two spermathecae as an apomorphy of all Conopidae. Smith and Peterson (1987) and Speight (1969) describe *Dalmanniinae* as having two spermathecae, whereas Skevington et al. (2010) describe them as having only one. Smith and Peterson (1987) and Speight (1969) describe *Stylogastrinae* as having two spermathecae. Smith and Peterson (1987) note four

spermathecae in Conopinae and Myopinae (including *Zodion* and *Sicus*). In the present research, it is found that the size, location, and degree of sclerotization of spermathecae are highly variable. Even in specimens that are carefully prepared, spermathecae can often be lost.

While not as a part of phylogenetic analysis, a number of other characters have been included in diagnoses of species of Conopidae. These characters include the presence of a pterostigma and the confluence of wing cells bm and dm. These characters were examined, but were not phylogenetically informative.

4.4.5. Conclusions

The present analysis represents the first comprehensive analysis of the phylogenetic systematics of Conopidae. Both molecular and morphological data contribute to a robust hypothesis of relationships within the family. The monophyly of both Schizophora and Conopidae is confirmed. The monophyly of five subfamilies is confirmed, with the reinstatement of the subfamily Zodioninae. It is proposed to remove *Parazodion* from Dalmanniinae and place it within Zodioninae. Likewise, *Sicus* should be removed from Myopinae, although its current status is uncertain pending further analysis. Relationships between subfamilies are determined with strong support. Conopinae and Zodioninae form a monophyletic clade most recognizable by the absence of an elongate, ventrally folded labellum. Wing vein characters define the clade (Conopinae+Zodioninae)+*Sicus*. Characters of the male and female abdomen, including modifications to the female fifth sternite, sometimes developed into a ventral genital plate, are autapomorphies of the Conopidae

(excluding *Dalmannia* and *Stylogaster*). A modification of the female terminalia to include sclerotized hooks is autapomorphous to Conopidae (excluding *Stylogaster*). This development is likely associated with the piercing of the host cuticle during oviposition. While absent in *Stylogaster*, a similar function may be served by the sclerotized hooks observed on eggs of members of that genus.

Morphological characters from all adult body regions contribute informative apomorphic states. Gross modifications of some structures, including antennae and wing venation, define some clades. Male and female terminalia would appear to be of high value for species identification in some groups. Members of *Zodion*, *Parazodion*, and *Stylogaster*, in particular, display a variety of structural variations that will be of future value. In the remaining subfamilies, the terminalia appear to be quite uniform across the diversity of the group. In the case of Conopinae, the lack of resolution in the cladogram may indicate a rapid and recent radiation of the group with a great variety of body shapes, but little genetic or genitalic variation.

5. Revision of the genera of Conopidae based on morphological data

5.1. Introduction

Conopidae have been the subject of sporadic, but considerable taxonomic effort over the past 250 years. Species of Conopidae were among the original species descriptions of Linnaeus (1758, 1761). The major figures in eighteenth and nineteenth century insect taxonomy all contributed in some way to the systematics of Conopidae, including Fabricius (1775, 1782, 1787, 1794, 1805), Latreille (1796, 1802), Say (1823, 1829), Robineau-Desvoidy (1830, 1853), Wiedemann (1830), Macquart (1834, 1835, 1840, 1843, 1846, 1851), Rondani (1856, 1857, 1863, 1865), Bigot (1859, 1887), and Loew (1847, 1853, 1863, 1866). It was Williston (1882, 1883, 1885, 1888, 1892a, 1892b, 1893), however, that produced the first major works focused on members of Conopidae. Meunier (1899, 1912, 1916) described the first confirmed fossil specimens of Conopidae. Kröber took a global approach, describing over twenty genera and 200 species in a series of 39 taxonomic papers (e.g., Kröber 1915a, 1936a, 1939a, 1940a) published in the first half of the twentieth century. The Afrotropical and Oriental regions were given early taxonomic attention by Brunetti (1912, 1923, 1925a, 1925b, 1925c, 1925d, 1929) and Chen (1939) respectively. Early regional taxonomic revisions were completed for *Stylogaster* Macquart, 1835 (Aldrich, 1930; Lopes, 1937) and *Dalmannia* Robineau-Desvoidy, 1830 (Bohart, 1938). Conopidology in the second half of the twentieth century has been dominated by the work of Camras. Working on all subfamilies, from all parts of the world, Camras has described over a dozen genera and subgenera and 150

species in over 40 publications (e.g., Camras, 1955a, 1961, 1994a, 2004). Smith has also contributed to present knowledge of Conopidae, mainly through his contributions to world catalogues (1969, 1975, 1980, 1989). Stuke has also been prolific, contributing a handful of new descriptions and revisions, as well as numerous regional faunal lists (e.g., 2001, 2005a, 2008a). The most important taxonomic work on Conopidae in the past twenty years is the revision of Australian species by Schneider (2010), in which five new genera and one new subfamily are described.

Current catalogues (Camras, 1965; Chvála and Smith, 1988; Papavero, 1971; Smith, 1975, 1980, 1989) offer a combined list of nearly 800 valid, extant species of Conopidae, organized into four (or five) subfamilies and 56 genera and subgenera. Zimina (1960, 1974) divides the subfamilies Conopinae and Myopinae each into four tribes based on species found in the former USSR. Some of the subsequent regional catalogues (Camras, 1965, 2000, 2001; Papavero, 1971; Smith, 1980; Smith and Peterson, 1987) have adopted this tribal classification, each with varying degrees of modification. A summary of these tribal classifications is given in Table 5.1. Due to their geographical focus, none of these previous classifications include all world genera of Conopidae.

Biogeographical theories for Conopidae are practically non-existent. This is likely due to the lack of a robust classification. While some genera (e.g., *Physocephala* Schiner, 1861) are found globally, others are more limited in their range. For example, thirteen genera of Conopidae are endemic to Australia

(Schneider, 2010). In order to properly revise the present classification, as many genera, both global in range and locally endemic, as possible must be examined and included. Only then can biogeographical hypotheses be formulated for Conopidae.

Identification tools for Conopidae are limited to region. Keys to genera exist for most geographic regions (Chvála, 1961; Schneider, 2010; Skevington et al., 2010; Smith, 1969; Smith and Peterson, 1987; Zimina, 1970, 1975), excluding the Oriental and Afrotropical regions. There presently exists no dichotomous key to world genera of Conopidae.

Previous phylogenetic analysis based on molecular and morphological data (Chapters 3 and 4) hypothesizes at least five monophyletic subfamilies of Conopidae: Conopinae, Dalmanniinae, Myopinae, Stylogastrinae, and Zodioninae. These analyses offer characteristic apomorphies for clades including each subfamily as well as clades showing relationships between subfamilies. While suites of characters are proposed that vary within subfamilies, the taxon sampling of these previous studies does not allow conclusions to be drawn about character evolution within subfamilies. Existing characters must be supplemented with new characters selected to clarify phylogenetic relationships within subfamilies of Conopidae.

Chapter 4 concludes that members of *Zodion* and *Parazodion* form a monophyletic clade that is sister to Conopinae. This hypothesis differs from the traditional placement of *Zodion* within Myopinae and *Parazodion* within Dalmanniinae. The placement of *Parazodion* within Dalmanniinae is based almost exclusively on the shape of the female terminalia (e.g., Camras, 1953a). The analysis

in Chapter 4 suggests that the terminalia of *Dalmannia* and that of *Parazodion* represent independent modifications of female abdominal segment 7. This conclusion leaves the status of the other genera included in Dalmanniinae (*Baruerizodion* and *Pseudomyopa*), based on the female terminalia, as uncertain.

Two genera of Conopidae are currently subdivided into subgenera.

Physoconops Szilady, 1926 is divided into seven subgenera (Camras, 2004), with subgeneric status uncertain for four Afrotropical species (Smith, 1980). Chapter 4 indicates that *Physoconops sensu lato* represents a monophyletic clade, but only three species and two subgenera are tested. *Conops* Linnaeus, 1758 is divided into six subgenera (Camras, 2000). Chapter 4 includes five species and three subgenera of *Conops*. Each subgenus is recovered as monophyletic, but *Conops sensu lato* is not. Further research with members of as many subgenera as possible is necessary to determine the status of these two genera and their included subgenera.

This chapter aims to revise the genera of Conopidae. A phylogenetic hypothesis for the family, including representatives of as many genera as possible, will be created using a phylogenetic analysis of morphological characters. In addition to characters shown to be informative in Chapter 4, new characters and character states will be included. The resultant phylogenetic hypothesis will be used to produce a revised subfamily and tribal classification. Characteristic apomorphies for newly proposed and existing groups will be presented. Also, a dichotomous key to world genera of Conopidae will be produced.

5.2. Materials and methods

5.2.1. Taxon sampling

A total of 163 species of Conopidae are included. These species represent all described, currently valid genera and subgenera of Conopidae (Table 5.2). For the nine genera for which morphological specimens are not available, original and subsequent literature descriptions are used to determine as many character states as possible. For the remaining 154 species, male and female exemplars are examined, where available. Also included are seven species from seven other dipteran families to serve as outgroup taxa. *Lonchoptera tristis* (Lonchopteridae) is used to root all trees.

Both male and female adult specimens of available taxa were examined, where possible. These specimens were obtained from and have been deposited at the following institutions: American Museum of Natural History, New York, USA (AMNH); Australian Museum, Sydney, New South Wales, Australia (AMS); Australian National Insect Collection, CSIRO, Canberra, Australia (ANIC); The Natural History Museum, London, UK (BMNH); California Academy of Sciences, San Francisco, CA, USA (CAS); Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, ON, Canada (CNC); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); Utah State University, Logan, Utah, USA (EMUS); Field Museum of Natural History, Chicago, IL, USA (FMNH); Florida State Collection of Arthropods, Gainesville, FL, USA (FSCA); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); Muséum National d'Histoire Naturelle, Paris, France

(MNHN); Natal Museum, Pietermaritzburg, South Africa (NMSA); Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI); R.M. Bohart Museum of Entomology, University of California-Davis, Davis, CA, USA (UCDC); National Museum of Natural History, Washington D.C., USA (USNM); personal collection of Dr. Milan Chvála, Charles University, Prague, Czech Republic; personal collection of Dr. Amnon Friedberg, Tel Aviv University, Tel Aviv, Israel.

5.2.2. *Regarding Caenoconops, Chrysidiomyia, and Callosiconops*

Evenhuis et al. (2008) include *Caenoconops* in their list of post-1930 genera for which type species had not been designated. They determine that the proper authorship for the genus is *Caenoconops* Anonymous in Imperial Institute of Entomology, 1940, and that the type species is *Ca. subapicalis* Kröber, 1939a. They state that Smith's (1980) designation of *Ca. rhodesiensis* (Brunetti, 1925a) as the type species is incorrect. Evenhuis et al.'s explanation, while clear, is complicated by a pair of prior taxonomic publications. Kröber (1939a) designates *Conops bicolor* a junior synonym of *Caenoconops rhodesiensis*, itself originally described in *Conops* by Brunetti (1925a). Camras (2000) proposes a series of changes to classification: he notes that the specimens of *Ca. rhodesiensis* examined by Kröber were actually misidentified *Conops bicolor*, thereby removing *Co. bicolor* from synonymy with *Ca. rhodesiensis*; he designates *Caenoconops subapicalis* as a junior synonym of *Caenoconops bicolor*; he transfers *Ca. rhodesiensis* to *Physoconops*; he transfers *Physoconops claripennis* to *Caenoconops*; and he describes *Caenoconops friedbergi*.

Accounting for this labyrinthine trio of papers, and without the holotypes of

all species involved at hand, the following interpretation is made of the present state of *Caenoconops*, in accordance with Article 67.1.2. of the ICZN (1999). The type species is *Caenoconops subapicalis* Kröber, 1939a, which is now a junior synonym of *Ca. bicolor* (Kröber, 1931), by subsequent designation (Anonymous in Imperial Institute of Entomology, 1940). The other valid species are *Ca. claripennis* and *Ca. friedbergi*, with *rhodesiensis* currently placed in *Physoconops*.

Also as part of their effort to clarify type species for genus group names, Evenhuis et al. (2008) note that the original description of *Chrysidiomyia* Kröber, 1940a was a *nomen nudum*. The Australian catalogue of Smith (1989) is the first to include a type species and therefore the correct authorship is *Chrysidiomyia* Smith, 1989.

Following examination of many specimens, Schneider (2010) proposes that the differences between *Chrysidiomyia* and *Callosiconops* included by Kröber (1940a) in his original descriptions are not sufficient to justify separate genera and synonymises them. Unfortunately, she chooses *Callosiconops* as the junior synonym, despite the correct author-date of *Chrysidiomyia* being Smith, 1989. This error is corrected here with *Chrysidiomyia* Smith, 1989 considered a junior synonym of *Callosiconops* Kröber, 1940a.

5.2.3. Morphological characters analyzed

Following is a list of all morphological characters included in the phylogenetic analysis. Morphological terminology follows that of Cumming and Wood (2009) and the conopid-specific terminology of Chapter 4. Character states

for all available pinned specimens are given. In instances where male or female specimens are not available (Table 5.2), characters are determined from literature descriptions or else left as unknown. Many of the characters included here have been discussed and used in previous morphological and taxonomic research, particularly in Chapter 4. Notes on the initial definition and suspected informative qualities of each character, as well as the original reference where applicable, is discussed in Chapter 4, as well as section 5.4. The plesiomorphic state of each character, as determined by outgroup analysis, is included as state “0”.

Head

1. Ptilinum: (0) absent; (1) present. A ptilinum is present in all examined taxa except Syrphidae, Phoridae, and Lonchopteridae.
2. Central ocellus: (0) present; (1) absent. The central ocellus is absent in Pyrgotidae and all examined specimens of Conopinae except *Atrichoparia*, *Camrasiconops*, *Callosiconops*, *Jelte*, *Neoconops*, *Physoconops* (absent only in *P. microvalvus*, *P. sepulchralis*, *P. notatifrons*, *P. quadripunctatus*, and *P. rhodesiensis*), *Pleurocerina*, *Pleurocerinella*, *Smartiomyia*, and *Tammo*.
3. Lateral ocelli: (0) present; (1) absent. Lateral ocelli are absent in Pyrgotidae, *Physoconops quadripunctatus*, *Heteroconops gracilis*, and all examined members of *Archiconops*, *Brachyceraea*, *Caenoconops*, *Conops* (except *C. nigripes*), *Euconops*, *Leopoldius*, *Neobrachyceraea*, *Mallochoconops*, *Physocephala*, *Pseudophysocephala*, *Setosiconops*, and *Tanyconops*.

4. Ocellar tubercle: (0) present, (1) absent. The ocellar tubercle is completely absent in Pyrgotidae, *Physoconops quadripunctatus*, *Heteroconops gracilis*, and all examined members of *Archiconops*, *Conops* (all except *C. flavipes*, *C. nigripes*, and *C. vesicularis*), *Dacops*, *Euconops*, *Mallochoconops*, *Physocephala*, *Pseudophysocephala*, *Setosiconops*, and *Tanyconops*.
5. Vertex: (0) divided; (1) complete. The vertex is divided by a large, triangular ocellar tubercle in most examined taxa. In Pyrgotidae and all members of Conopinae, the ocellar tubercle is complete and surrounds the ocellar tubercle, if present.
6. Length of vertex: (0) restricted to less than half of the depth of the frons; (1) expanded to meet ptilinal suture. The vertex is expanded no farther than the midpoint of the frons in nearly all included taxa. In all examined members of *Stylogaster* (except *S. biannulata* and *S. stylata*) the vertex extends deep into the frons and in some cases meets the ptilinal suture.
7. Vertex: (0) reduced, triangular, or round; (1) large, square plate. The vertex is present as a large, square, setose plate, with the ocellar tubercle displaced forward in all examined members of *Physoconops* (*Gyroconops*).
8. Vertex: (0) variable in shape, without grooves; (1) triangular in shape, with longitudinal grooves. The vertex forms a sharp triangle with broad, longitudinal grooves in all members of *Caenoconops*, as well as *Physoconops rhodesiensis*.

9. Vertex: (0) variable; (1) with prominent lateral ridge and very fine longitudinal grooves. The vertex of all examined members of *Conops* (*Smithiconops*) features a prominent lateral ridge bisected by longitudinal ridges.
10. Texture of frons: (0) almost entirely smooth; (1) with extensive lateral grooves. In all examined members of *Atrichoparia*, *Camrasiconops*, *Callosiconops*, *Conops* (*C. verus*, *Asiconops*, *Ceratoconops*, and *Diconops* only), *Heteroconops*, *Neoconops*, *Pleurocerina*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*, the frons has extensive lateral grooves. All other examined taxa have the frons entirely smooth, or with only minor rugosity.
11. Posterior margin of compound eye: (0) round; (1) with triangular, shiny notch. All examined members of *Conops* (except *C. flavipes*, *C. nigripes*, *C. vesicularis*, and *Smithiconops*), *Caenoconops*, *Dacops*, *Jelte*, *Physocephala*, *Physoconops* (except *P. microvalvus*, *P. sepulchralis*, and *Gyroconops*), *Pseudophysocephala*, and *Tropidomyia* have a triangular, shiny notch in the posterior margin of the compound eye.
12. Fronto-orbital bristles: (0) present; (1) absent. Bristles on the frons or orbital region are absent in Psilidae, Pyrgotidae, Syrphidae and all examined members of Conopidae (except *Stylogaster biannulata*, *S. breviventris*, *S. decorata*, *S. inca*, *S. neglecta*, *S. rectinervis*, and *S. stylata*).

13. Frontal setae: (0) absent or dense; (1) confined to two convergent medial rows. In all examined members of *Parazodion* and *Zodion*, there are two distinct, convergent rows of dark setae on the frons.
14. Ocellar bristles: (0) present; (1) absent. Ocellar bristles are absent in Pyrgotidae, Syrphidae, all examined members of *Baruerizodion*, *Dalmannia*, *Notoconops*, and Conopinae, and some species of *Stylogaster* (*S. biannulata*, *S. frauci*, *S. pauliani*, *S. stylata*, *S. westwoodi*, and *S. sp.*).
15. Postocellar bristles: (0) present; (1) absent. Postocellar bristles are absent in Pyrgotidae, Syrphidae, and all examined members of *Baruerizodion*, *Dalmannia*, *Notoconops*, and Conopinae.
16. Gena: (0) very small; (1) expanded to be at least one-third of the total height of the head. The gena are absent, very small, or only slightly developed in all examined specimens. In all examined members of *Myopa*, *Paramyopa*, *Pseudomyopa*, *Myopotta*, and *Melanosoma*, however, the gena is expanded to be over one-third of the total head height.
17. Occipital setae: (0) variable; (1) long, dense, white. The setae of the occiput is absent, sparse, short, or black in most examined taxa. In all examined members of *Dalmannia*, *Myopa*, *Myopotta*, and *Paramyopa*, the setae on the occiput is long, dense, and white.
18. Compound eye: (0) ommatidia uniform across width; (1) ommatidia larger anteriorly. In all examined members of *Stylogaster*, the ommatidia are distinctly larger anteriorly.

19. Facial fovea: (0) absent; (1) present. A concave facial fovea beneath the antennal bases is present in all specimens examined except Phoridae, Syrphidae, Lonchopteridae, and all members of *Stylogaster*.
20. Facial fovea: (0) absent or normal; (1) reduced. In all examined members of *Tropidomyia*, the facial fovea is reduced to a small concavity at the base of the antennae.
21. Lunule: (0) not developed; (1) expanded, visible between antennal bases and ptilinum. The lunule is developed and projecting forward over the base of the antennae in all members of Conopinae (except *Atrichoparia*, *Callosiconops*, *Camrasiconops*, *Euconops*, *Heteroconops*, *Mallachoconops*, *Neoconops*, *Pleurocerina*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*).
22. Facial carina: (0) absent; (1) present. A facial carina, if only weakly developed, is present in Strongylophthalmyiidae, Pyrgotidae, Psilidae, Lauxaniidae, and all examined members of Conopidae.
23. Prominent facial carina: (0) absent; (1) present. In all examined members of *Stylogaster* and *Tropidomyia*, the facial carina is strongly developed and projects beyond the facial ridge.
24. Facial ridge: (0) absent; (1) present. A facial ridge, extending from the antennal bases to the subcranial cavity is present in all examined taxa except Lonchopteridae, Phoridae, Syrphidae, and all examined members of *Tropidomyia*.

25. Pointed facial ridge: (0) absent; (1) present. The facial ridge meets the subcranial cavity at a pointed 90° angle in all examined members of *Atrichoparia*, *Heteroconops*, *Microconops*, *Neoconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*.
26. Parafacial: (0) bare or with light setae; (1) with row of dark setae. All examined members of *Pleurocerinella* have a distinct row of dark setae on the parafacial.
27. Scape: (0) quadrate; (1) elongate. The scape is at least twice as long as wide in specimens of *Pseudoconops* and all examined members of Conopinae (except *Neobrachyceraea* and *Brachyceraea*).
28. Pedicel: (0) quadrate; (1) elongate. The pedicel is quadrate in all outgroup taxa, except Pyrgotidae. In all members of Conopidae (except *Notoconops*) the pedicel is elongate, with the length being at least one and one half times the width at the base.
29. Transverse dorsal ridge on pedicel: (0) absent; (1) present. A distinct, transverse dorsal ridge is present near the base of the pedicel in all examined members of *Camrasiconops* and *Pleurocerina*.
30. Pedicel: (0) narrow; (1) broad. In Lonchopteridae and all examined members of *Dalmannia* and *Notoconops*, the pedicel is at least twice the width of the scape. In all other examined taxa, the width of the pedicel is at most one and one half times that of the scape.

31. First flagellomere: (0) parallel sided or tapered; (1) distinctly rounded ventrally. In all examined members of *Atrichoparia*, the first flagellomere is distinctly rounded ventrally.
32. First flagellomere: (0) short; (1) elongate. In Lauxaniidae, Phoridae, *Stylogaster inca*, *S. neglecta*, and all examined members of *Heteroconops*, *Neoconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*, the first flagellomere is more than twice as long as the combined length of the scape and pedicel.
33. Location of arista: (0) dorsal; (1) apical. In members of Conopinae, the arista is located at the apex of the first flagellomere.
34. Arista: (0) filiform; (1) thickened. All outgroup taxa have a filiform arista. All examined members of Conopidae (except *Melanosoma* and *Notoconops*) have a thickened arista.
35. Arista: (0) complete, projecting from first flagellomere; (1) reduced and retracted into first flagellomere. In all examined members of *Heteroconops*, *Neoconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*, the arista is barely as long as wide and is partly retracted within the first flagellomere.
36. Second aristomere: (0) as wide as other segments; (1) expanded ventrally. The second aristomere is expanded ventrally, sometimes greatly so, in all examined members of Conopinae (except *Conops* (*Sphenconops*)).
37. Anterior margin of subcranial cavity: (0) broad, straight or rounded; (1) pointed anteriorly. The anterior margin of the subcranial cavity projects

forward to reach a narrow point where it meets the facial carina in all examined members of *Stylogaster* and Conopinae.

38. Anterior margin of subcranial cavity: (0) flat; (1) with prominent bulb. In all examined members of *Neobrachyceraea*, a prominent bulb is present where the facial carina meets the subcranial cavity.
39. Setae on maxillary palpi: (0) present; (1) absent. Setae on the maxillary palpi are absent in all examined members of *Archiconops*, *Atrichoparia*, *Callosiconops*, *Conops* (except *C. flavipes*, *C. nigripes*, and *C. vesicularis*), *Dacops*, *Heteroconops*, *Jelte*, *Neoconops*, *Notoconops*, *Physocephala*, *Physoconops* (except *Gyroconops*, *Physoconops microvalvus*, *P. rhodesiensis*, and *P. sepulchralis*), *Pleurocerina*, *Pseudophysocephala*, *Setosiconops*, *Smartiomyia*, *Tanyconops*, *Tropidomyia*, and *Stylogaster*. All mouthparts are completely absent in *Notoconops*. For this character and the following six characters, *Notoconops* is coded as unknown.
40. Maxillary palpus: (0) elongate; (1) absent or length less than half of the width of prementum. The maxillary palpi are reduced or completely absent in all examined members of *Stylogaster* and Conopinae.
41. Clypeus: (0) reduced, bare; (1) broad, microsetose. In all examined members of *Neoconops*, the clypeus is broad and microsetose.
42. Prementum: (0) unmodified; (1) elongate and fused. The prementum length is equal to or less than half of the width of the head in all outgroup taxa. The prementum is fused into an elongate proboscis in all members of Conopidae.

In all examined members of *Leopoldius*, the prementum is fused into a proboscis, but is short; they are coded as (1).

43. Prementum: (0) short; (1) elongate. The prementum has a length greater than the width of the head in all examined members of Conopidae (except *Myopa occulta* and members of *Abrachyglossum*, *Baruerizodion*, *Heteroconops*, *Leopoldius*, *Pleurocerinella*, *Pseudomyopa*, *Tammo*, and *Tanyconops*).
44. Labellum: (0) folded back and at least as long as prementum; (1) not folded and less than half of the length of the prementum. The labellum is folded back along the prementum and is at least the same length as the prementum in all outgroup taxa and most members of Conopidae. In all members of *Parazodion*, *Robertsonomyia*, *Zodiomyia*, *Zodion*, and Conopinae, the labellum is less than one half of the length of the prementum and projects forward from the apex of the prementum.
45. Shape of labella: (0) broad, separate; (1) filiform, fused. The labella are broad and separate in all outgroup taxa, as well as all members of Conopinae, *Parazodion*, *Robertsonomyia*, *Zodiomyia*, and *Zodion*. In all other members of Conopidae, the labella are filiform and fused for at least a portion of their length.
46. Labella: (0) equal to or narrower than prementum; (1) square, broader than prementum. In all examined members of *Abrachyglossum* and *Leopoldius*, the labella are square and much broader than the prementum.

Thorax (including legs)

47. Basisternum shape: (0) broad; (1) reduced to short, narrow single sclerite; (2) reduced to narrow sclerite divided posteriorly [unordered]. The basisternum is broad in all outgroup taxa as well as in all examined members of Conopinae, *Baruerizodion*, *Carbonosicus*, *Dalmannia*, *Notoconops*, *Sicus*, and *Stylogaster*. It is reduced to a narrow, single sclerite in all examined members of *Myopa*, *Pseudoconops*, *Thecophora*, *Myopotta*, *Pseudomyopa*, and *Paramyopa*. In all examined members of *Parazodion*, *Robertsonomyia*, *Zodiomyia*, and *Zodion* the basisternum is reduced to a narrow, elongate sclerite that is divided anteriorly.
48. Posterolateral extensions of the basisternum: (0) absent; (1) present. Posterolateral extensions of the basisternum are lacking in all outgroup taxa. They are present in all examined members of Conopidae. Although Schneider (2010) noted the presence of posterolateral extensions on the basisternum in her description of *Notoconops*, they were not present on the specimen available for the present research.
49. Setae on posterolateral extensions of the basisternum: (0) absent; (1) present. The posterolateral extensions of the basisternum are elongate, narrow, and with setae in all examined members of Conopidae (except members of Conopinae, *Carbonosicus*, *Sicus*, and *Stylogaster*).
50. Foretibial apical spurs: (0) absent; (1) present. Foretibial apical spurs are present in all examined members of *Stylogaster*.

51. Shape of metafemur: (0) parallel or spindle-shaped; (1) distinctly broadened basally. The hind femur has a distinct shape in all examined members of *Physocephala* and *Pseudophysocephala*.
52. Double row of spines on ventral surface of femora: (0) absent; (1) present. A distinct double row of black spines on the ventral surface of all femora is present in all examined members of *Baruerizodion*, *Melanosoma*, *Myopa*, *Myopotta*, *Paramyopa*, *Pseudoconops*, *Pseudomyopa*, *Robertsonomyia*, *Scatocemyia*, *Thecophora*, and *Zodiomyia*.
53. Apical shiny patch on metatibia: (0) absent; (1) present. A defined, shiny patch near the apex of the metatibia is present in all examined members of Conopinae, *Parazodion*, *Robertsonomyia*, *Zodiomyia*, and *Zodion*.
54. Prominent row of setae on mesofemur: (0) absent; (1) present. There is a distinct row of setae on the posterior surface of the mesofemur in all examined members of Conopidae (except *Dacops*, *Notoconops*, *Physocephala*, and *Pseudophysocephala*).
55. Male pro- and mesocoxa: (0) bare or with sparse setae; (1) with dense patch of long, pale setae. Males of *Stylogaster biannulata*, and *S. stylata* have a patch of long, pale setae on the pro- and mesocoxa.
56. Metacoxa: (0) normal; (1) with diagonal, pale marking. *Stylogaster breviventris* and *S. rectinervis* have a diagonal, pale marking on the metacoxa.

57. Pleural sclerites: (0) bare and shiny with setae and/or bristles; (1) entirely micropilose. In all examined members of *Callosiconops*, all pleural sclerites are entirely micropilose.
58. Ventral half of proepisternum: (0) with setae and/or bristles; (1) bare. Setae and/or bristles are present on the ventral half of the proepisternum of all outgroup taxa as well as all examined members of Conopidae (except *Baruerizodion*, *Dacops*, *Physocephala*, *Pseudophysocephala*, and *Scatocemyia*).
59. Dorsal half of proepisternum: (0) bare; (1) with patch of setae. A patch of setae is present on the dorsal half of the proepisternum in Pyrgotidae and all examined members of *Pseudoconops* and *Thecophora*.
60. Postpronotal bristles: (0) present; (1) absent. Postpronotal bristles are absent in Psilidae, Pyrgotidae, Strongylophthalmyiidae, Syrphidae, and all members of Conopidae (except *Stylogaster biannulata*, *S. frauci*, *S. pauliani*, *S. stylata*, *S. westwoodi*, and *S. sp.*).
61. Supra-alar bristles: (0) 0 or 1; (1) 2. There are two supra-alar bristles in *Stylogaster decorata*, *S. inca*, and *S. neglecta*.
62. Bristles on anepimeron: (0) absent; (1) present. The anepimeron is bare or with only small setae in most examined taxa. Defined bristles on the anepimeron are present in Pyrgotidae, Strongylophthalmyiidae, and all examined members of *Stylogaster*.

63. Bristles on anepisternum: (0) absent; (1) present. Bristles on the anepisternum are present only in Strongylophthalmyiidae, Pyrgotidae, and Lauxaniidae.
64. Katepisternum: (0) bare; (1) with bristles and/or setae. The katepisternum is bare in Lonchopteridae, Phoridae, Syrphidae, and all examined members of *Notoconops* and *Stylogaster*.
65. Scutellum: (0) developed, with bristles; (1) greatly reduced, lacking bristles. In all examined members of *Archiconops*, *Brachyceraea*, *Caenoconops*, *Conops* (all except *C. flavipes*, *C. nigripes*, *C. vesicularis*, and *Diconops*), *Dacops*, *Mallochoconops*, *Neobrachyceraea*, *Physocephala*, *Physoconops* (all except *P. microvalvus*, *P. sepulchralis*, and *Gyroconops*), *Pleurocerinella*, *Pseudophysocephala*, *Tammo*, and *Tropidomyia*, the scutellum is greatly reduced and lacking bristles.
66. Scutellar bristles: (0) zero, one, or two pairs; (1) greater than two pairs. In Psilidae and all examined members of *Parazodion*, *Robertsonomyia* (all except *R. pearsoni*), and *Zodion* there are at least two pairs of distinct bristles on the scutellum.

Wing

67. Wing pattern: (0) partly or completely opaque or darkened; (1) completely hyaline. In Phoridae, Strongylophthalmyiidae, Syrphidae and all examined members of *Atrichoparia*, *Camrasiconops*, *Callosiconops*, *Heteroconops*,

Microconops, *Neoconops*, *Notoconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops* the wings are completely hyaline.

68. Wing pattern: (0) hyaline or pattern variable; (1) wing distinctly darker anteriorly. In all examined members of *Caenoconops*, *Dacops*, *Jelte*, *Physocephala*, *Physoconops* (all except *P. quadripunctatus*, *P. microvalvus*, *P. sepulchralis*, and *Gyroconops*), *Pleurocerina*, *Pseudophysocephala*, and *Tropidomyia* the wing anterior to vein CuA₁ is partly or entirely darkened, whereas as the wing posterior to vein CuA₁ is hyaline.
69. M vein: (0) parallel to vein R₄₊₅; (1) deflected towards vein R₄₊₅. The M vein is parallel to vein R₄₊₅ in all outgroup taxa. In all examined members of Conopidae (except *Notoconops*), the M vein is deflected toward, or joins vein R₄₊₅.
70. Petiole of vein R₄₊₅+M: (0) absent or short; (1) elongate. Vein M is curved such that it meets vein R₄₊₅ at a 90° angle and the petiole formed from their union is greater than the length of cross-vein dm-cu in all examined members of *Atrichoparia* (except *A. sp. B*), *Heteroconops*, *Smartiomyia*, and *Tanyconops*.
71. Sc vein: (0) incomplete, or ends at a point before four-tenths of the length of the costa; (1) ends at or beyond a point four-tenths of the length of the costa. Vein Sc is either incomplete or ends before a point four-tenths of the length of the costa in all outgroup taxa as well as all examined members of *Notoconops* and *Stylogaster*. Vein Sc ends at or beyond a point four-tenths of the length of the costa in all other examined members of Conopidae.

72. R₁ vein: (0) ends at or before a point six-tenths of the length of the costa; (1) ends beyond a point six-tenths of the length of the costa. Vein R₁ ends beyond a point six-tenths of the length of the costa in all examined members of Conopinae, *Carbonosicus*, *Parazodion*, *Robertsonomyia*, *Sicus*, *Zodiomyia*, and *Zodion*.
73. Veins Sc and R₁: (0) separate for their entire length; (1) fused before reaching costa. Veins Sc and R₁ are fused before reaching the costa in all examined members of *Melanosoma*, *Myopa*, *Myopotta*, *Paramyopa*, *Pseudoconops*, *Pseudomyopa*, *Scatocemyia*, and *Thecophora*.
74. Costa: (0) even in width along length; (1) thickened at insertion of Sc+R₁. In all examined members of *Pseudoconops*, *Scatocemyia*, and *Thecophora* the costa is greatly thickened at the insertion of Sc+R₁.
75. Vein R₂₊₃: (0) ends beyond endpoint of vein R₁; (1) ends at or near endpoint of vein R₁. Vein R₂₊₃ meets the costa at a point at least two tenths of the length of the costa beyond the end point of vein R₁ in all examined taxa except members of Conopinae, *Carbonosicus*, *Myopotta*, *Parazodion*, *Robertsonomyia*, *Sicus*, *Zodiomyia*, and *Zodion*.
76. Crossvein sc-r: (0) absent; (1) present. A crossvein between veins Sc and R₁ is present in all examined members of Conopinae, *Parazodion*, *Robertsonomyia*, *Stylogaster*, *Zodiomyia*, and *Zodion*.
77. Angle between vein CuA₂ and cross-vein dm-cu: (0) absent or acute; (1) obtuse. The angle formed between vein CuA₁ and cross-vein dm-cu is obtuse,

with cross-vein dm-cu nearly parallel to the wing margin in *Physoconops quadripunctatus* and all examined members of *Archiconops* and *Conops* (all except *C. flavipes*, *C. nigripes*, and *C. vesicularis*).

78. Vein CuA_2+A_1 : (0) absent or shorter than crossvein dm-cu; (1) longer than crossvein dm-cu. The vein formed by the union of veins CuA_2 and A_1 is longer than crossvein dm-cu in Pyrgotidae and all examined members of Conopidae. However, in all examined members of Conopinae (except *Atrichoparia*, *Heteroconops*, *Neoconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*), vein CuA_2+A_1 is shorter than dm-cu.
79. Vein CuA_2 : (0) straight; (1) curved. Vein CuA_2 is curved along its length in Syrphidae as well as all examined members of Conopinae, *Parazodion*, *Robertsonomyia*, *Zodiomyia*, and *Zodion*.
80. Cell cup: (0) narrow; (1) broad. In all examined members of *Robertsonomyia* and *Zodiomyia* cell cup is broad and vein CuA_2 meets vein A_1 at a nearly 90° angle.
81. Vena spuria: (0) absent; (1) present. A spurious vein, sometimes only present as a weak fold, is present in Syrphidae, Pyrgotidae, and all examined members of Conopinae.
82. Width of alula: (0) absent or narrow; (1) broad. The alula is broad in most examined taxa. It is absent or reduced to being less than one fourth of the width of the wing in Phoridae, Lonchopteridae, and all examined members of *Stylogaster*.

83. Wing margin: (0) normal; (1) expanded. The wing margin is expanded such that the costa ends well before the apex of the wing in all examined members of *Archiconops*.

Female abdomen

84. Tergite 2: (0) normal; (1) with a shiny, pollinose band. All examined members of *Australoconops* possess a distinct band of pollinosity on the posterior half of tergite 2 in both males and females.
85. Sternites 2 and 3: (0) present; (1) absent. Abdominal sternites 2 and 3 are absent in all examined members of *Stylogaster*.
86. Patch of bristles on Sternite 2: (0) absent; (1) present. There is a patch of bristles on sternite 2 in *Conops nigripes*, *Physoconops microvalvus*, and *Siniconops elegans*.
87. Tergite 5 and sternite 5: (0) separate; (1) fused. Abdominal tergite 5 and sternite 5 are fused in all examined members of Conopinae, *Parazodion*, *Robertsonomyia*, *Zodiomyia*, and *Zodion*.
88. Tergite 6 and sternite 6: (0) separate; (1) fused. Abdominal tergite 6 and sternite 6 are at least partly fused in all examined members of Conopidae (except *Baruerizodion*, *Dalmannia*, and *Notoconops*). In Chapter 4, the complete fusion of tergite 6 and sternite 6 into a ring-like structure is observed in all members of *Stylogaster*. In the present analysis, the partial fusion of tergite 6 and sternite 6 is recorded instead.

89. Tergite 7 and sternite 7: (0) separate; (1) fused. Abdominal tergite 7 and sternite 7 are fused and ring-like in Lauxaniidae, Psilidae, Pyrgotidae, Strongylophthalmyiidae, and all examined members of Conopidae (state unknown in *Notoconops*).
90. Sternite 6: (0) unmodified; (1) with rows of spicules. Rows of spicules cover the surface of sternite 6 in all examined members of Conopidae (except *Baruerizodion*, *Dalmannia*, *Parazodion*, and *Stylogaster*).
91. Sternite 5: (0) unmodified; (1) with rows of spicules. In all examined members of Conopidae (except *Baruerizodion*, *Dalmannia*, and *Stylogaster*), sternite 5 has rows of spicules and may or may not be expanded ventrally into a genital plate.
92. Spicules confined to tip of ventral genital plate: (0) absent; (1) present. There are only a few rows of spicules at the apex of the ventral genital plate in all examined members of *Heteroconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*.
93. Medial lobe on ventral genital plate: (0) absent; (1) present. In all examined members of *Abrachyglossum* and *Leopoldius*, the ventral genital plate is broad and rounded with a medial lobe.
94. Syntergite 8+9: (0) absent or unmodified; (1) fused with cerci and elongate. In all examined members of *Dacops*, the anterior portion of syntergite 8+9 is retracted into segment 7. Also, the posterior portion of syntergite 8+9 is

fused with the cerci and projected into a ventrally-directed, elongate appendage.

95. Segments 5, 6, 7: (0) normal; (1) narrowed. In all examined members of *Pseudophysocephala*, segments 5, 6, and 7 are distinctly narrower than segment 4.
96. Segment 7: (0) absent or parallel to tergite 6; (1) deflected ventrally at 90° to segment 6. Segment 7 projects posteriorly from segment 6 in all outgroup taxa as well as all examined members of *Dalmannia*, *Notoconops*, and *Stylogaster*. In all other examined members of Conopidae, segment 7 meets segment 6 at a 90° angle.
97. Segment 7: (0) absent or broad; (1) compressed laterally along entire length; (2) compressed laterally only in posterior half; (3) narrowed in posterior half [unordered]. Segment 7 is compressed laterally, forming a sharp, narrow point in all examined members of *Baruerizodion* and *Dalmannia*. In all examined members of *Parazodion*, segment 7 is broad and bulbous at the base and laterally compressed posteriorly. In all examined members of *Paramyopa*, segment 7 is broad at the base and narrowed to a small tube in the posterior half.
98. Epiproct: (0) present; (1) absent. The epiproct is absent in Pyrgotidae as well as all examined members of Conopidae (state unknown in *Notoconops*).

99. Elongate, sclerotized hypoproct: (0) absent; (1) present. The hypoproct is sclerotized and elongate well beyond the cerci in all examined members of *Stylogaster*.
100. Two square lobes on sternite 8: (0) absent; (1) present. Sternite 8 is present as two well-sclerotised lobes in all examined members of Conopidae (except *Stylogaster*; state unknown in *Notoconops*).
101. Lateral lobes on sternite 8: (0) absent; (1) present. Elongate lateral lobes are present on sternite 8 in all examined members of *Stylogaster* (except *decorata* and *neglecta*).
102. Sclerotized posteroventral hooks on syntergite 8+9: (0) absent; (1) present. In all examined members of Conopidae (except *Stylogaster*), the posteroventral surfaces of syntergite 8+9 are developed into a pair of sharp, sclerotized hooks (state unknown in *Notoconops*).

Male abdomen

103. Sternites 2-4: (0) partly or entirely membranous; (1) broad, sclerotized plates. In *Conops flavipes*, *C. vesicularis*, and all examined members of *Archiconops*, sternites 2 through 4 are broad, sclerotised plates.
104. Tergites 3 and 4: (0) narrow and/or tapering; (1) broad and parallel-sided. In *Conops flavipes*, *C. vesicularis*, and all examined members of *Abrachyglossum* and *Leopoldius*, tergites 3 and 4 are as broad as the thorax and parallel-sided.

105. Tergites 2 and 3: (0) broad, rectangular; (1) petiolate. In all examined members of *Brachyceraea*, *Caenoconops*, *Dacops*, *Neobrachyceraea*, *Physocephala*, *Physoconops* (all except *P. quadripunctatus*, *P. sepulchralis*, and *Gyroconops*), *Pseudophysocephala*, and *Tropidomyia*, tergite 2 is extremely narrow and is longer than any other tergite. Also in these taxa, tergite 3 is distinctly narrowed anteriorly.
106. Sternite 5: (0) unmodified; (1) broad, with setae or spicules. Sternite 5 is wider and broader than all other sternites and has thick setae or spicules on the posterior margin in all examined members of Conopidae (except *Dalmannia*, *Notoconops*, and *Stylogaster*).
107. Sternite and tergite 5: (0) separate; (1) fused. Sternite and tergite 5 are fused into a broad ring in all examined members of *Archiconops*.
108. Syntergosternite 7+8: (0) absent; (1) present. Tergite 7, and sternite 8 are fused into a single pre-genital sclerite in all examined members of Pyrgotidae, Strongylophthalmyiidae, Lauxaniidae, and Conopidae.
109. Broad, hemispherical syntergosternite 7+8: (0) absent; (1) present. Syntergosternite 7+8 is absent or present as a narrow band in all outgroup taxa as well as *Dalmannia*, *Notoconops*, and New World members of *Stylogaster*. In all other examined members of Conopidae, syntergosternite 7+8 is present as a large, hemispherical, dorsal sclerite.

110. Apex of abdomen: (0) rounded or pointed; (1) square. In *Conops nigripes*, *Physoconops microvalvus*, *P. sepulchralis*, and *Siniconops elegans*, the apex of the abdomen is square.
111. Sternite 8: (0) absent; (1) present. The apical portion of syntergosternite 7+8, here described as sternite 8, is present as a clearly differentiated portion of the sclerite in all examined members of Conopidae (except *Baruerizodion*, *Dalmannia*, *Notoconops*, and *Stylogaster*).
112. Dense, long, black, setae on sternite 8: (0) absent; (1) present. In all examined members of *Carbonosicus* and *Sicus*, sternite 8 features a dense patch of long, black setae.
113. Elongate cerci: (0) absent; (1) present. The cerci are elongate to a length of at least three times their width in Pyrgotidae, Strongylophthalmyiidae, and all examined members of *Stylogaster*.
114. Cercal attachment: (0) broad; (1) narrow, sclerotized stalk. The sclerotized portion of the cercal attachment is a narrow stalk in all examined members of Conopinae, *Parazodion*, *Robertsonomyia*, and *Zodion*.
115. Epandrium: (0) two separate lobes beyond cerci; (1) fused beyond cerci. The epandrium is fused into a single plate beyond the cerci in all examined members of Conopinae.
116. Medial spine on epandrium: (0) absent; (1) present. A medial spine is present at the fusion point of the lobes of the epandrium in all examined members of *Australoconops* and *Microconops*.

117. Posterior hump on epandrium: (0) absent; (1) present. A posterior hump where the cerci attach to the epandrium is present in all examined members of Conopinae (except *Atrichoparia*, *Callosiconops*, *Camrasiconops*, *Heteroconops*, *Neoconops*, *Pleurocerina*, *Setosiconops*, and *Smartiomyia*).

5.2.4. Parsimony analysis

All characters were equally weighted and were treated as unordered. Parsimony analysis was conducted using TNT v1.1 (Goloboff et al., 2008). A traditional search involved generating 1000 random-addition sequence Wagner trees and performing TBR branch-swapping. Bootstrap resampling support values (boot) were determined in TNT by a traditional search with 1000 replicates. Total Bremer supports (TBS) (Bremer, 1988, 1994) were determined in TNT by performing a search for trees suboptimal by up to 1000 steps and a relative fit difference of 1.0.

5.3. Results

5.3.1. Parsimony analysis

A total of 117 characters are included in the analysis. Characters included from each body region are as follows: head – 46 characters (39.3%); thorax, including legs – 20 characters (17.1%); wing – 17 characters (14.5%); female abdomen, including terminalia – 19 characters (16.2%); male abdomen, including terminalia – 15 characters (12.8%). No characters are constant and all are parsimony informative. A full character matrix is included (Table 5.3.).

Parsimony analysis of all available pinned specimens (161 taxa) recovers 47

equally parsimonious trees (length 218; consistency index (CI) – 0.550; retention index (RI) - 0.957). This likely does not represent all possible trees. Most groups of congeneric taxa included in the analysis represent identical character sets. An exponentially large number of possible topologies for each clade of identical congeners is possible, however, none would prove to be more informative than the 47 trees recovered. One of these trees, chosen to best preserve existing generic classification, is shown in Fig. 5.1 with bootstrap and Bremer support values for each node.

The strict consensus of 47 trees (not shown) differs from Fig. 5.1 at only four points: the clade *Camrasiconops*+*Pleurocerina* is collapsed; the clade *Robertsonomyia mexicana*+*R. palpalis*+*R. parva* is collapsed; the clade *Paramyopa*+*Myopa*+*Myopotta* is collapsed; and near the base of the tree four nodes are collapsed to form a polytomy including Conopidae (*s.s.*), *Notoconops*, Lauxaniidae, Psilidae, Pygotidae, and Strongylophthalmyiidae.

The illustrated tree (Fig. 5.1) is well supported with 51 of 83 nodes (61%) having a bootstrap support value (boot) greater than 50%. A clade including all members of Schizophora is recovered as monophyletic with strong support (boot – 70; TBS – 2; morphological autapomorphies (MAA) – 1:1, 19:1, 22:1, 24:1, 64:1, 89:1, 108:1; other morphological apomorphies and reversals (MA) – 60:1, 82:1). A clade including all members of Conopidae (except *Notoconops*) is recovered with strong support (boot - 82; TBS – 4; MAA – 34:1, 42:1, 43:1, 45:1, 48:1, 54:1, 69:1, 88:1; MA – 28:1, 78:1, 98:1).

A clade including all members of Conopinae is recovered with strong support (boot – 100; TBS – 11; MAA – 33:1, 36:1, 115:1; MA – 5:1, 14:1, 15:1, 27:1, 37:1, 40:1, 49:0, 78:0, 81:1). A clade including all members of *Zodion*, plus members of *Parazodion*, *Robertsonomyia*, and *Zodiomyia* is recovered (boot – 65; TBS – 1; MAA – 47:2; MA – 66:1). A clade including all members of *Sicus* and *Carbonosicus* is recovered (boot – 62; TBS – 1; MAA – 112:1; MA – 49:0). A clade including all members *Myopa*, *Melanosoma*, *Paramyopa*, *Pseudomyopa*, *Myopotta*, *Thecophora*, *Pseudoconops*, and *Scatocemyia* is recovered with strong support (boot – 79; TBS – 3; MAA – 47:1, 73:1; MA – 52:1). A clade including all members of *Dalmannia* and *Baruerizodion* is recovered (boot – >50; TBS – 1; MAA – 97:1; MA – 14:1, 15:1, 88:0). A clade including all members of Stylogastrinae is recovered with strong support (boot – 100; TBS – 13; MAA – 6:1, 18:1, 50:1, 85:1, 99:1; MA – 19:0, 23:1, 37:1, 39:1, 40:1, 62:1, 64:0, 76:1, 82:0, 101:1, 113:1).

Relationships between newly defined subfamilies of Conopidae are also determined. A clade including all members of Conopinae, *Parazodion*, *Robertsonomyia*, *Zodiomyia*, and *Zodion* is recovered with strong support (boot – 93; TBS – 7; MAA – 44:1, 53:1, 87:1, 114:1; MA – 45:0, 76:1, 79:1). A clade including all members of Conopinae, *Carbonosicus*, *Parazodion*, *Robertsonomyia*, *Sicus*, *Zodiomyia*, and *Zodion* is recovered with strong support (boot – 79; TBS – 2; MAA – 72:1; MA – 75:1). Conopidae (excluding *Baruerizodion*, *Dalmannia*, *Notoconops*, and *Stylogaster*) is recovered with strong support (boot – 80; TBS – 4; MAA – 90:1, 91:1, 106:1, 111:1; MA – 109:1). Conopidae (excluding *Notoconops* and *Stylogaster*) is

recovered with strong support (boot – 65; TBS – 1; MAA – 49:1, 71:1, 100:1, 102:1; MA – 12:1, 96:1).

Some relationships within subfamilies are determined. A clade including *Conops flavipes*, *C. vesicularis* and all members of *Abrachyglossum* and *Leopoldius* is recovered (boot – >50; TBS – 1; MAA – 104:1). A clade including *Physoconops quadripunctatus* and all members of *Archiconops* and *Conops* (excluding *C. flavipes*, *C. nigripes*, and *C. vesicularis*) is recovered (boot – >50; TBS – 1; MAA – 77:1; MA – 39:1). A clade including all members of *Brachyceraea* and *Neobrachyceraea* is recovered with strong support (boot – 60; TBS – 1; MA – 27:0). A clade including *Physoconops rhodesiensis* and all members of *Caenoconops* is recovered with strong support (boot – 65; TBS – 1; MAA – 8:1). A clade including all members of *Dacops*, *Physocephala*, and *Pseudophysocephala* is recovered with strong support (boot – 88; TBS – 3; MA – 4:1, 54:0, 58:1). A clade including all members of *Jelte*, *Physoconops* (except *P. microvalvus*, *P. quadripunctatus*, *P. rhodesiensis*, *P. sepulchralis*, and *Gyroconops*), and *Tropidomyia* is recovered (boot – >50; TBS – 1; MA – 3:0). A clade including all members of *Australoconops* and *Microconops* is recovered with strong support (boot – 54; TBS – 1; MAA – 116:1). A clade including *Conops nigripes*, *Physoconops microvalvus*, *P. sepulchralis*, and *Siniconops elegans* is recovered with strong support (boot – 55; TBS – 1; MAA – 86:1, 110:1). A clade including all members of *Physoconops* (*Gyroconops*) is recovered with strong support (boot – 63; TBS – 1; MAA – 7:1). A clade including *Tammo rufa* and all members of *Pleurocerinella* is recovered with strong support (boot – 53; TBS – 2; MA – 43:0,

65:1). A clade including all members of *Atrichoparia*, *Callosiconops*, *Camrasiconops*, *Heteroconops*, *Neoconops*, *Pleurocerina*, *Setosiconops*, *Smartiomyia*, and *Tanyconops* is recovered (boot – >50; TBS – 1; MA – 10:1, 39:1, 67:1). A clade including all members of *Melanosoma*, *Myopa*, *Myopotta*, *Paramyopa*, and *Pseudomyopa* is recovered with strong support (boot – 59; TBS – 1; MAA – 16:1). A clade including all members of *Pseudoconops*, *Scatocemyia*, and *Thecophora* is recovered with strong support (boot – 59; TBS – 1; MAA – 74:1).

5.3.2. Character states of genera for which pinned specimens are not available

The genus *Anticonops* Kröber, 1936b was erected to accommodate the type species, *A. abdominalis*. No other species have been assigned to it since. It is included in the tribe Conopini in Smith's (1980) Afrotropical catalogue. Based on Kröber's (1936b) original description and Camras' (2000) redescription, the following important character states can be determined: scape and pedicel elongate; first flagellomere equal in length to scape and pedicel combined; arista apical, not retracted into first flagellomere; prementum twice as long as width of head; wing not hyaline; female abdominal sternite 5 with spicules, but ventral genital plate not present; female abdominal sternite 6 with spicules; female abdominal tergite 7 elongate.

The genus *Delkeskampomyia* Kröber, 1940a was erected to accommodate the type species, *D. fasciata*. No other species have been assigned to it since. Smith's (1989) Australasian catalogue includes the genus in Conopinae, but does not include tribal classifications. Schneider (2010) could not locate the single identified

specimen of this genus. Based on Schneider's (2010) translation of Kröber's original (1940a) description, the following important character states can be determined: lateral ocelli and ocellar tubercle present; central ocellus absent; frons with lateral grooves; first flagellomere elongate; arista stylate, retracted into first flagellomere; prementum shorter than head width; wing hyaline; petiole of $R_{4+5}+M$ present, elongate; male abdomen not petiolate.

The genus *Macroconops* Kröber, 1927a was erected to accommodate the type species, *M. helleri*. Only *M. sinensis* Ôuchi, 1942 has been assigned to it since. Smith's (1975) Oriental catalogue includes the genus in Conopinae, but does not include tribal classifications. Kröber's (1927a) original description states that *Macroconops* is very similar to *Siniconops maculifrons* (Kröber, 1916e), but with a greatly enlarged arista. Kröber describes a small ventral genital plate, but from the illustration included, it is clear that the specimen is a male with a large abdominal sternite 5 and syntergosternite 7+8 produced into a point.

The genus *Microbrachyceraea* Kröber, 1940b was erected as a new genus for the type species, *Microconops pendleburyi*. No other species have been assigned to it since. Smith's (1975) Oriental catalogue includes the genus in Conopinae, but does not include tribal classifications. Based on Brunetti (1927) and Kröber's (1940b) original descriptions, the following important character states can be determined: facial fovea present, normal; facial carina present; scape quadrate; pedicel narrow, elongate, and without transverse dorsal ridge; first flagellomere slightly longer than

pedicel; arista stylate, apical, not retracted into first flagellomere; vein CuA₂ curved; vein CuA₂+A₁ short; male abdomen petiolate.

The genus *Neobrachyglossum* Kröber, 1915g was erected to accommodate the type species, *M. punctatum*. No other species have been assigned to it since. Chvála and Smith's (1988) Palaearctic catalogue includes it in Conopini. The sole specimen was deposited at the Hungarian Natural History Museum (HNHM) and was likely destroyed during the Soviet attack and fire that destroyed the collection in 1956 (Skevington & Marshall, 1998). Based on Kröber's (1915g) original description, the following important character states can be determined: prementum short, fleshy; first flagellomere as long as scape and pedicel combined; arista apical, stylate, not retracted into first flagellomere; wing similar to *Conops*; abdomen slightly narrowed. All of these character states are present in all species of *Leopoldius*.

The genus *Neozodion* Szilady, 1926 was erected to accommodate the type species, *N. pruinsum*. No other species have been assigned to it since. Papavero's (1971) Neotropical catalogue includes it in Myopinae. The sole specimen was deposited at the HNHM and was likely destroyed during the Soviet attack and fire that destroyed the collection in 1956 (Skevington & Marshall, 1998). Szilady (1926) describes the single, female specimen as very similar to *Zodion*, but with abdominal segments 2-4 closely appressed and a ventral extension on abdominal sternite 5. These character states are present in many species of *Zodion*, and no other characters are offered to distinguish *Neozodion* from *Zodion*.

The genus *Stenoconops* Kröber, 1939d was erected to accommodate the type species, *S. niger*. No other species have been assigned to it since. Smith's (1989) Australasian catalogue includes the genus in Conopinae, but does not include tribal classifications. Schneider (2010) studied the only known specimen, the female holotype, and concluded that *Stenoconops* is a valid genus. Based on Schneider's (2010) re-description, the following important character states can be determined: lateral ocelli and ocellar tubercle present; central ocellus absent [although Kröber (1939d) describes three ocelli as present]; frons with lateral grooves; cephalic bristles absent; facial ridge not meeting subcranial cavity at 90° angle; first flagellomere not elongate; arista stylate, not retracted into first flagellomere; maxillary palpus absent; prementum elongate; apical shiny patches on metafemur present; scutellum developed, with two pairs of bristles; wing hyaline; petiole of R₄₊₅+M present, length not stated; vein R₁ ending near end of R₂₊₃; angle between vein CuA₁ and crossvein dm-cu acute; petiole of CuA₂+A₁ short; vena spuria present; ventral genital plate present.

Five fossil species have been assigned to Conopidae. *Poliomyia recta* Scudder, 1878 is described from the Green River shale. *Hoffeinsia baltica*, *Palaeomyopa tertiaria*, *Palaeomyopa hennigi* Stuke, 2003b, and *Palaeosicus loewi* Meunier, 1916 are all described from Baltic amber. In his analysis of the Baltic amber species, Hennig (1966) states that *Poliomyia* likely does not belong in Conopidae. He also notes that the type of *Palaeomyopa tertiaria* is missing. Hennig examined Meunier's specimens of *Palaeosicus* and concluded that they are synonymous with the

description of *Palaeomyopa*. Thus, two fossil genera of Conopidae, *Palaeomyopa* and *Hoffeinsia*, are recognized at present.

Based on Hennig's (1966) detailed discussion of the specimens, the following important character states for *Palaeomyopa* can be determined: arista thickened, mid-dorsal; second aristomere not expanded ventrally; scape quadrate; pedicel elongate; facial fovea and medial carina present; ptilinum present; facial ridge present and not meeting subcranial cavity at 90° angle; lunule absent; maxillary palpi elongate; three ocelli and ocellar tubercle present; ocellar and postocellar bristles present; vein M deflected towards vein R₄₊₅, but not petiolate; vein Sc ends at a point four tenths of the length of the costa; vein R₁ ends at a point before six tenths of the length of the costa; vein Sc and R₁ separate; crossvein sc-r absent; vein R₂₊₃ ends well beyond end of vein R₁; vein CuA₂+A₁ longer than crossvein dm-cu; vein CuA₂ straight; cell cup narrow; vena spuria absent; alula broad; female abdominal sternite 6 with spicules. While Hennig describes fronto-orbital bristles, it is difficult to determine if these are true bristles or merely large setae. The prementum and labella are not clear on the specimens observed. Hennig also suggests that a ventral genital plate arises from female abdominal sternite 4. This is likely a misinterpretation, as in many modern specimens, the ventral genital plate arises from the fifth segment but is displaced anteriorly so as to be ventral to the fourth segment.

Based on Stuke's (2005b) original description and figures, the following important character states for *Hoffeinsia* can be determined: arista and first

flagellomere missing; scape elongate; pedicel elongate; facial fovea and medial carina present; ptilinum present; facial ridge present and not meeting subcranial cavity at 90° angle; lunule absent; maxillary palpi elongate; prementum short, broad, unfused; labella broad, separate, short; three ocelli and ocellar tubercle present; ocellar, postocellar, and fronto-orbital bristles present; katapisternum and propleuron bare; humeral, notopleural, supra-alar, post-alar, dorsocentral, prescutellar, and scutellar bristles present; all femora bare; vein M not deflected towards vein R₄₊₅; vein Sc ends at a point before four tenths of the length of costa; vein R₁ at a point before six tenths of the length of costa; vein Sc and R₁ separate; crossvein sc-r absent; vein R₂₊₃ ends well beyond end of vein R₁; vein CuA₂+A₁ longer than crossvein dm-cu; vein CuA₂ straight; cell cup narrow; vena spuria absent; alula missing; male abdominal characters uncertain.

5.4. Discussion

5.4.1. Taxonomic revision of some species of Conopidae

The following taxonomic revisions are proposed for some individual species and genera of Conopidae based on phylogenetic analysis and the hypothesized cladogram (Fig. 5.1). The proposed new status of these species and genera reflects morphological character states as recorded as part of this research. Complete descriptions for proposed tribal groups, including these taxa are included in section 5.4.2.

Asiconops and *Smithiconops* are removed as subgenera of *Conops* and elevated to genus status, **stat. nov.** *Ceratoconops*, *Diconops*, and *Sphenoconops* are

transferred from subgenera of *Conops* to subgenera of *Asiconops*, **comb. nov.**

Physoconops quadripunctatus, originally described by Kröber (1915a) in *Conops* and transferred to *Physoconops* by Camras (2000), is now transferred to *Asiconops* as the type species of a new subgenus, *Aegloconops*, **subgen. nov.** *Conops (Conops) verus* is transferred to *Asiconops (Asiconops)*, **comb. nov.** *Conops (Conops) nigripes* is transferred to *Siniconops*, **comb. nov.**

Physoconops sepulchralis and *Physoconops microvalvus* are both transferred to *Siniconops*, **comb. nov.** *Jelte* is transferred to a subgenus of *Physoconops*, **comb. nov.** *Gyroconops* is removed from *Physoconops* and elevated to genus status, **stat. nov.** *Physoconops rhodesiensis* is transferred to *Caenoconops*, **comb. rev.** A new genus, *Schedophysoconops*, is erected with *Physoconops notatifrons* as its type, **gen. nov.**

Neobrachyglossum is designated a junior synonym of *Leopoldius*, **syn. nov.**

Neozodion is designated a junior synonym of *Zodion*, **syn. nov.**

Asiconops (Aegloconops) **subgen. nov.** (Fig. 5.22)

Type species: *Conops quadripunctatus* Kröber, 1915f: 38, present designation.

Diagnosis

Aegloconops can be distinguished from other members of *Asiconops (s.l.)* by the combination of narrow frons; fronto-facial spots; reduced facial carina; short, wide, arista; short prementum; and narrow second abdominal segment in the male.

Description

Head. Occipital setae sparse, short, dark. Vertex round, not distinct. Frons slightly wider than long; no setae or bristles; smooth, concave, elevated at anterior margin. Fronto-facial spot present. Ocellar tubercle and ocelli absent. Ocellar and postocellar bristles absent. Compound eye oval with triangular notch in posterior margin. Facial foveae deep, blends into gena; medial carina very small. Gena present, small, less than one tenth of head height; anterior margin of subcranial cavity pointed anteriorly at junction with medial carina. Lunule well-developed, united with facial ridge. Scape elongate, length four times the width; pedicel twice as long as scape; pedicel elongate, length five times the width; first flagellomere short, half of the length of scape and pedicel combined; first flagellomere bare; arista short, wide; second aristomere expanded ventrally. Maxillary palpi absent; prementum elongate, one and one quarter times as long as width of head; labella short, length one tenth of length of prementum; labella ovate, pointed, without setae.

Thorax. Basisternum square, posterolateral extensions pointed; proepimeron, anepimeron, and anepisternum bare; two proepisternal setae; small patch of bristles in posterodorsal portion of katepisternum; dorsum of thorax without prominent bristles; scutellum reduced, without bristles. Shiny patches at apex of all tibia; prominent row of setae on posterior surface of mesofemur.

Wing. Dark pattern at apex of wing, anterior to vein R_{4+5} , otherwise hyaline; petiole of $R_{4+5}+M$ half as long as crossvein $dm-cu$; vein Sc ends at midpoint of costa; vein R_1 ends at a point seven tenths of the length of the costa; vein R_{2+3} ends only slightly

beyond the end of R_1 ; crossvein sc-r present; petiole of $CuA_{2+}+A_1$ half as long as crossvein dm-cu; vein CuA_2 curved along its length; vena spuria present; alula half as wide as wing.

Female abdomen. Sternites 1-4 present, but narrow; tergite 5 and sternite 5 partially fused; ventral genital plate half as long as height of tergite 6, rounded, broader than tall, covered with irregular rows of spicules; tergite 6 and sternite 6 fused anteriorly; sternite 6 with rows of spicules; tergite 7 and sternite 7 fused.

Male abdomen. Tergite 2 equal in length to, but distinctly narrower than, tergites 1 and 3; sternite 2 and 3 present, narrow; spicules present on posterior margin of sternite 5. Syntergosternite 7+8 round, hemispherical; sternite 8 broad, bare, shiny. Cerci large, rounded and connected to the epandrium by a sclerotized stalk, densely setose. Epandrium strongly fused beyond cerci, quadrate, bare except for setae on posterior margin, very small posterior hump where cerci attach.

Measurements. Total length (excluding antennae) = 10 mm; wing length = 6 mm.

Geographical distribution

Afrotropical: Congo, South Africa, Zaire, Zimbabwe.

Etymology

The name is constructed from the Greek term *aeglo-*, meaning brilliant or radiant, and *Conops*. The name is masculine.

Schedophysoconops **gen. nov.** (Fig. 5.41)

Type species: *Physoconops notatifrons* Camras, 1962b: 219, present designation.

Diagnosis

Similar to *Physoconops* (*s.l.*), but with a fronto-facial spot, two ocelli, and a shorter prementum.

Description

Head. Occipital setae sparse, short, dark. Vertex round, not distinct. Frons slightly wider than long; no setae or bristles; smooth with small rugose area at anterior margin. Fronto-facial spot present. Ocellar tubercle round, nondistinct; two ocelli present. Ocellar and postocellar bristles absent. Compound eye oval with triangular notch in posterior margin. Facial foveae deep, blends into gena; medial carina very small. Gena present, small, less than one quarter of head height; anterior margin of subcranial cavity pointed anteriorly at junction with medial carina. Lunule well-developed, united with facial ridge. Scape elongate, length four times the width; pedicel one and one half times as long as scape; pedicel elongate, length four times the width; first flagellomere short, less than half of the length of the scape and pedicel combined; first flagellomere bare; arista short, wide; second aristomere greatly expanded ventrally, nearly reaching apex of third aristomere. Maxillary palpi absent; prementum elongate, one and one third times as long as width of head; labella short, length one tenth of length of prementum; labella ovate, pointed, without setae.

Thorax. Basisternum square, posterolateral extensions pointed; proepimeron, anepimeron, and anepisternum bare; one proepisternal seta; small patch of bristles in posterodorsal portion of katepisternum; dorsum of thorax without prominent

bristles; scutellum reduced, without bristles. Shiny patches at apex of all tibia; prominent row of setae on posterior surface of mesofemur.

Wing. Dark pattern anterior to vein CuA_2 , hyaline posterior; petiole of $R_{4+5}+M$ half as long as crossvein dm-cu; vein Sc ends at point halfway along costa; vein R_1 ends at point seven tenths of the way along costa; vein R_{2+3} ends only slightly beyond end of R_1 ; crossvein sc-r present; petiole of $CuA_{2+}+A_1$ half as long as crossvein dm-cu; vein CuA_2 curved along its length; vena spuria present; alula half as wide as wing.

Female abdomen. Sternites 1-4 present, but narrow; tergite 5 and sternite 5 partially fused; ventral genital plate two thirds as long as height of tergite 6; rounded, broader than tall, covered with irregular rows of spicules; tergite 6 and sternite 6 fused anteriorly; sternite 6 with rows of spicules; margin between tergite 6 and tergite 7 straight; tergite 7 and sternite 7 fused; row of long setae on sternite 7; cerci broad, cupped, square, with long setae, attached narrowly; sternite 8 bilobed, square posteriorly, with long setae; syntergite 8+9 with long, broad, posterior sclerotized hooks.

Male abdomen. Males are not known for this genus.

Measurements. Total length (excluding antennae) = 9–11mm; wing length = 5–7mm.

Geographical distribution

Afrotropical: Cameroon, Kenya, Nigeria, Uganda, Zambia.

Etymology

The name is constructed from the greek term *schedo-*, meaning near or almost, and *Physoconops*. The name is masculine.

5.4.2. *Proposed classification of Conopidae*

Based on the present analysis, the following classification is proposed. Family, subfamily, and tribal ranks are designated based on an apomorphy-based phylogenetic concept. A list of apomorphic character states defining each group is included. Previous authors' interpretations of character states are provided using present terminology (*sensu* Cumming and Wood, 2009 and Chapter 4). Most previous catalogues of Conopidae utilized tribal classifications without diagnosis of tribal-group characters. These previous classifications are summarized in Table 5.1.

Chapter 4 examined phylogenetic relationships within Conopidae using DNA sequence data and many of the same morphological characters presented here, albeit with a smaller taxon set. That research recovered the same monophyletic clades with the same morphological apomorphies listed here. Also in Chapter 4, the past character interpretations and proposed apomorphic character states for Conopidae and its component subfamilies are reviewed. To avoid repetition of that work, only discussion of novel character states and tribal and subtribal relationships are included here. A list of species examined in the present analysis, either with specimens or through literature review, is included for each genus-group. Proposed taxonomic changes are also included.

CONOPIDAE Latreille, 1802 (Figs. 5.2-5.50)

Type genus *Conops* Linnaeus, 1758: 604. Included subfamilies: Conopinae, Dalmaniinae, Myopinae, Palaeomyopinae, Sicinae, Stylogastrinae, Zodioninae.

Uncontroverted morphological autapomorphies: prementum fused into a tube (42); posterolateral extensions of the basisternum present (48); and M vein deflected to meet or end near vein R_{4+5} (69). The pedicel is elongate in all members of Conopidae (28), but this character state is also observed in Pyrgotidae. The arista is thickened in all members of Conopidae (34), but has been secondarily reversed to the filiform state in *Melanosoma*. The prementum is longer than the width of the head in all members of Conopidae (43), but it has been secondarily shortened in *Myopa occulta*, *Abrachyglossum*, *Baruerizodion*, *Heteroconops*, *Leopoldius*, *Pseudomyopa*, *Tanyconops* and all members of Pleurocerinellini. The labella are filiform and fused (45) in Conopidae, but have been reversed to a broad and separate state in Conopinae and Zodioninae. There is a prominent row of setae on the posterior surface of the mesofemur in Conopidae (54); this has been lost in *Dacops*+*Physocephala*+*Pseudophysocephala*. All members of Conopidae (except some *Stylogaster* - (*S. biannulta*+*S. stylata*)+(*S. frauci*+ *S. pauliani*+*S. westwoodi*+*S. sp.*)) are lacking bristles on the postpronotum (60). The petiole of vein CuA_2+A_1 is longer than crossvein $dm-cu$ (78) in all members of Conopidae; this character has been reversed independently in three lineages: *Callosiconops*, *Pleurocerina*+*Camrasiconops*, and Conopinae excluding Pleurocerini. Female abdominal tergite and sternite 6 are at least partially fused in all members of Conopidae (88); this fusion has been lost in Dalmanniinae. The male epiproct is absent in all members of Conopidae (98); this state is also observed in Pyrgotidae.

Chapter 4 recovers Conopidae as monophyletic with the same set of apomorphic character states as recovered in the present analysis. Latreille (1802) initially described Conopsariae, including *Conops*, *Zodion*, *Myopa*, and *Stomoxys* [now in Muscidae], with the following characters: prementum elongate, cylindrical; labellum sometimes elongate, filiform, folded ventrally; maxillary palpi, when present, elongate; antennae sometimes longer than head; arista either apical or dorsal. According to the present analysis, the cylindrical prementum is apomorphic to Conopidae and the remaining characters describe various states across conopid subfamilies.

Schneider (2010) included *Notoconops*, as the type genus of the subfamily Notoconopinae, in Conopidae based on the absence of a dorsal notch on the pedicel; a bare anepisternum; vein R₁ bare; the absence of vibrissae; absence of mid coxal prongs; costa lacking breaks; veins Sc and R₁ separate; cell cup acute; vein A₁ complete. In the present analysis, none of these character states are found to be apomorphic to Conopidae. Also, the eyes and frons of *Notoconops* are sexually dimorphic, a condition not observed in any members of Conopidae. Furthermore, *Notoconops* lacks all but one (78 - vein CuA₂+A₁ elongate) of the apomorphic characters of Conopidae. For these reasons, *Notoconops* cannot be included in Conopidae. Its proper family classification is unknown and it should be left as *incertae sedis* within Schizophora pending further evidence of its proper placement.

Stuke (2005b) describes the single male fossil specimen of *Hoffeinsia* and places it in Conopidae due to its similarity to *Palaeomyopa*. He lists the

characteristics of *Hoffeinsia* as: absence of facial foveae; broad parafacial; extremely short prementum; and distinct chaetotaxy of the head and thorax. The absence of facial foveae is found within Conopidae in *Stylogaster*. The size of the parafacial is variable within Conopidae. Based on Stuke's description and figures, the prementum does not appear to be fused and elongate; an autapomorphy of Conopidae. Additionally, the chaetotaxy of the head and thorax is unlike any other examined member of Conopidae. Furthermore, *Hoffeinsia* lacks all but one (78 - vein CuA_2+A_1 elongate) of the apomorphic characters of Conopidae. For these reasons, *Hoffeinsia* cannot be included in Conopidae. Its proper family classification is unknown and it should be left as *incertae sedis* within Schizophora pending further evidence of its proper placement.

CONOPINAE Latreille, 1802 (Figs. 5.19-5.50)

Type genus *Conops* Linnaeus, 1758: 604. Included tribes: Asiconopini, Brachyceraeini, Caenoconopini, Conopini (s.s.), Gyroconopini, Microconopini, Physocephalini, Pleurocerinellini, Pleurocerini, Siniconopini, Tropicomyiini. Genera *incertae sedis*: *Euconops* and *Mallachoconops*. Uncontroverted morphological autapomorphies: apical, stylate arista (33); and epandrium fused beyond cerci (115). The vertex is complete and undivided in Conopinae (5), but this character state is also observed in Pyrgotidae. Ocellar bristles are absent in all members of Conopinae (14); this character state is also observed in Pyrgotidae, Syrphidae, Dalmanniinae, and some species of *Stylogaster* (*S. biannulata*+*S. stylata*+*S. frauci*+*S. pauliani*+*S. westwoodi*+*S. sp.*). Postocellar bristles are absent in all members of

Conopinae (15); this character state is also observed in Pyrgotidae, Syrphidae, and Dalmanniinae. The scape is elongate in all members of Conopinae (27); this character state has been reversed in Brachyceraeini and is also observed in *Pseudoconops*. The second aristomere is expanded ventrally in all members of Conopinae and has been reversed in *Asiconops* (*Sphenoconops*) (36). The anterior margin of the subcranial cavity is projects forward to a narrow point (37) and the maxillary palpi are reduced or absent (40) in Conopinae (37); these character states are also observed in Stylogastrinae. The posterolateral extensions of the basisternum have been reversed to blunt points in all members of Conopinae (49); a parallel reversal is observed in Sicinae. The petiole of vein CuA_2+A_1 is shorter than crossvein dm-cu (78) in all members of Conopinae (except *Atrichoparia*, *Heteroconops*, *Neoconops*, *Setosiconops*, *Smartiomyia*, and *Tanyconops*). A vena spuria is present in all members Conopinae (81), although sometimes only as a fold. This character state is also observed in Pyrgotidae and Syrphidae.

Chapter 4 recovers Conopinae as monophyletic with the same set of apomorphic character states, but only includes representatives of Asiconopini, Conopini (s.s.), Microconopini, Physocephalini, Pleurocerini, Tropicomyiini and *Euconops*. The following additional apomorphic character states are added: heavily sclerotized dorsal bridge of hypandrium forming nearly complete tube around phallus; single anterior arm on the hypandrium (absent in *Atrichoparia* sp. B); and absence of posterior surstyli.

Hendel (1936) suggests that the absence of ocelli is characteristic of all Conopinae, but Hennig (1966) notes that this is not the case. The presence of three ocelli on a well-developed ocellar tubercle is the plesiomorphic state within Conopidae. A reduction of the ocellar tubercle is apomorphic to Conopinae, but the loss of the central and lateral ocelli and the ocellar tubercle has occurred more than once within Conopinae (2,3,4). In a clade including all members of Conopinae, (except Pleurocerini, Gyroconopini, and Pleurocerinellini), the central ocellus is absent. In a clade including the Conopini+Asiconopini+*Euconops*+*Mallachoconops*+Brachyceraeini+Caenoconopini+Physocephalini+Tropidomyiini the lateral ocelli have been lost as well. Some reversal events have also occurred in regards to ocelli. All members of Tropidomyiini have regained the lateral ocelli. Within Tropidomyiini, all members of *Physoconops* (s.l.) have regained the central ocellus as well, although it is often very small. Parallel to these character changes, the central ocellus has been lost in members of *Heteroconops*+*Setosiconops*+*Tanyconops*, and all three ocelli have been lost in *Heteroconops gracilis*+*Setosiconops*+*Tanyconops*. This clade has also lost the ocellar tubercle completely. *Delkeskampomyia* and *Stenoconops* are each described as having two ocelli placing them within the *Heteroconops*+*Setosiconops*+*Tanyconops* clade. A parallel loss of the ocellar tubercle has occurred in Physocephalini and Asiconopini+*Euconops*+*Mallachoconops*.

A well-developed lunule (21) and the presence of a posterior hump on the epandrium (117) are autapomorphies of Conopinae excluding Pleurocerini. The lunule has been secondarily reduced in *Euconops*+*Mallachoconops*.

In addition to being an apomorphy of Stylogastrinae, the loss of the maxillary palpi (39) has occurred three times within Conopinae. This character state is an apomorphy of Asiconopini, Physocephalini+Tropidomyiini, and Pleurocerini. The maxillary palpi have been regained in *Camrasiconops*. The state of the maxillary palpi is unknown for *Delkeskampomyia*.

In addition to being an apomorphy of Pleurocerinellini, the reduction of the scutellum (65) is also an apomorphy of Asiconopini+*Euconops*+*Mallachoconops*+Brachyceraeini+Caenoconopini+Physocephalini+Tropidomyiini. This character has been reversed in *Euconops*, in which the scutellum is greatly enlarged with many bristles.

The petiole of CuA₂+A₁ (78) has been secondarily shortened in Conopinae. This character state has been reversed again to the long state in *Atrichoparia*+*Neoconops*+*Smartiomyia*+*Heteroconops*+*Setosiconops*+*Tanyconops*.

The distinctly petiolate shape to the male abdomen (105) is an apomorphy of Brachyceraeini+Caenoconopini+Physocephalini+Tropidomyiini that has arisen independently in *Siniconops microvalvus*.

Other characteristic states are observed in members of Conopinae but are not included in the present analysis. A prominent fronto-facial spot is present in many Afrotropical species of various tribes. A greatly elongate ventral genital plate is observed in many species, but the size and shape of the ventral genital plate is highly variable within genera. Both of these characters prove to be too homoplasious to contribute to higher-level classification.

ASICONOPINI **trib. nov.** (Figs. 5.20-5.22)

Type genus *Asiconops* Chen, 1939: 171. Genera included: *Anticonops* Kröber, 1936b: 285, *Archiconops* Kröber 1939a: 381, *Asiconops*, *Smithiconops* Smith, 2000: 221.

Uncontroverted morphological autapomorphy: angle between vein CuA₁ and crossvein dm-cu obtuse (77). Setae on the maxillary palpi are completely absent in Asiconopini (39); this character state is also observed in Physocephalini+ Trepidomyiini and most Pleurocerini.

The genus *Anticonops* is described based on one female specimen from the Congo. Kröber's (1936b) original description suggests that it is similar to *Conops*, but does not specify a species or subgenus. The extremely long prementum suggests a similarity to *Asiconops* (*s.l.*), but with a distinct condition of the female terminalia.

All of the genera currently placed in Asiconopini were previously placed in Conopini, with two of the genera being subgenera of *Conops*. The absence of an ocellar tubercle, maxillary palpi, scutellar bristles, and broad male abdominal tergites 3 and 4, as well as the presence of a characteristic acute angle between vein CuA₁ and crossvein dm-cu separate members of Asiconopini from Conopini as presently defined.

Species examined – *Anticonops abdominalis*; *Archiconops insularis*; *Archiconops pseudoerythrocephalus*; *Asiconops* (*Aegloconops*) *quadripunctatus* **comb. nov.** (*Conops*); *Asiconops* (*Asiconops*) *ater* **comb. nov.** (*Conops*); *Asiconops* (*Asiconops*) *aureomaculatus* **comb. nov.** (*Conops*); *Asiconops* (*Asiconops*) *australianus* **comb. nov.** (*Conops*); *Asiconops* (*Asiconops*) *chinensis* **comb. nov.** (*Conops*); *Asiconops*

(*Asiconops*) *nubeculosus* **comb. nov.** (*Conops*); *Asiconops* (*Asiconops*) *verus* **comb. nov.** (*Conops*); *Asiconops* (*Ceratoconops*) *ornatus* **comb. nov.** (*Conops*); *Asiconops* (*Diconops*) *geminatus* **comb. nov.** (*Conops*); *Asiconops* (*Diconops*) *trichus* **comb. nov.** (*Conops*); *Asiconops* (*Sphenoconops*) *brunneosericeus* **comb. nov.** (*Conops*); *Asiconops* (*Sphenoconops*) *nobilis* **comb. nov.** (*Conops*); *Smithiconops* *guineensis* **comb. nov.** (*Conops*); *Smithiconops* *rondanii* **comb. nov.** (*Conops*).

BRACHYCERAEINI Zimina, 1960 (Figs. 5.34-5.35)

Type genus *Brachyceraea* Röder, 1892: 366. Genera included: *Brachyceraea*, *Microbrachyceraea* Kröber, 1940b: 217, *Neobrachyceraea* Szilady, 1926: 587.

Uncontroverted morphological autapomorphy: scape quadrate (27). The single species of *Microbrachyceraea* possesses a quadrate scape and petiolate male abdomen, the two key characteristics of Brachyceraeini, thereby warranting its inclusion.

The presently proposed membership of Brachyceraeini matches the previously proposed definitions for the group. Zimina's (1960) original description of Brachyceraeini includes the following diagnostic characters: antennae shortened; basisternum broad with very small posterolateral extensions; vein R_{2+3} parallel to R_1 and meeting the costa midway between the end of R_1 and R_{4+5} . Hennig (1966) also suggests that the reduced antenna is likely a shared, derived apomorphy of the *Brachyceraea*. The present analysis confirms the characteristic antennal shape is due to a reduction in the scape. The other characters included by Zimina are plesiomorphic to Conopinae.

Species examined – *Brachyceraea brevicornis*; *Microbrachyceraea pendleburyi*
Neobrachyceraea elongata; *Neobrachyceraea obscuripennis*.

CAENOCONOPINI **trib. nov.** (Fig. 5.36)

Type genus *Caenoconops* Anonymous in Imperial Institute of Entomology, 1940: 365.

Genus included: *Caenoconops*. Uncontroverted morphological autapomorphy:
 vertex triangular in shape with longitudinal grooves (8).

Previous catalogues included *Caenoconops* in Conopini. The condition of the vertex, the absence of scutellar bristles, the petiolate male abdomen, the notched posterior margin of the eye, and the presence of a characteristic dark anterior/hyaline posterior wing pattern separate members of Caenoconopini from Conopini as presently defined.

Species examined - *Caenoconops bicolor*; *Caenoconops claripennis*; *Caenoconops friedbergi*; *Caenoconops rhodesiensis* **comb. rev.** (*Conops*).

CONOPINI Latreille, 1802 (Figs. 5.43-5.45)

Type genus *Conops* Linnaeus, 1758: 604. Genera included: *Abrachyglossum* Kröber, 1919: 142, *Conops*, *Leopoldius* Rondani, 1843: 35. Uncontroverted morphological autapomorphy: male abdominal tergites 3 and 4 broad and parallel-sided (104).

Previous classifications variously included members of Asiconopini, Caenoconopini, Physocephalini, Siniconopini, and Tropicomyiini within Conopini. See notes on each of those respective tribes for means to distinguish them from Conopini. Zimina's (1960) definition of Conopini includes the following key characteristics: facial foveae present; arista three-segmented; vein R₁ ending near

the end of R_{2+3} ; basisternum quadrangular. In the present analysis, each of these character states is plesiomorphic to Conopinae (*s.l.*). Smith and Peterson (1987) include no key characteristics of Conopini in their key to Nearctic genera, except that the key characteristics of *Physocephala* are absent.

Species examined – *Abrachyglossum capitatum*; *Conops flavipes*; *Conops vesicularis*; *Leopoldius coronatus*; *Leopoldius punctatum* **comb. nov.** (*Neobrachyglossum*); *Leopoldius signatus*.

GYROCONOPINI **trib. nov.** (Fig. 5.48)

Type genus *Gyroconops* Camras, 1955b: 174. Included genus: *Gyroconops*.

Uncontroverted morphological autapomorphy: vertex large, square, and setose, with ocelli displaced forward (7).

Previously placed as a subgenus of *Physoconops*, members of *Gyroconops* have been variously placed within Conopini and Physocephalini. As presently defined, members of Gyroconopini can be distinguished from *Physoconops* by the characteristic shape of the vertex and frons, the developed scutellum, the non-petiolate male abdomen, the presence of maxillary palpi, the absence of a notch in the posterior margin of the eye, and the absence of a characteristic dark anterior/hyaline posterior wing pattern.

Species examined – *Gyroconops abbreviatus* **comb. nov.** (*Physoconops*); *Gyroconops parvus* **comb. nov.** (*Physoconops*); *Gyroconops sylvosus* **comb. nov.** (*Physoconops*).

MICROCONOPINI trib. nov. (Figs. 5.49-5.50)

Type genus *Microconops* Kröber, 1915g: 77. Included genera: *Australoconops* Camras 1961: 64, *Microconops*. Uncontroverted morphological autapomorphy: presence of a medial spine on the epandrium (116).

Chapter 4 also recovers a monophyletic Microconopini using molecular and morphological analysis of species of both *Australoconops* and *Microconops*. Members of Microconopini have not been placed within any tribe in previous classifications.

Species examined – *Australoconops perbellum*; *Australoconops phaeomeros*; *Australoconops unicinctus*; *Microconops nigrithorax*; *Microconops ornatus*; *Microconops similis*; *Microconops tasmaniensis*.

PHYSOCEPHALINI Smith and Peterson, 1987 (Figs. 5.37-5.39)

Type genus *Physocephala* Schiner, 1861: 137. Included genera: *Dacops* Speiser, 1923: 99, *Physocephala*, *Pseudophysocephala* Kröber, 1939a: 374. Uncontroverted morphological autapomorphies: prominent row of setae on mesofemur absent (54). The ocellar tubercle is absent (4); this character state is also observed in *Asiconopini*+*Euconops*+*Mallachoconops* and *Heteroconops gracilis*+*Tanyconops*+*Setosiconops*. The ventral half of the proepisternum is bare in all members of Physocephalini (58); this character state is also observed in *Baruerizodion* and *Scatocemyia*.

Chapter 4 also recovers a monophyletic Physocephalini using molecular and morphological analysis and including representatives of only *Physocephala*. A

characteristic shape of the metafemur is listed as an autapomorphy of the clade, but this character is recovered in the present analysis as an autapomorphy of *Physocephala*+*Pseudophysocephala*.

The original usage of this tribal classification by Camras (1965) was in a Nearctic catalogue without diagnosis. Sabroskey (1999) notes that this makes the name unavailable. Smith and Peterson (1987) include Physocephalini in their key to Nearctic genera and this action makes them the authors of the name. They include only *Physocephala* in the tribe and list the following as key characteristics: crossvein r-m well beyond the middle of cell dm; prosepisternum bare; metafemur thickened in basal half; ocelli absent.

While *Physocephala* has been included in Conopini in some classifications, the tribe Physocephalini has included members of the present Pleurocerinellini and Trepidomyiini in past catalogues. In addition to the apomorphies of the tribe, Physocephalini can be distinguished from Conopini by the absence of maxillary palpi, the absence of scutellar bristles, the petiolate male abdomen, the notched posterior margin of the eye, and the presence of a characteristic dark anterior and hyaline posterior wing. Differences between Physocephalini, Pleurocerinellini, and Trepidomyiini are discussed below.

Species examined – *Dacops abdominalis*; *Dacops kaplanae*; *Physocephala bimarginipennis*; *Physocephala maculipes*; *Physocephala madagascariensis*; *Physocephala marginata*; *Physocephala rufipes*; *Physocephala tibialis*; *Pseudophysocephala constricta*; *Pseudophysocephala platycephala*.

PLEUROCERINELLINI Zimina, 1974 (Figs. 5.46-5.47)

Type genus *Pleurocerinella* Brunetti, 1923: 368. Included genera: *Pleurocerinella*, *Tammo* Stuke, 2008b: 50. Uncontroverted morphological autapomorphies: none. In all members of Pleurocerinellini, the prementum is reduced from the elongate state plesiomorphic to Conopidae (43); the reduced state is also observed in *Abrachyglossum*+*Leopoldius*, *Baruerizodion*, *Heteroconops*, *Myopa occulta*, *Pseudomyopa*, and *Tanyconops*. The scutellum is greatly reduced and lacking bristles (65) in all members of Pleurocerinellini; this character state is also observed in Asiconopini+*Euconops*+*Mallachoconops*+Brachyceraeini+Caenoconopini+Physocephalini+Tropidomyiini.

Zimina (1974) first described this tribe and included only the Palaearctic species, *Pleurocerinella tibialis*. The original tribal description, translated by Clements & Vincent (2001), includes the following diagnostic characters: pedicel elongate; three ocelli present; prementum short; labella “massive”; crossvein sc-r present; vein R₄₊₅+M present; pleura and coxae bare. While all of these character states are observed in the present analysis, only the shortened prementum is apomorphic to the tribe. Zimina (1974) suggests that Pleurocerinellini is intermediate between Conopinae and Myopinae, as it has the morphological characters of Conopinae, except ocelli are present. In the present analysis, the absence of ocelli is not apomorphic to Conopinae. Members of Pleurocerinellini display all character states apomorphic to Conopinae.

Previous classifications have included *Pleurocerinella* within Physocephalini. Members of Pleurocerinellini can be distinguished from members of Physocephalini by the presence of ocelli and an ocellar tubercle, a shortened prementum, a non-petiolate male abdomen, the absence of a notch in the posterior margin of the eye, the absence of a characteristic dark anterior and hyaline posterior wing pattern, the presence of maxillary palpi, the presence of a prominent row of setae on the mesofemur, and the presence of setae on the ventral half of the proepisternum. Species examined – *Pleurocerinella albohalterata*; *Pleurocerinella copelandi*; *Pleurocerinella srilankai*; *Pleurocerinella tibialis*; *Pleurocerinella* sp.; *Tammo rufa*.

PLEUROCERINI trib. nov. (Figs. 5.23-5.31)

Type genus *Pleurocerina* Macquart, 1851: 164. Included genera: *Atrichoparia* Schneider, 2010: 33, *Callosiconops* Kröber, 1940a: 75, *Camrasiconops* Schneider, 2010: 78, *Delkeskampomyia* Kröber, 1940a: 71, *Heteroconops* Kröber, 1915g: 80, *Neoconops* Kröber, 1915g: 75, *Pleurocerina*, *Setosiconops* Schneider, 2010: 157, *Smartiomyia* Kröber, 1940a: 72, *Stenoconops* Kröber, 1939d: 606, *Tanyconops* Schneider, 2010: 170. Uncontroverted morphological apomorphies: none. The frons has extensive lateral grooves (10) in all members of Pleurocerini; there has been a parallel development of this character state in *Asiconops* (s.s.)+*Ceratoconops*+*Diconops*. Setae on the maxillary palpi are absent (39) in all members of Pleurocerini, except *Camrasiconops*; this character state is also observed in *Asiconopini* and *Physocephalini*+*Tropidomyiini*. The wings are completely hyaline (67) in all members of Pleurocerini except *Pleurocerina*; this character state has

arisen independently in Phoridae, Syrphidae, Strongylophthalmyiidae, and *Microconops*. Although not available for examination, the original, or subsequent, descriptions of *Delkeskampomyia* and *Stenoconops* both include mention of these apomorphic character states. Their inclusion in Pleurocerini is thus warranted.

Chapter 4 also recovers a monophyletic Pleurocerini using molecular and morphological analysis and including representatives of *Atrichoparia*, *Camrasiconops*, *Pleurocerina*, *Heteroconops*, and *Smartiomyia*. Members of Pleurocerini have not been placed within any tribe in previous classifications.

The facial ridge meeting the subcranial cavity at a 90° angle (25) is an apomorphy of *Atrichoparia*+*Heteroconops*+*Neoconops*+*Setosiconops*+*Smartiomyia*+*Tanyconops*. This character cannot be assessed in *Delkeskampomyia*. The same character state has arisen independently in *Microconops*.

An extremely elongate first flagellomere (32) is an apomorphy of *Stylogaster inca*+*S. neglecta*, and is observed in Lauxaniidae and Phoridae. This character state is also an apomorphy of *Heteroconops*+*Neoconops*+*Setosiconops*+*Smartiomyia*+*Tanyconops*. This latter clade also shares a stylate arista that is reduced and retracted into the first flagellomere (35) and reduction of spicules on the ventral genital plate to a few apical rows (92). The status of these characters is unknown in *Stenoconops* and *Delkeskampomyia*.

While both species of *Setosiconops* and the one species of *Tanyconops* are recovered in a monophyletic clade with members of *Heteroconops*, the possible synonymy is considered here as unconfirmed. Some characters of *Heteroconops*,

especially regarding number of ocelli, are highly variable. Revision of all species of *Heteroconops* will be necessary to confirm a possible taxonomic revision for *Setosiconops* and *Tanyconops*.

Species examined – *Atrichoparia curticornis*; *Atrichoparia* sp. A; *Atrichoparia* sp. B; *Camrasiconops ater*; *Callosiconops hirsutus* **comb. rev.**; *Callosiconops rufus* **comb. nov.** (*Chrysidiomyia rufa*); *Callosiconops rugifrons* **comb. nov.** (*Chrysidiomyia*); *Delkeskampomyia fasciata*; *Heteroconops antennatus*; *Heteroconops gracilis*; *Heteroconops* sp.; *Neoconops brevistylus*; *Neoconops longicornis*; *Pleurocerina brevis*; *Pleurocerina longicornis*; *Pleurocerina luteiceps*; *Pleurocerina turneri*; *Pleurocerina vespiformis*; *Setosiconops robustus*; *Smartiomyia arena*; *Smartiomyia obscura*; *Stenoconops niger*; *Tanyconops longicaudus*.

SINICONOPINI **trib. nov.** (Fig. 5.33)

Type genus *Siniconops* Chen, 1939: 197. Included genera: *Macroconops* Kröber, 1927a: 125, *Siniconops*. Uncontroverted morphological autapomorphies: patch of bristles on female abdominal sternite 2 (86); apex of male abdomen square (110). While only a male is described and the number of ocelli is not mentioned, the stated similarity to *Siniconops maculifrons* justifies placement of *Macroconops* within Siniconopini.

Members of Siniconopini have been previously placed in Conopini. In addition to the two autapomorphic characters, members of Siniconopini can be distinguished from Conopini by the presence of two ocelli and a narrow second male abdominal segment.

Species examined – *Macroconops helleri*; *Siniconops elegans*; *Siniconops microvalvus* **comb. nov.** (*Conops*); *Siniconops nigripes* **comb. nov.** (*Conops*); *Siniconops sepulchralis* **comb. nov.** (*Physocephala*).

TROPIDOMYIINI Zimina, 1960 (Figs. 5.40-5.42)

Type genus: *Tropidomyia* Williston, 1888: 11. Included genera: *Physoconops* Szilady, 1926: 588, *Schedophysoconops* gen. nov., *Tropidomyia*. Uncontroverted morphological autapomorphies: none. Members of Tropidomyiini are characterized by the presence of lateral ocelli (3); this character state is present in many other conopid taxa, but it represents an autapomorphic character reversal in Tropidomyiini.

Chapter 4 also recovers a monophyletic Tropidomyiini using molecular and morphological analysis and including only representatives of *Physoconops*. Zimina (1960) describes the tribe Tropidomyiini, with the following characteristics: facial fovea absent; basisternum with anterolateral extensions; arista two-segmented; vein R_1 not ending near end of R_{2+3} . Hennig (1966) suggests that the absence of facial fovea is a secondary loss in *Tropidomyia*. In the present analysis, reduction of the facial fovea and facial ridge (20, 24) along with a strongly developed facial carina (23) are apomorphies of *Tropidomyia*, not Tropidomyiini (*s.l.*). The condition of the basisternum, arista, and wing veins in Tropidomyiini is plesiomorphic to the Conopinae.

While usually placed within its own tribe, *Tropidomyia* has been placed in Physocephalini by some authors. Members of Tropidomyiini can be distinguished

from Physocephalini by the presence of lateral ocelli, an ocellar tubercle, a prominent row of setae on the mesofemur, and setae or bristles on the ventral half of the proepisternum.

Species examined - *Physoconops (Aconops) antennatus*; *Physoconops (Aconops) costatus*; *Physoconops (Aureoconops) aureolus*; *Physoconops (Jelte) neotropicum* **comb. nov.** (*Jelte neotropica*); *Physoconops (Kroeberoconops) argentinus*; *Physoconops (Kroeberoconops) hermanni*; *Physoconops (Kroeberoconops) rufipennis*; *Physoconops (Pachyconops) brachyrhynchus*; *Physoconops (Pachyconops) bulbirostris*; *Physoconops (Pachyconops) guianicus*; *Physoconops (Physoconops) discalis*; *Physoconops (Physoconops) fronto*; *Physoconops (Physoconops) obscuripennis*; *Physoconops (Shannonconops) apicalis*; *Schedophysoconops notatifrons* **comb. nov.** (*Physoconops*); *Tropidomyia alexanderi*; *Tropidomyia aureifacies*; *Tropidomyia bimaculata*; *Tropidomyia ornata*; *Tropidomyia* sp.

Incertae sedis within Conopinae (Figs. 5.19, 5.32)

Genera: *Euconops* Kröber, 1915g: 76, *Mallachoconops* Camras, 1955b: 160. *Euconops* and *Mallachoconops* are each monotypic and their respective species are included in the present analysis. The present analysis recovers the two species in a monophyletic clade albeit it with little support. The only apomorphy for the group is a secondary reduction of the lunule (21). As they cannot with confidence be placed in any described tribe, these two genera remain genera *incertae sedis* within Conopinae. In Chapter 4, molecular and morphological analysis failed to place a representative of *Euconops* with any other clade within Conopinae with any support.

Species examined – *Euconops bellus*; *Mallachoconops atratulus*.

DALMANNIINAE Hendel, 1916 (Fig. 5.5-5.6)

Type genus *Dalmannia* Robineau-Desvoidy 1830: 248. Included genera:

Baruerizodion Papavero, 1970: 121, *Dalmannia*. Uncontroverted morphological autapomorphies: female abdominal sternite and tergite 6 separate (88); female abdominal segment 7 compressed laterally along entire length (97). Ocellar bristles are absent in all members of Dalmanniinae (14); this character state is also observed in Pyrgotidae, Syrphidae, Conopinae, and some species of *Stylogaster*. Postocellar bristles are absent in all members of Dalmanniinae (15); this character state is also observed in Pyrgotidae, Syrphidae, and Conopinae.

Chapter 4 recovers Dalmanniinae as monophyletic with the same set of apomorphic character states, but only includes representatives of *Dalmannia*. The following additional apomorphic character states are added: phallus coiled and setose; and posterior surstyli absent. Hendel's (1916) original mention of Dalmanniinae does not specify included genera and character states. The mention only state that Dalmanniinae possesses an unbroken costa and "[other primitive characteristics]".

Zimina (1960) describes the tribe Dalmanniini with the following key characteristics: female with long, curved "ovipositor"; phallus elongate and "band-shaped"; veins Sc and R₁ ending not near one another; cell cup short; lower pleural sclerites bare. According to the present analysis, the male and female terminalia characters are both autapomorphies of Dalmanniinae. For the wing and pleural

characters, Dalmanniinae retains the condition plesiomorphic to Conopidae. The presence of an “ovipositor” has previously been used to define Dalmanniinae, and in the present analysis, modification to female abdominal segment 7 is an autapomorphy of the subfamily. Superficially similar, yet distinct, modifications to the female terminalia have occurred in other subfamilies (e.g. *Paramyopa*, *Parazodion*, and *Tanyconops*).

While all other authors have afforded Dalmanniinae subfamily status, it was described by Zimina (1960) as a tribe of Myopinae. According to the present analysis, in addition to its apomorphic character states, Dalmanniinae can be distinguished from Myopinae by a broad basisternum, unfused veins Sc and R₁, absence of spicules on female abdominal sternites 5 and 6, absence of spicules on male abdominal sternite 5, narrow male syntergosternite 7+8, and absence of male abdominal sternite 8.

Species examined – *Baruerizodion steyskali*; *Dalmannia aculeata*; *Dalmannia nigriceps*; *Dalmannia vitiosa*.

MYOPINAE Macquart, 1834 (Figs. 5.7-5.14)

Type genus *Myopa* Fabricius, 1775: 798. Included tribes: Myopini (s.s.), Thecophorini. Uncontroverted morphological autapomorphies: basisternum short, narrow, single sclerite (47); veins Sc and R₁ fused before reaching costa (73). A double row of black spines is present on the ventral surface of all femora (52) in all members of Myopinae; this character state is also observed in *Baruerizodion* and *Robertsonomyia*+*Zodiomyia*.

Chapter 4 recovers Myopinae as monophyletic with the same set of apomorphic character states, but only includes representatives of *Myopa*, *Thecophora*, and *Pseudoconops*. The following additional apomorphic character state is added for those taxa: two, separate, anterior arms on the hypandrium. Macquart (1834) originally described the Myopariae, including *Myopa*, *Stachynia* [now *Dalmannia*], and *Zodion*, with the following diagnostic characters: veins $R_{4+5}+M$ not petiolate; alula small; prementum elongate; labellum sometimes elongate and folded back along prementum. In the present analysis, both petiolate and non-petiolate states of vein $R_{4+5}+M$ are observed in genera of Myopinae. The prementum in Myopinae is in the state plesiomorphic to Conopidae. The elongate and ventrally directed labellum is an autapomorphy of Conopidae.

In addition to the present members of Myopini (s.s.) and Thecophorini, previous classifications also included genera presently placed within Dalmanniinae, Sicinae, and Zodioninae within Myopinae. See discussions of those subfamilies for details in distinguishing the members of each respective subfamily.

MYOPINI Macquart, 1834 (Figs. 5.7-5.11)

Type genus *Myopa* Fabricius, 1775: 798. Included genera: *Melanosoma* Robineau: Desvoidy, 1853: 122, *Myopa*, *Myopotta* Zimina, 1969: 671, *Paramyopa* Kröber, 1916e: 91, *Pseudomyopa* Pearson, 1974: 148. Uncontroverted morphological autapomorphies: gena expanded to be over one third of head height (16).

Chapter 4 recovers Myopini as monophyletic with the same apomorphic character state, but only includes representatives of *Myopa*. Zimina (1960)

described the tribe Myopini, including *Melanosoma*, *Myopa*, and *Thecophora*, with the following key characteristics: veins Sc and R₁ fused before reaching costa; costa thickened at end of R₁; lower pleural sclerites pilose. According to the present analysis, the first two characters are apomorphies of Myopinae and Thecophorini respectively and the third character state is not observed.

Pearson (1974) included *Pseudomyopa* in Dalmanniinae based on the presence of an elongate “appendage on the penis.” This structure is not present in the specimens included in the present analysis. All other characters of *Pseudomyopa* are in agreement with the present definition of Myopini.

Species examined – *Melanosoma bicolor*; *Melanosoma hyalipenne*; *Myopa buccata*; *Myopa clausa*; *Myopa occulta*; *Myopa vesiculosa*; *Myopa* sp.; *Myopotta pallipes*; *Myopotta rubripes*; *Paramyopa oestracea*; *Pseudomyopa camrasi*.

THECOPHORINI **trib. nov.** (Figs. 5.12-5.14)

Type genus *Thecophora* Rondani, 1845: 15. Included genera: *Pseudoconops* Camras, 1962a: 183, *Scatocemyia* Camras 1957a: 13, *Thecophora*. Uncontroverted morphological autapomorphies: costa thickened at insertion of Sc+R₁ (74).

Chapter 4 recovers a monophyletic Thecophorini using molecular and morphological analysis and including representatives of *Pseudoconops* and *Thecophora*. Additional uncontroverted morphological autapomorphies provided are: dorsal half of proepisternum with patch of setae; hypandrium with broad, setose, anterior plate; and a repeated segment of DNA sequence in the D2 expansion

section of the 28S gene region. The first character state is found by the present analysis to be an autapomorphy of *Pseudoconops*+*Thecophora*.

Species examined – *Pseudoconops antennatus*; *Scatocemyia plaumanni*; *Thecophora africana*; *Thecophora atra*; *Thecophora australiana*; *Thecophora metallica*; *Thecophora modesta*; *Thecophora occidensis*.

†PALAEOMYOPINAE Camras, 1994

Type genus *Palaeomyopa* Meunier, 1899: 145. Included genus: †*Palaeomyopa*.

Uncontroverted morphological autapomorphies: none. Hennig (1966) offers one possible apomorphy for *Palaeomyopa*: a bend in vein CuA₂. This is not to be confused with the curved vein CuA₂ observed in Conopinae+Zodioninae, which is in the opposite direction.

Hennig (1966) suggests that the antennae of *Palaeomyopa* are in a “primitive” state. Camras (1994) suggests that the elongate pedicel and “peculiar” arista are apomorphies of Palaeomyopinae. The present analysis demonstrates that Palaeomyopinae retains the conopid groundplan state for all antennal characters (27-36).

Likewise, Hennig (1966) notes the presence of a “short, thick proboscis” with elongate maxillary palpi. If this is so, then the palpi retain a condition plesiomorphic to Conopidae, but the prementum and labella would represent apomorphic states, possibly convergent with the condition observed in *Leopoldius*. Camras (1994) includes reduced mouthparts as a plesiomorphic condition in his description of Palaeomyopinae. However, Hennig (1966) also states that mouthparts are absent or

else very difficult to diagnose in the fossil specimens of *Palaeomyopa*. Further examination of existing specimens will be necessary to assess these potential apomorphies.

Camras (1994) and Hennig (1966) both note that *Palaeomyopa*, *Stylogaster*, and *Tropidomyia* all possess a strong medial carina and weak, if not absent, facial foveae. He suggests that this is a plesiomorphic condition in the prior two genera, but is secondarily derived in *Tropidomyia*. The illustration in Hennig (1966) clearly shows the presence of a facial fovea and medial carina in *Palaeomyopa*, suggesting a condition plesiomorphic to Conopidae for these characters (19, 20, 22, 23).

Hennig (1966) also notes the presence of fronto-orbital bristles (12), a plesiomorphic condition in Palaeomyopinae. Although the degree of setation varies throughout Conopidae, the presence of true bristles on the frons is limited to some species of *Stylogaster*. In the present analysis, the absence of fronto-orbital bristles is an apomorphy of Conopidae excluding Stylogastrinae. If bristles are truly present in *Palaeomyopa*, it would suggest excluding it from this clade, but closer examination is necessary.

Hennig's (1966) and Camras' (1994) interpretation of the ventral genital plate as arising from the fourth abdominal sternite leads each of them to conclude this is the groundplan state of the Conopidae excluding Stylogastrinae. However, if the ventral genital plate arises from the fifth sternite and has merely been displaced in the available specimen, then there is nothing in the female abdominal characters to distinguish it from Myopinae.

This leaves Palaeomyopinae without any clear apomorphic character states. This is unsurprising for a fossil species. Only further specimens and further examination will reveal possible apomorphies for Palaeomyopinae.

Species examined – *Palaeomyopa tertiaria*.

SICINAE Zimina, 1960 (Figs. 5.3-5.4)

Type genus *Sicus* Scopoli, 1763: 1004. Included genera: *Carbonosicus* Zimina, 1958: 933, *Sicus*. Uncontroverted morphological autapomorphies: male sternite 8 with dense, long, black setae (112). A secondary reversal to reduced posterolateral extensions of the basisternum is present in members of Sicinae (49); a parallel reversal has occurred in members of Conopinae.

Chapter 4 did not test the monophyly of Sicinae, because only one species of *Sicus* was included in the analysis. Zimina (1958) first suggests the tribe Sicini, including the genera *Carbonosicus* and *Sicus*, but does not give diagnostic characters for the group. According to Sabroskey (1999), the lack of a description or diagnosis renders the genus-group name invalid. In Zimina (1960), however, a diagnosis of the tribe is provided with the following key characteristics: basisternum broad; veins Sc and R₁ parallel; cell cup elongate; long red bristles present on sides of mesonotum. According to the present analysis, the first three characters states are plesiomorphic to Conopidae.

Species examined – *Carbonosicus carbonarius*; *Sicus abdominalis*; *Sicus ferrugineus*.

STYLOGASTRINAE Williston, 1885 (Fig. 5.2)

Type genus *Stylogaster* Macquart, 1835: 38. Included genus: *Stylogaster*.

Uncontroverted morphological autapomorphies: ommatidia distinctly larger anteriorly (18); facial fovea absent (19); protibial, apical spurs present (50); katepisternum bare (64); alula narrow (82); female abdominal sternite 2 and 3 absent (85); female hypoproct sclerotized and elongate (99). The vertex is expanded to more than half of the length of the frons, sometimes reaching the ptilinum (6) in all members of *Stylogaster* (except *biannulata* and *stylata*). The facial carina is strongly developed (23) in all members of Stylogastrinae; this character state has arisen independently in *Tropidomyia*. The anterior margin of the subcranial cavity projects forward to a narrow point in Stylogastrinae (37); this character state is also observed in Conopinae. Maxillary palpi are absent (39, 40) in all members of Stylogastrinae; this character state is also observed in some members of Conopinae. Bristles are present on the anepimeron (62) in all members of Stylogastrinae; this character state is also observed in Strongylophthalmyiidae and Pyrgotidae. Crossvein sc-r is present (76) in all members of Stylogastrinae; this character state is also present in Conopinae. The male cerci are elongate (113) in all members of Stylogastrinae; this character state is also observed in Pyrgotidae and Strongylophthalmyiidae.

Chapter 4 recovers Stylogastrinae as monophyletic with the same set of apomorphic character states. The following additional apomorphic character states are added for those taxa: bi- or tri-lobed posterior surstyli; male abdominal tergite 6

broad, hemispherical, internal; phallapodeme and ejaculatory apodeme broadened into wide, thin lobe; sperm pump modified into a sclerotized sphere with lateral lobes and a long sperm duct; and phallus with two distinct, sclerotized segments. See the note in Chapter 4 about alternate spelling of this subfamily name and discussion of past status as a separate family.

Species examined – *Stylogaster biannulata*; *Stylogaster breviventris*; *Stylogaster decorata*; *Stylogaster frauci*; *Stylogaster inca*; *Stylogaster neglecta*; *Stylogaster pauliani*; *Stylogaster rectinervis*; *Stylogaster stylata*; *Stylogaster westwoodi*; *Stylogaster* sp.

ZODIONINAE Rondani, 1856 (Figs. 5.15-5.18)

Type genus *Zodion* Latreille, 1797: 162. Included genera: *Robertsonomyia* Malloch, 1919: 205, *Zodiomyia* Camras, 1957c: 163, *Zodion*. Uncontroverted morphological autapomorphy: basisternum reduced to a narrow sclerite divided posteriorly (47).

Chapter 4 recovers Zodioninae as monophyletic with the same set of apomorphic character states, but only includes representatives of *Zodion* and *Parazodion*. The following additional apomorphic character states are added for those taxa: a developed, fleshy hypoproct in the male; a leaf-shaped phallus with a single, central, sclerotized rod; and two, separate, anterior arms on the hypandrium.

Rondani (1856) originally describes Zodionina, including only *Zodion*, based on the presence of a dorsal arista, an elongate prementum, and reduced labellum. Zimina (1960) redefines the tribe Zodionini, within Myopinae and containing only *Zodion*, with the following key characteristics: labella not elongate; crossvein sc-r

present; vein $R_{4+5}+M$ usually petiolate. Each of these characters are plesiomorphic, either to Conopidae or Conopinae+Zodioninae.

Robertsonomyia and *Zodion* have been placed within Myopinae in most previous classifications. Members of Zodioninae can be distinguished from Myopinae by the short, broad labella, the shape of the basisternum, the presence of shiny patches near the apex of the tibia, the extended vein R_1 , the unfused veins Sc and R_1 , the presence of crossvein sc-r, the ending of vein R_{2+3} near the end of vein R_1 , the curved vein CuA_2 , and the male cerci attached by a narrow, sclerotized stalk. Species examined – *Parazodion schmidtii*; *Parazodion* sp.; *Robertsonomyia mexicana*; *Robertsonomyia palpalis*; *Robertsonomyia parva*; *Robertsonomyia pearsoni*; *Zodiomyia sumbaensis*; *Zodion cinereum*; *Zodion erythrurum*; *Zodion fulvifrons*; *Zodion griseum*; *Zodion intermedium*; *Zodion pictum*; *Zodion pruinsum* **comb. nov.** (*Neozodion*).

5.4.3. Evolution of character states within Conopidae

In addition to those characters previously discussed that are apomorphic to certain clades, the following characters are present in varying states within Conopidae. As such, these characters can help to determine relationships between subfamily clades within Conopidae.

The absence of fronto-orbital bristles (12) is an apomorphy of Conopidae excluding Stylogastrinae. This character state, however, is also observed in Pyrgotidae, Psilidae, Syrphidae, and a clade of Old World *Stylogaster* (*S. frauci*+ *S. pauliani*+*S. westwoodi*+*S.* sp.). Other apomorphies of Conopidae excluding

Stylogastrinae include: the extension of vein Sc to a point beyond four tenths of the length of the costa (71); female sternite 8 divided into two, sclerotized lobes (100); and presence of sclerotized posteroventral hooks on female syntergite 8+9 (102).

Chapter 4 recovers Conopidae excluding *Stylogaster* as monophyletic with the same set of apomorphic character states. The following additional apomorphic character states are added for those taxa: male abdominal tergite 6 narrow, bare, and fused with syntergosternite 7+8; and postgonites present.

Elongate, narrow, posterolateral extensions of the basisternum (49) is an apomorphy of Conopidae excluding Stylogastrinae and has been independently reversed in Sicinae and Conopinae. An equally parsimonious explanation is the independent evolution of this character state in three subfamilies: Dalmanniinae, Myopinae, and Zodioninae. Unfortunately, this character cannot be diagnosed in Palaeomyopinae.

A clade including ((Conopinae+Zodioninae)+Sicinae)+Myopinae is defined by a number of modifications to the female and male abdomen. These apomorphic character states include: presence of spicules on female abdominal sternites 5 and 6 (91, 90); the deflection of female abdominal segment 7 ventrally (96); male abdominal sternite 5 broad and with spicules (106); male abdominal sternite 8 present (111); and male abdominal syntergosternite 7+8 broad and hemispherical (109). The spicules on female sternite 6 have been secondarily lost in *Parazodion* and the deflection of female segment 7 has arisen independently in *Baruerizodion*. The broad male syntergosternite 7+8 has arisen independently in Old World

Stylogaster (i.e., *S. frauci*+*S. pauliani*+*S. westwoodi* +*S. sp.*). While the male character states are unknown, Palaeomyopinae possesses all three of the female abdominal character states apomorphic to this clade.

Chapter 4 recovers ((Conopinae+Zodioninae)+Sicinae)+Myopinae as monophyletic with the same set of apomorphic character states. The following additional apomorphic character state is added: anterior surstyli present.

Hennig (1966) suggests *Palaeomyopa* as a possible adelphotaxon to Conopidae excluding Stylogastrinae. He also suggests it as possibly an ancestral form of either Conopinae or Myopinae (including *Zodion* and *Dalmannia* in his analysis). In regards to wing venation, Hennig notes that the absence of crossvein sc-r and the equally spaced insertions of Sc, R₁, and R₂₊₃ along the costa suggest that *Palaemyopa* has retained the plesiomorphic wing condition. Camras (1994) describes the wing venation of Palaeomyopinae as plesiomorphic. In the present analysis, *Palaeomyopa* lacks all of the wing characters apomorphic to (Conopinae +Zodioninae)+Sicinae (72, 75), Myopinae (73), and Stylogastrinae (76), respectively. There remains equal likelihood that Palaeomyopinae represents an adelphotaxon to (Conopinae+Zodioninae)+Sicinae, or Myopinae, or is an ancestral form of either.

The extension of vein R₁ to a point beyond six tenths of the length of the costa and near to the end of R₂₊₃ (72, 75) are apomorphies of (Conopinae+Zodioninae)+Sicinae. Chapter 4 recovers (Conopinae+Zodioninae)+Sicinae as monophyletic with the same set of apomorphic character states. It does not add any additional apomorphic character states.

Elongate, filiform, partly fused labella that fold back along the prementum are the groundplan conditions within Conopidae. The reduction of the labella to a shortened, separate, broad state (44, 45) are autapomorphies of Conopinae+Zodioninae. Additional apomorphies of this clade include: the presence of a shiny patch near the apex of the metatibia (53); the presence of crossvein sc-r (76); vein CuA₂ curved (79); female abdominal tergite and sternite 5 fused (87); and male cerci attached by a narrow, sclerotized stalk (114).

Chapter 4 recovers Conopinae+Zodioninae as monophyletic with the same set of apomorphic character states. It does not add any additional apomorphic character states.

5.4.4. *Biogeography of Conopidae*

While an overall biogeographical pattern is difficult to determine for Conopidae (*s.l.*), a number of intra-subfamilial observations can be made that may facilitate future investigation.

Stylogastrinae has a Southern distribution. The subfamily is absent from the Palaearctic and only two species are found in the Nearctic region. The bulk of the diversity appears to be found in the Neotropics. Furthermore, both Chapter 4 and the present analysis recover four Old World species of *Stylogaster* as a monophyletic clade within the subfamily. This phylogeny and distribution pattern suggests a possible origin of *Stylogaster* in South America with a single invasion and radiation in the Old World.

In the present analysis, Dalmanniinae is divided into the holarctic *Dalmannia* and the Neotropical *Baruerizodion*. Two species of *Dalmannia* are included in Smith's (1975) Oriental catalogue, but they are both from China's Jiangsu province, which is not conventionally considered part of the Oriental region.

Myopinae (*s.l.*) and Thecophorini are each global in distribution with little pattern evident in the present analysis. Myopini (*s.s.*), however, displays an interesting pattern. Three species of *Myopa* are included in Papavero's (1971) Neotropical catalogue, but they are all from the Chihuahua state of Mexico, which is not conventionally considered part of the Neotropical region. The species of *Myopa* included in Smith's (1975) Oriental catalogue are all from Northern China or Northern India. A single species of *Myopa* is recorded from Australia. *Melanosoma* and *Myopotta* are recorded only from the Palearctic. Myopini can thus be described as mainly Holarctic, with *Paramyopa* and *Pseudomyopa* being the sole representatives of the tribe in Africa and South America respectively.

Sicinae is limited in generic and species diversity. It is also exclusive to the Palearctic region and the northern reaches of the Oriental region.

Within Zodioninae, *Zodion* is global in distribution. *Parazodion*, *Robertsonomyia*, and *Zodiomyia*, however, are endemic to the Neotropics, the New World, and the Oriental region, respectively.

Conopinae is truly global in distribution, but closer analysis of its component tribes reveals some biogeographical pattern. Pleurocerini is the adelphotaxon of the remaining Conopinae and is one of two tribes composed entirely of Australian

endemic genera. The remaining tribes of Conopinae are each restricted to a specific area, with notable exceptions. Conopini and Pleurocerinellini are both exclusively Old World, but absent from Australia. A single species of *Conops*, *pruinus* Bigot, 1887, is recorded from the New World, but this identification and/or locality information should likely be questioned. Gyroconopini is found only in the New World. The distribution of Siniconopini is limited to the far eastern Palaearctic and Oriental regions. Microconopini is exclusively Australian. Members of Brachyceraeini are found only in the Palaearctic and Oriental regions. Caenoconopini is the only tribe endemic to the Afrotropical region. Asiconopini and Physocephalini are both global in distribution, with some genera and subgenera being endemic to certain regions.

The remaining tribe, Tropidomyiini, presents an odd distribution amongst its three included genera. *Schedophysoconops* is exclusively Afrotropical, but is monotypic. *Tropidomyia* is circumtropical in distribution. *Physoconops* is endemic to the New World. Four species of *Physoconops* from the Afrotropical and Oriental regions are reclassified here. The two remaining Oriental species (*P. jutogensis* Nayar, 1968 and *P. borneensis* Kröber, 1940a) need to be re-examined, but are likely not *Physoconops*.

5.4.5. Conclusions

The present analysis represents the most comprehensive phylogenetic analysis of relationships within Conopidae to date. Representatives of all extant and two fossil genera are included. Only nine genera were unavailable for observation

and are included in analysis as literature descriptions. Parsimony analysis of a 117-character morphological database recovers a phylogenetic hypothesis for the family. The first ever classification including all described world genera is proposed based on this phylogenetic hypothesis.

All previously proposed subfamilies are recovered with strong support and numerous autapomorphic character states. Generic membership of most subfamilies (except Conopinae and Stylogastrinae) is revised. The previously proposed tribe Sicini is elevated to subfamily rank. Relationships between subfamilies are also recovered with strong support. Placement of the fossil subfamily Palaeomyopinae is ambiguous, but analysis places it within the ((Conopinae+ Zodioninae)+Sicinae)+Myopinae clade.

Well-supported and well-defined clades within both Conopinae and Myopinae are recovered. Each of these tribal groups is distinguishable morphologically, but relationships between tribes in Conopinae are not fully resolved. This may be due to a rapid evolution of a wide diversity of autapomorphic genera within a short time span in evolutionary history.

A number of changes to classification are proposed. Both *Notoconops* and *Hoffeinsia* are removed from Conopidae. Both Sicini and Zodionini are removed from Myopinae and elevated to subfamilial status. A new tribe is proposed within Myopinae to accommodate *Thecophora*, *Scatocceomyia*, and *Pseudoconops*. Two genera are removed from Dalmanniinae and placed in Myopinae and Zodioninae respectively. Conopinae is divided into eleven tribes, seven of which are newly

described. Some examined species are transferred to different or new genera and subgenera based on the phylogram recovered.

The phylogenetic hypothesis and classification proposed here will facilitate future revisionary work within Conopidae. Variation within autapomorphic character states of each subfamily and tribe will provide new character data for future research. Also, the present results will provide a phylogenetic framework for ongoing research into the evolution of mimicry, hilltopping mating behaviour, and host-parasitoid interactions involving species of Conopidae.

5.5. Key to world genera of Conopidae.

The following key is to all extant genera of Conopidae. Only adult male and female characters are used. Internal, genitalic characters, requiring dissection are not used. Morphological terminology follows that of Cumming and Wood (2009). Confirmed ranges of each genus are given based on current catalogues with the following abbreviations: AF – Afrotropical, AU – Australasian, NA – Nearctic, NT – Neotropical, OR – Oriental, PA – Palaearctic.

1. Labella subequal in length to prementum, filiform, at least partly fused, folded back along prementum (Figs. 5.2, 5.3, 5.6, 5.12); metatibia without apical shiny patch; vein CuA₂ straight (Figs. 5.2, 5.3, 5.6, 5.12); female abdominal tergite and sternite 5 separate; male cerci broadly attached 2
- Labella, shorter than prementum, broad, separate for entire length, projecting forward from apex of prementum (Figs. 5.15, 5.29); shiny patch present near

- apex of metatibia (Fig. 5.22); vein CuA₂ curved along its length (Figs. 5.16, 5.20); female abdominal tergite and sternite 5 fused; male cerci attached by narrow, sclerotized stalk 14
2. Body elongate, light coloured, with long, narrow legs and mouthparts; ommatidia distinctly larger at anterior margin; facial foveae absent; anterior margin of subcranial cavity projecting forward at junction with medial carina; facial carina strongly developed; maxillary palpi absent; protibial, apical spurs present; katapisternum bare; anepimeral bristles present; crossvein sc-r present; alula narrow; female abdominal sternite 2 and 3 absent; female hypoproct sclerotized and elongate; elongate lateral lobes on female abdominal sternite 8 usually present; male cerci elongate (Fig. 5.2) Stylogastrinae (AF, AU, NA, NT, OR) ... *Stylogaster* Macquart, 1835
- Body robust, colour variable, legs short and robust, mouthparts variable; ommatidia uniform (Figs. 5.3, 5.6, 5.10); facial foveae present (Figs. 5.3, 5.6, 5.10); anterior margin of subcranial cavity straight or round (Figs. 5.3, 5.6, 5.10); facial carina weakly developed (Figs. 5.3, 5.6, 5.10); maxillary palpi present (Fig. 5.3); protibial, apical spurs absent; katapisternum with bristles or setae (Fig. 5.3); anepimeral bristles absent (Fig. 5.3); crossvein sc-r absent (Figs. 5.3, 5.6, 5.10); alula broad (Figs. 5.3, 5.6, 5.10); female abdominal sternite 2 and 3 present; female hypoproct absent; elongate lateral lobes on female abdominal sternite 8 absent; male cerci short, round 3

3. Posterolateral extensions of basisternum short, blunt; vein R_1 ends posterior to halfway point of costa; male abdominal sternite 8 with dense, long, black setae (Figs. 5.3, 5.4) *Sicinae* ... 4
- Posterolateral extensions of basisternum elongate, narrow (Fig. 5.5); vein R_1 ends at or before halfway point of costa (Figs. 5.6, 5.10); male abdominal sternite 8 bare or with sparse, short, or pale setae 5
4. Entirely black except for yellow-orange head, antennae, and wing bases; frons, anepisternum, proepisternum, proepimeron, and katepisternum covered with long, dense setae (Fig. 5.4) (PA) *Carbonosicus* Zimina, 1958
- Entirely reddish-brown; frons, anepisternum, proepisternum, proepimeron, and katepisternum bare or with sparse or short setae (Fig. 5.3) (OR, PA)
..... *Sicus* Scopoli, 1763
5. Ocellar and postocellar bristles absent (Figs. 5.5, 5.6); basisternum broad; veins Sc and R_1 separate for entire length (Fig. 5.6); female abdominal tergite and sternite 6 completely separate; female abdominal segment 7 laterally compressed along entire length (Figs. 5.5, 5.6); phallus visible, elongate, ribbon-shaped, setose along entire length..... *Dalmanniinae* ... 6
- Ocellar and postocellar bristles present (Fig. 5.10); basisternum short, narrow, single sclerite; veins Sc and R_1 fused before reaching costa (Figs. 5.10, 5.14); female abdominal tergite and sternite 6 at least partly fused; female abdominal segment 7 rounded at least in basal half (Fig. 5.12); phallus usually not visible *Myopinae* ... 7

6. Body dark and large (>8mm in length); pedicel equal in width to scape; setae on occiput sparse, short, black; setae on frons sparse; prementum shorter than head width; ventral half of proepisternum bare; femora thickened, with double row of black spines ventrally; female abdominal segment 7 deflected ventrally (Fig. 5.5) (NT) *Baruerizodion* Papavero, 1970
- Body usually with distinct black and yellow patterning, small (<8mm); pedicel at least twice as wide as scape; setae on occiput dense, long, white; dense setae on frons; prementum length equal to or greater than head width; ventral half of proepisternum with setae; femora narrow, without spines; female abdominal segment 7 not deflected ventrally (Fig. 5.6) (NA, PA)
..... *Dalmannia* Robineau-Desvoidy, 1830
7. Gena expanded to be at least one third of total head height (Figs. 5.7, 5.9); anterior margin of subcranial cavity rounded (Fig. 5.9); costa uniform thickness along entire length (Fig. 5.9) Myopini ... 8
- Gena less than one third of head height (Fig. 5.12); anterior margin of subcranial cavity straight (Fig. 5.12); costa thickened at endpoint of Sc+R₁ (Fig. 5.14) Thecophorini ... 12
8. Large (body 10mm), very setose; female abdominal segment 7 broad basally and modified into narrow tube apically (Fig. 5.7) (AF)
..... *Paramyopa* Kröber, 1916c
- Body size and degree of setation variable; female abdominal segment 7 broad for entire length (Fig. 5.8) 9

9. Abdomen narrow; thoracic and abdominal setae sparse; arista filiform; setae on frons sparse; length of prementum at least 1.5 times the width of the head; double row of ventral femoral spines very small (Fig. 5.8) (OR, PA)
..... *Melanosoma* Robineau-Desvoidy, 1853
- Abdomen broad; thoracic and abdominal setae dense; arista thick (Fig. 5.10); setae on frons dense (Fig. 5.10); length of prementum equal to or less than width of head (Fig. 5.10); double row of ventral femoral spines well-developed 10
10. Setae on occiput short and sparse; prementum shorter than head width; labella short, thickened (Fig. 5.9) (NT) *Pseudomyopa* Pearson, 1974
- Setae on occiput long and dense (Fig. 5.10); prementum usually longer than head width (Fig. 5.10); labella elongate, filiform (Fig. 5.11) 11
11. Fronto-facial spot absent; katapisternum with distinct bristles; vein R_{2+3} ending well beyond end of R_1 ; male abdominal sternite 8 broad, dull (Fig. 5.10) (AU, NA, OR, PA) *Myopa* Fabricius, 1775
- Prominent fronto-facial spot; katapisternum lacking bristles, setae only; vein R_{2+3} ending near end of R_1 ; male abdominal sternite 8 very narrow, shiny (Fig. 5.11) (PA) *Myopotta* Zimina, 1969
12. Body elongate (>7mm) reddish brown; scape at least twice as long as wide; length of maxillary palpi more three times the width of the prementum; abdominal tergite 2 more than twice as long as all other abdominal tergites (Fig. 5.12) (AF) *Pseudoconops* Camras, 1962a

- Body robust (usually <7mm) mostly black (Figs. 5.13, 5.14); second abdominal segment equal to third segment (Figs. 5.13, 5.14); scape quadrate (Figs. 5.13, 5.14); length of maxillary palpi less than three times the width of the prementum 13
- 13. Length of prementum more than twice the width of the head; proepisternum bare; male sternite 8 wide (Fig. 5.13) (NT) *Scatocemyia* Camras, 1957a
- Length of prementum less than twice the width of the head; proepisternum with setae; male sternite 8 narrow (Fig. 5.14) (AF, NA, NT, OR, PA)
..... *Thecophora* Rondani, 1845
- 14. Arista mid-dorsal (Figs. 5.15, 5.16); second aristomere equal to first; scape quadrate (Figs. 5.15, 5.16); ocellar tubercle well-developed (Figs. 5.15, 5.16); ocellar and postocellar bristles present (Figs. 5.15, 5.16); anterior margin of subcranial cavity rounded (Figs. 5.15, 5.16); maxillary palpal length at least equal to prementum width (Fig. 5.16); basisternum narrow, divided posteriorly, with elongate and narrow posterolateral extensions; more than two pairs of scutellar bristles usually present; vena spuria absent (Fig. 5.16); epandrium separate beyond cerci *Zodioninae* ... 15
- Arista stylate and apical (Fig. 5.20); second aristomere usually expanded ventrally; scape at least twice as long as wide (except for *Brachyceraeini*) (Fig. 5.20); ocellar tubercle reduced or absent (Fig. 5.19); ocellar and postocellar bristles absent (Fig. 5.19); anterior margin of subcranial cavity projecting forward at junction with medial carina (Fig. 5.20); maxillary palpi

- reduced or absent (Fig. 5.20); basisternum broad, posterolateral extensions short and blunt (Fig. 5.20); zero or one pair of scutellar bristles (Fig. 5.19); vena spuria present (Fig. 5.20); epandrium fused beyond cerci
 Conopinae ... 18
15. Frons width less than length; ventral genital plate absent; spicules on female abdominal sternite 6 absent; female abdominal segment 7 and terminalia laterally compressed and narrowed to a sharp point; males with only setae on abdominal sternite 5, no spicules (Fig. 5.15) (NT)
 Parazodion Kröber, 1927a
- Frons square or wider than long (Figs. 5.16-5.18); female abdominal sternite 5 developed into ventral genital plate (Fig. 5.18); spicules on female abdominal sternite 6 present; female abdominal segment 7 and terminalia not modified into a sharp point (Fig. 5.18); males with spicules on abdominal sternite 5 16
16. Setae on frons in two distinct rows; black spines on femora absent; petiole of veins $CuA_2 + A_1$ more than one and one half times as long as crossvein dm-cu; cell cup narrow, vein CuA_2 meets vein A_1 at acute angle (Fig. 5.16) (AF, NA, NT, OR, PA) *Zodion* Latreille, 1797
- Setae on frons sparse, not in rows (Fig. 5.17); double row of black spines present on ventral surface of all femora; petiole of veins $CuA_2 + A_1$ less than one and one half times as long as crossvein dm-cu (Figs. 5.17, 5.18); cell cup broad, vein CuA_2 meets vein A_1 at nearly a 90° angle (Figs. 5.17, 5.18)..... 17

17. Pedicel less than three times as long as scape; vertex restricted to posterior half of frons; compound eyes not more than three fourths of head height; maxillary palpi longer than width of prementum; posterolateral extensions of basisternum with setae; metatibia narrow; petiole of veins $R_{4+5}+M$ absent or shorter than crossvein dm-cu (Fig. 5.17) (NA, NT) *Robertsonomyia* Malloch, 1919
- Pedicel more than three times longer than scape; vertex extending nearly to ptilinum; compound eyes enlarged, nearly entire height of head; maxillary palpi shorter than width of prementum; posterolateral extensions of basisternum bare; metatibia swollen; petiole of veins $R_{4+5}+M$ longer than crossvein dm-cu (Fig. 5.18) (OR) *Zodiomyia* Camras, 1957c
18. Entire body brilliant metallic blue; pronotal lobes and apex of abdomen bright orange; scutellum strongly developed, triangular, with bristles (Fig. 5.19) (AF) *Euconops* Kröber, 1915g
- Body colour variable, not metallic blue; abdomen variable, not bright orange at apex; scutellum reduced or slightly developed, with or without bristles (Figs. 5.44, 5.46) 19
19. Ocelli and ocellar tubercle absent (Figs. 5.19, 5.21, 5.22); maxillary palpi absent (Figs. 5.20, 5.21); angle between vein CuA_1 and crossvein dm-cu obtuse (Figs. 5.20-5.22) Asiconopini ... 20

- Ocelli number variable; ocellar tubercle absent or present; maxillary palpi absent or present; angle between vein CuA₁ and crossvein dm-cu acute (Figs. 5.23, 5.40, 5.48) 27
- 20. First flagellomere elongate, equal in length to scape and pedicel combined; ventral genital plate absent; female abdominal segment 7 elongate (AF)
..... *Anticonops* Kröber, 1936b
- First flagellomere not elongate, shorter than scape and pedicel combined (Figs. 5.20-5.22); ventral genital plate present (Fig. 5.21); female abdominal segment 7 normal (Fig. 5.21) 21
- 21. Very large (body >10mm), robust, dark; wing margin expanded, costa ends well before wing apex; male abdominal sternites 2-4 broad, sclerotized plates; male abdominal tergite and sternite 5 fused into a broad, ring-like structure (Fig. 5.20) (AF, OR) *Archiconops* Kröber, 1939a
- Body size variable, usually >10mm, colour variable; wing margin normal, costa ends at or near wing apex (Figs. 5.21, 5.22); sclerotized portion of male abdominal sclerites 2-4 narrow (Fig. 5.22); male abdominal tergite and sternite 5 at most partly fused (Fig. 5.22) 22
- 22. Vertex prominent with fine longitudinal grooves; posterior margin of compound eye round; height of ventral genital plate greater than height of tergite 6 (Fig. 5.21) (AF) *Smithiconops* Camras, 2000

- Vertex not distinct; posterior margin of compound eye with triangular, shiny notch; height of ventral genital plate less than height of tergite 6 (Fig. 5.22)
..... *Asiconops* (*s.l.*) ... 23
- 23. Frons smooth; male second abdominal segment distinctly narrower than first and third segments (Fig. 5.22) 24
- Frons with extensive lateral grooves; male second abdominal segment about equal in width to first and third segments 25
- 24. Second aristomere equal in width to first; frons twice as wide as long; frons without distinct spots; prementum more than twice as long as head width; male abdominal syntergosternite 7+8 produced into sharp point posteriorly (NT) *Asiconops* (*Sphenonops*) Camras, 1955b
- Second aristomere ventrally expanded; frons barely wider than long; four distinct spots on frons; prementum barely longer than head width; male abdominal syntergosternite 7+8 rounded posteriorly (Fig. 5.22) (AF)
..... *Asiconops* (*Aegloconops*) subgen. nov.
- 25. Sclerotized swellings on occiput, behind notch in compound eye (NT)
..... *Asiconops* (*Ceratoconops*) Camras, 1955b
- Occiput without swellings 26
- 26. First flagellomere less than half of the length of the scape and pedicel combined; posterolateral extensions of basisternum blunt, rounded; scutellum reduced, lacking bristles (AF, AU, NT, OR, PA)
..... *Asiconops* (*s.s.*) Chen, 1939

- First flagellomere greater than half of the length of the scape and pedicel combined; extensions of basisternum pointed; scutellum developed, with bristles (NT) *Asiconops* (*Diconops*) Camras, 1957a
- 27. Frons with extensive lateral grooves (Figs. 5.23, 5.28, 5.29); wings completely hyaline (except *Pleurocerina*) (Figs. 5.24, 5.26, 5.27, 5.29-5.31); petiole of vein CuA_2+A_1 longer or shorter than crossvein dm-cu; epandrium without posterior hump; Australasian (Figs. 5.23-5.31) *Pleurocerini* ... 28
- Frons mostly smooth, with minor rugosity (Figs. 5.33, 5.35, 5.36, 5.39, 5.42, 5.43); wings with some dark colouration (except *Microconops*) (Figs. 5.36, 5.37, 5.39-5.41, 5.48, 5.50); petiole of vein CuA_2+A_1 shorter than crossvein dm-cu (Figs. 5.35, 5.37, 5.39-5.41, 5.48, 5.50); epandrium with posterior hump where cerci attached; global 37
- 28. Wing pattern distinct, darker anterior to vein CuA_2 and hyaline posterior (Fig. 5.23) (AU) *Pleurocerina* Macquart, 1851
- Wings entirely hyaline (Figs. 5.24-5.31) 29
- 29. Maxillary palpi absent (Fig. 5.24) (AU) *Camrasiconops* Schneider, 2010
- Maxillary palpi present (Fig. 5.29) 30
- 30. Parafacial not expanded; facial ridge meets subcranial cavity at obtuse angle; petiole of vein CuA_2+A_1 shorter than crossvein dm-cu 31
- Parafacial expanded (Fig. 5.29); facial ridge meets subcranial cavity at 90° angle (Fig. 5.29); petiole of vein CuA_2+A_1 longer than crossvein dm-cu (Figs. 5.26, 5.30) 32

31. All pleural sclerites microsetose (Fig. 5.25) (AU)
 Callosiconops Kröber, 1940a
- Pleural sclerites bare or with sparse setae (AU) *Stenoconops* Kröber, 1939d
32. Arista elongate, not retracted into first flagellomere; first flagellomere
 distinctly rounded ventrally and less than twice as long as the combined
 length of the scape and pedicel (Fig. 5.26)(AU) .. *Atrichoparia* Schneider, 2010
- Arista extremely short, partially retracted into first flagellomere; first
 flagellomere not distinctly rounded, more than twice as long as the combined
 length of the scape and pedicel (Figs. 5.27, 5.29) 33
33. Three ocelli and ocellar tubercle present; clypeus broad and microsetose;
 vein M meets vein R_{4+5} at acute angle; petiole of vein $R_{4+5}+M$ shorter than
 crossvein dm-cu (Fig. 5.27) (AU) *Neoconops* Kröber, 1915g
- Number of ocelli variable; ocellar tubercle absent or present; clypeus narrow
 and bare; vein M meets vein R_{4+5} at 90° angle; petiole of vein $R_{4+5}+M$ longer
 than crossvein dm-cu (Figs. 5.29-5.31) 34
34. Three ocelli and ocellar tubercle present (Fig. 5.28) (AU)
 Smartiomyia Kröber, 1940a
- Zero or two ocelli present; ocellar tubercle absent or present 35
35. Frons with dense setae; ocelli and ocellar tubercle absent; prementum longer
 than head width (Fig. 5.29) (AU) *Setosiconops* Schneider, 2010
- Frons bare or with sparse setae; zero or two ocelli present; ocellar tubercle
 absent or present; prementum shorter than head width 36

36. Ocelli and ocellar tubercle absent; female abdominal segment 7 greatly elongate ventrally and pointed (Fig. 5.30) (AU) ... *Tanyconops* Schneider, 2010
- Zero or two ocelli present; ocellar tubercle absent or present; female abdominal segment 7 blunt, not greatly expanded ventrally (Fig. 5.31) (AU) ...
 Delkeskampomyia Kröber, 1940a OR *Heteroconops* Kröber, 1915g

Note – Members of *Heteroconops* vary in the absence and presence of ocelli and ocellar tubercles. Those with two ocelli cannot reliably be distinguished from *Delkeskampomyia*. However, only one specimen of *Delkeskampomyia* is known to exist. The present designation persists, pending revision of these two genera.

37. Frons large, square, flat; ocelli and ocellar tubercle absent; lunule not well-developed (Fig. 5.32) (NT) *Mallachoconops* Camras, 1955b
- Frons size and shape variable; ocelli number variable; ocellar tubercle absent or present; lunule well developed (Fig. 5.33) 38
38. Two ocelli and ocellar tubercle present; patch of bristles on female abdominal sternite 2 (Fig. 5.33) Siniconopini ... 39
- Number of ocelli variable; ocellar tubercle absent or present; female abdominal sternite 2 without bristles 40
39. Arista normal, distinctly narrower than first flagellomere; male abdominal syntergosternite 7+8 square at apex (Fig. 5.33) (OR, PA)
 Siniconops Chen, 1939

- Arista greatly expanded, as broad and long as first flagellomere; male abdominal syntergosternite 7+8 pointed at apex (PA) *Macroconops* Kröber, 1927a
- 40. Scutellum reduced, bristles absent; male abdomen petiolate, segment 2 elongate and distinctly narrower than all other segments (Figs. 5.36, 5.39, 5.40) 41
- Scutellum reduced or developed, bristles absent or present; male abdomen not petiolate, segment 2 equal to or only slightly longer and narrower than other segments (Figs. 5.43, 5.44, 5.46, 5.47, 5.49) 56
- 41. Scape quadrate; ocelli absent; ocellar tubercle present; posterior margin of compound eye round; wing pattern not distinct (Figs. 5.34, 5.35) *Brachyceraeini* ... 42
- Scape elongate, length greater than twice the width (Figs. 5.36-5.41); ocelli number variable; ocellar tubercle absent or present; posterior margin of compound eye with triangular, shiny notch (Figs. 5.38-5.40); wing pattern distinct, darker anterior to vein CuA₂ and hyaline posterior (Figs. 5.37-5.41) 44
- 42. Anterior margin of subcranial cavity with prominent bulb; posterolateral extensions of basisternum blunt; katepisternum with strong bristles (Fig. 5.34) (OR) *Neobrachyceraea* Szilady, 1926
- Anterior margin of subcranial cavity without bulb; posterolateral extensions of basisternum pointed; katepisternum with weak setae only (Fig. 5.35) 43

43. Large, body length >5mm (Fig. 5.35) (PA) *Brachyceraea* Röder, 1892
- Small, body length ≤5mm (OR) *Microbracerceraea* Kröber, 1940b
44. Ocelli absent; ocellar tubercle present; vertex triangular with longitudinal grooves; maxillary palpi present (Fig. 5.36) (AF)
..... *Caenoconopini* ... *Caenoconops* Kröber, 1939a
- Ocelli number variable; ocellar tubercle absent or present; vertex shape variable, but without longitudinal grooves; maxillary palpi absent (Figs. 5.37-5.40) 45
45. Ocelli and ocellar tubercle absent (Fig. 5.39); ventral half of proepisternum bare (Figs. 5.37-5.39); prominent row of setae on posterior surface of mesofemur absent *Physocephalini* ... 46
- Two or three ocelli present; ocellar tubercle present (Fig. 5.42); ventral half of proepisternum with setae and/or bristles; prominent row of setae on posterior surface of mesofemur present *Tropidomyiini* .. 48
46. Metafemur parallel-sided; females with distinct extended appendage on syntergite 8+9 (Fig. 5.37) (AF) *Dacops* Speiser, 1923
- Metafemur with distinct shape, broad basally, narrowed apically (Fig. 5.39); females without appendage on syntergite 8+9 47
47. Female abdominal segments 5 to 7 narrower than segment 4 (Fig. 5.38) (AF, OR) *Pseudophysocephala* Kröber, 1939a
- Female abdominal segments 5 to 7 approximately equal in width to segment 4 (Fig. 5.39) (AF, AU, NA, NT, OR, PA) *Physocephala* Schiner, 1861

48. Two ocelli present; global (Figs. 5.41-5.42) 49
- Three ocelli present; Neotropical (Fig. 5.40) *Physoconops (s.l.)* ... 50
49. Facial fovea reduced; medial carina strongly developed; facial ridge reduced or absent (Fig. 5.41) (AF, NT, OR, PA) *Tropidomyia* Williston, 1888
- Facial fovea large, complete from antennae to subcranial cavity; medial carina present, but not strongly developed; facial ridge strong, complete to subcranial cavity (Fig. 5.42) (AF) *Schedophysoconops* gen. nov.
50. First flagellomere elongate, greater than twice the length of the scape and pedicel combined (NT) *Physoconops (Jelte)* Stuke, 2008b
- Length of first flagellomere equal to or less than length of scape and pedicel combined 51
51. Pedicel narrow, width equal to or less than width of scape; first flagellomere nearly equal in length to scape and pedicel combined (NT)
..... *Physoconops (Aconops)* Kröber, 1919
- Pedicel broad, width greater than width of scape; first flagellomere shorter than length of scape and pedicel combined 52
52. Apex of male abdomen sharply pointed (NT)
..... *Physoconops (Shannonconops)* Camras, 1955b
- Apex of male abdomen rounded 53
53. Petiole of CuA₂+A₁ less than half of the length of crossvein dm-cu (NA, NT)
..... *Physoconops (Pachyconops)* Camras, 1955b
- Petiole of CuA₂+A₁ greater than half of the length of crossvein dm-cu 54

54. Frons twice as wide as long; vertex triangular; pedicel normal, length less than twice that of scape 55
- Frons width less than double the length; vertex round, non-distinct; pedicel elongate, at least twice as long as scape (NA, NT)
..... *Physoconops* (s.s.) Szilady, 1926
55. Vertex extends to midpoint of frons; prementum length more than twice the width of the head; bright, gold pollinosity on thorax and abdomen (NT)
..... *Physoconops* (*Aureoconops*) Camras, 2004
- Vertex restricted to posterior half of frons; prementum length less than twice the width of the head; pollinosity variable, not gold (NT)
..... *Physoconops* (*Kroeberoconops*) Camras, 1955b
56. Ocelli absent (Fig. 5.43); male abdominal segments 3 and 4 broad and parallel-sided (Fig. 5.43) Conopini ... 57
- Two or three ocelli present; male abdominal segments 3 and 4 tapered, narrower than other segments (Figs. 5.46, 5.47) 59
57. Prementum longer than head width; labella narrow, tapered; ventral genital plate elongate, tapered; male abdominal sternites 2-4 broad, sclerotized plates (Fig. 5.43) (AF, NT, OR, PA) *Conops* Linnaeus, 1758
- Prementum shorter than head width (Figs. 5.44, 5.45, 5.47, 5.49); labella broad, quadrate; ventral genital plate broad, with a medial lobe; male abdominal sternites 2-4 narrow, partly membranous 58

58. First flagellomere with dorsal ridge of black setae (Fig. 5.44) (PA)
 Abrachyglossum Kröber, 1919
- First flagellomere bare (Fig. 5.45) (PA) *Leopoldius* Rondani, 1843
59. Prementum shorter than head width (Fig. 5.47); first flagellomere elongate,
 length greater than the length of the scape and pedicel combined (Fig. 5.46);
 scutellum reduced, bristles absent *Pleurocerinellini* ... 60
- Prementum longer than head width (Figs. 5.48, 5.49); first flagellomere
 length variable (Figs. 5.48-5.50); scutellum developed, bristles present 61
60. First flagellomere more than one and one half times the length of the scape
 and pedicel together; parafacial setae non-distinct; distinct fronto-facial spot;
 one seta on proepisternum (Fig. 5.46) (AF) *Tammo* Stuke, 2008b
- First flagellomere more than one and one half times the length of the scape
 and pedicel together; parafacial with a distinct dark row of setae; fronto-
 facial spot absent; two setae on proepisternum (Fig. 5.47) (AF, OR, PA)
 Pleurocerinella Brunetti, 1923
61. Three ocelli (central ocellus sometimes weakly developed); vertex large,
 square, and setose; ocelli displaced forward to midpoint of head; medial spine
 on epandrium absent (Fig. 5.48) (NA, NT)
 Gyroconopini ... *Gyroconops* Camras, 1955b
- Two ocelli; vertex rounded, restricted to posterior quarter of frons (Fig.
 5.49); ocelli in posterior quarter of frons; medial spine on epandrium
 Microconopini ... 62

62. First flagellomere elongate, length greater than the length of the scape and pedicel combined; parafacial expanded; facial ridge meets subcranial cavity at 90° angle; wings completely hyaline; abdomen without distinct pollinose bands (Fig. 5.49) (AU) *Microconops* Kröber, 1915g
- First flagellomere short, length less than scape and pedicel combined; parafacial not expanded; facial ridge meets subcranial cavity at obtuse angle; wings with at least some dark patterning; abdominal tergite 2 with distinct pollinose band (Fig. 5.50) (AU) *Australoconops* Camras, 1961

6. General conclusion

The current state of knowledge of the evolutionary biology of Conopidae is comparable to any given family group in Diptera. The species of Conopidae have been the subject of over two hundred years of effort by skilled systematists. With 800 valid species described, the family ranks as small to medium in terms of species diversity within Diptera. Systematic work on these species has been limited to regional classifications including poorly diagnosed tribal and subfamily groups. Likewise, the life history and ecology of a select number of species of Conopidae have been the focus of concerted research. The conclusions of previous research, however, have been limited by the lack of a robust phylogenetic hypothesis.

Species of Conopidae are of interest ecologically due to a number of life history traits that they display. A review of the literature reveals that most of the general knowledge of conopid ecology is based on few observations and very few species. All species are suspected to be obligate endoparasitoids with larval and pupal life stages contained entirely within adult insect hosts. Generally, these hosts are aculeate Hymenoptera, with cricket and cockroach hosts being a notable exception in members of Stylogastrinae. While conopid-host interaction has been the subject of ecological and behavioural research, the conopid diversity represented in these studies is extremely small. Pollinating Hymenoptera are the most often recorded hosts of Conopidae. With global pollinator populations in decline, it is important to be aware of the impact of conopid species on vital

pollinating species. More knowledge of Conopidae and its interactions with its host species is necessary.

Amongst amateur and professional entomologists, species of Conopidae are known as convincing mimics of wasps and bees. There has been little previous quantitative research completed on the ecology of these mimetic complexes or the morphology of the conopid mimics. No previous studies have examined the phylogenetic patterns of mimicry within Conopidae. Chapter 5 of this thesis includes observations of phylogenetic patterns of mimicry. Mimicry of Sphecidae (Hymenoptera), in the form of a distinctly petiolate abdomen, has arisen only twice in Conopidae, once in Brachyceraeini+(Caenoconopini+(Physocephalini+Tropidomyiini)) and once in *Siniconops maculifrons*. The mimicry is heightened in Caenoconopini+(Physocephalini+Tropidomyiini) with the anterior portion of the wing darker, making it look narrower. Characteristic black and yellow abdominal patterning is common throughout Diptera as a form of hymenopteran mimicry. This pattern is present in two distantly related groups of Conopidae: Conopini and Dalmaniinae. The question remains as to whether this evolutionary pattern of mimicry is related to host preference. While the existence of species of Conopidae that are mimics of the hosts of their offspring would be fascinating from an ecological and behavioural perspective, it has not yet been demonstrated in the scientific literature.

Hilltopping mating behaviour is suspected to be an evolutionary response to sparsely distributed insect populations. As parasitoids with highly mobile hosts,

species of Conopidae are likely to benefit from a mating strategy involving geographically and temporally focused mating. Despite great amounts of unpublished knowledge of Conopidae on hilltops, only a single report of hilltopping in Conopidae is found in the scientific literature. Chapter 2 of this thesis concludes that though hilltopping is a common strategy amongst Conopidae of eastern Canada, it is not universal. Within subfamilies and genera, species are found that are obligate hilltoppers, are facultative hilltoppers, or do not utilize hilltopping at all. Whether this pattern is phylogenetic or related to host-choice is an important question for future research.

The phylogenetic placement of Conopidae within Diptera has been the source of debate over the past 150 years. Previous morphological and molecular analyses have included at most two or three species of Conopidae in larger analyses of relationships within Schizophora. Determining the closest adelphotaxon to Conopidae has never been the focus of these studies. A number of possible adelphotaxa have been proposed, including Syrphidae, the remaining Schizophora, and any one of a number of families within Diopsoidea or Tephritoidea.

DNA sequence-based phylogenetic analysis has been very informative in the past in determining phylogenetic histories. Multiple gene regions and adequate taxon sampling are necessary, however, to maximize resolution. In Chapter 3 of this thesis, sequence data from ten gene regions, all previously proposed conopid subfamilies, and seventeen other families of Diptera are analyzed. While analysis methods produce differing results, an adelphotaxon within the subfamily

Lauxaniioidea is proposed as a novel hypothesis. Also in this chapter, it is confirmed that including data from multiple gene regions from both mitochondrial and nuclear genomes is necessary to maximize phylogenetic resolution.

The conclusions of the family placement analysis lead directly to a similar molecular approach taken in Chapter 4 to investigate phylogenetic relationships within Conopidae. DNA sequence data from five gene regions and 23 different genera and subgenera of Conopidae are included in a parsimony analysis. To these data are added 113 morphological characters. A combined, total evidence analysis recovers, and separate alternate and subset analyses confirm, five monophyletic subfamilies within Conopidae. Relationships between subfamilies are also determined. The inclusion of morphological data, especially male and female genitalic characters, allows autapomorphic morphological character states to be determined for the proposed subfamilies of Conopidae. Molecular methods require carefully prepared specimens. For many taxa, molecular-grade specimens were not available for DNA amplification and sequencing. The lack of resolution within Conopinae and *Sicus* is likely due to the lack of sufficient taxon sampling.

While not suitable for DNA sequencing, representatives of more than 80 additional species, representing over 30 additional genera and subgenera are added for the analysis in Chapter 5. Using the characters defined in Chapter 4, and adding a number of new characters, a parsimony analysis is conducted. While the degree of branch support is reduced compared to previous molecular analyses, a number of monophyletic clades are recovered. This phylogenetic hypothesis is used as the

basis of a new classification of conopid genera, the first ever to include all global genera. Following an apomorphy-based, phylogenetic concept, a number of apomorphic character states are found to diagnose and describe new and revised subfamilies, tribes, genera, and subgenera. The inclusion of a key to world genera of Conopidae is the first of its kind produced for this family of flies.

The exemplar approach employed throughout this thesis, and especially in Chapter 5, facilitates unambiguous character coding but does introduce some limitations to applicability. While the new classification proposed in Chapter 5 includes a number of taxonomic changes based on the recovered cladogram, the status of unexamined species remains uncertain. Further revisionary work, particularly within Conopinae, will be necessary to determine the taxonomic status of other currently described species according to the newly proposed classification. Also, the evolution of other characters, including colour characters, awaits analysis of a larger, or more targeted, taxon set.

By employing a deductive approach and a broad range of quantitative biological techniques, I have been able to contribute to the existing knowledge of conopid evolutionary biology. Field observation, literature review, and museum specimen analysis have allowed new conclusions to be drawn about the life history of Conopidae in regards to hilltopping. The amplification and sequencing of DNA sequence data from a wide diversity of conopid and non-conopid specimens has allowed a series of large, molecular phylogenetic datasets to be created. Analysis of these molecular datasets using a variety of comparative and phylogenetic methods

has allowed conclusions to be drawn about the placement of Conopidae within Schizophora and the monophyly of subfamily clades within Conopidae. The description of morphological characters has allowed for the creation of a large character dataset. Using this dataset, I was able to produce a phylogenetic hypothesis for all described extant and fossil genera of Conopidae. By combining the molecular and morphological hypotheses with a review of the taxonomic history of Conopidae, I was able to produce a new classification for the family including apomorphic character descriptions for seven subfamilies, thirteen tribes, and a newly described genus and subgenus. Not only does this thesis increase the knowledge of the evolutionary biology of Conopidae, but it also provides a basis for future systematic, ecological, and behavioural work involving species of Conopidae.

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Tables.

Table 2.1. Specimens of Conopidae (Diptera) from the CNC collected in the Ottawa area, noting those collected on hilltops (see text for coordinates of hilltop locations). M- males; F – females. Reprinted from Mei et al. 2008 under a Creative Commons Attribution 3.0 license.

Subfamily	Species	Total # in Ottawa Area (# on Hilltop)	Hilltop Locations
Conopinae	<i>Physocephala furcillata</i>	43M, 16F (3M, 2F)	Rigaud, Masham
	<i>P. marginata</i>	27M, 1F (23M)	Rigaud, King Mtn.
	<i>P. sagittaria</i>	8M, 2F (7M)	Rigaud
	<i>P. texana</i>	6M, 3F (2M)	Rigaud
Myopinae	<i>Myopa clausa</i>	33M, 2F (33M, 2F)	Rigaud, Masham, King Mtn.
	<i>M. vicaria</i>	21M, 12F (0)	
	<i>M. vesiculosa</i>	27M, 8F (14M)	Rigaud, King Mtn.
	<i>M. virginica</i>	4M, 4F (1M)	King Mtn.
	<i>Thecophora abbreviata</i>	5M, 13F (0)	
	<i>T. longicornis</i>	7M, 5F (2F)	King Mtn.
	<i>T. occidentalis</i>	14M, 13F (4M, 1F)	Rigaud
	<i>T. nigripes</i>	9M, 1F (2M)	Rigaud
	<i>T. propinqua</i>	3M, 2F (0)	
	<i>Zodion abitus</i>	3M, 4F (0)	
	<i>Z. americanum</i>	13M, 20F (3F)	Rigaud, King Mtn.
	<i>Z. fulvifrons</i>	31M, 10F (15M)	Rigaud, King Mtn.
	<i>Z. intermedium</i>	42M, 65F (23M, 7F)	Rigaud, Masham, King Mtn.
Dalmanniinae	<i>Dalmannia nigriceps</i>	17M, 4F (11M, 1F)	Rigaud, Masham, King Mtn.
	<i>D. vitiosa</i>	4M, 1F (3M)	Rigaud, Masham, King Mtn.

Table 3.1. List of taxa included in Chapter 3 analysis with GenBank accession numbers. Superfamily classifications follow McAlpine 1989. Reprinted from Gibson et al., 2010 with permission of Elsevier.

Taxa	Species	Author	Origin	Voucher #	COI	CytB	12S	28S	AATS
Empidoidea									
Brachystomatidae	<i>Heterophlebus versabilis</i>	(Collin, 1933)	Chile	2740	HM062531	N/A	HM062581	HM062609	HM062635
Aschiza									
Platypezoidea									
Platypezidae	<i>Platypeza</i> sp		USA (NC)	2753	HM062540	HM062563	HM062590	HM062618	HM062644
Lonchopteridae	<i>Lonchoptera tristis</i>	Meigen, 1824	Denmark	2747	HM062534	HM062558	HM062584	HM062612	HM062638
Phoridae	<i>Conicera (Conicera) dauci</i>	Meigen, 1830	Canada (QC)	2748	HM062538	HM062562	HM062588	HM062616	HM062642
Syrphoidea									
Syrphidae	<i>Toxomerus marginatus</i>	(Say, 1823)	Canada (ON)	2752	HM062546	HM062568	HM062596	HM062624	HM062649
Pipunculidae	<i>Pipunculus</i> sp		USA (NM)	2744	HM062539	N/A	HM062589	HM062617	HM062643
Schizophora									
Acalypttratae									
Conopoidea									
Conopidae									
Conopinae	<i>Physocephala marginata</i>	Say, 1823	Canada (QC)	1680	N/A	N/A	HM062570	HM062599	HM062626
	<i>Leopoldius coronatus</i>	(Rondani, 1857)	Germany	2481	HM062522	HM062548	HM062571	HM062598	HM062627
Dalmaninae	<i>Dalmanina nigriceps</i>	Loew, 1866	Canada (ON)	2259	HM062526	HM062551	HM062576	HM062604	HM062630
	<i>Dalmanina vitiosa</i>	Coquillett, 1892	Canada (QC)	2469	HM062527	HM062552	HM062577	HM062605	HM062631
Myopinae	<i>Myopa vesiculosa</i>	Say, 1823	Canada (QC)	2460	HM062523	HM062549	HM062572	HM062600	N/A
	<i>Thecophora occidentalis</i>	(Walker, 1849)	Canada (ON)	2731	HM062524	HM062550	HM062573	HM062601	HM062628
Stylogastrinae	<i>Stylogaster neglecta</i>	Williston, 1883	USA (NM)	2202	HM062528	HM062553	HM062578	HM062606	HM062632
	<i>Stylogaster stylata</i>	Fabricius, 1805	French Guiana	2606	HM062529	HM062554	HM062579	HM062607	HM062633
Zodioninae	<i>Zodion fulvifrons</i>	Say, 1823	Canada (QC)	2457	N/A	N/A	HM062574	HM062603	N/A
	<i>Zodion cinereum</i>	(Fabricius, 1794)	Italy	2492	HM062525	N/A	HM062575	HM062602	HM062629
Nerioidea									
Micropezidae	<i>Taeniaptera trivittata</i>	Macquart, 1835	USA (SC)	2758	HM062535	HM062559	HM062585	HM062613	HM062639
Diopsoidea									
Psilidae	<i>Chyliza scrobiculata</i>	Melander, 1920	Canada (BC)	2719	HM062542	N/A	HM062592	HM062620	HM062646
Strongylophthalmyidae	<i>Strongylophthalmyia angustipennis</i>	Melander, 1920	Canada (ON)	2741	HM062545	HM062567	HM062595	HM062623	HM062648
Tephritoidea									
Platystomatidae	<i>Lamprogaster nigripes</i>	Macquart, 1851	Australia (QD)	2743	HM062541	HM062564	HM062591	HM062619	HM062645
Tephritidae	<i>Campiglossa pygmaea</i>	(Novak, 1974)	USA (OR)	2745	HM062547	HM062569	HM062597	HM062625	HM062650
Pyrgotidae	<i>Pyrgota undata</i>	Wiedemann, 1830	Canada (ON)	1527	HM062543	HM062565	HM062593	HM062621	N/A
Pallopidae	<i>Toxoneura superba</i>	(Loew, 1861)	Canada (ON)	2751	HM062537	HM062561	HM062587	HM062615	HM062641
Lauxanoidea									
Lauxaniidae	<i>Minettia lupulina</i>	(Fabricius, 1787)	USA (OR)	2746	HM062532	HM062556	HM062582	HM062610	HM062636
Lauxaniidae	<i>Melanina</i> sp		Australia (QD)	495	HM062533	HM062557	HM062583	HM062611	HM062637
Sphaeroceroidae									
Sphaeroceridae	<i>Rachispoda</i> sp		Canada (ON)	2750	HM062544	HM062566	HM062594	HM062622	HM062647
Ephydroidea									
Drosophilidae	<i>Drosophila</i> sp		Chile	2742	HM062530	HM062555	HM062580	HM062608	HM062634
Calypttratae									
Muscoidea									
Muscidae	<i>Spilogona</i> sp		USA (OR)	2756	HM062536	HM062560	HM062586	HM062614	HM062640

Table 3.1. Continued.

Taxa	Species	Author	Origin	Voucher #	CAD	EF1a	PGD	TPI	white
Empidoidea									
Brachystomatidae	<i>Heterophlebus versabilis</i>	(Collin, 1933)	Chile	2740	HM062728	HM062658	HM062752	HM062682	HM062718
Aschiza									
Platypezoidea									
Platypezidae	<i>Platypeza</i> sp		USA (NC)	2753	HM062736	HM062666	HM062759	HM062691	N/A
Lonchopteridae	<i>Lonchoptera tristis</i>	Meigen, 1824	Denmark	2747	HM062731	HM062661	HM062754	HM062687	HM062704
Phonidae	<i>Conicera (Conicera) dauci</i>	Meigen, 1830	Canada (QC)	2748	HM062735	HM062664	HM062757	HM062688	N/A
Syrphoidea									
Syrphidae	<i>Toxomerus marginatus</i>	(Say, 1823)	Canada (ON)	2752	HM062742	HM062672	HM062762	HM062690	HM062701
Pipunculidae	<i>Pipunculus</i> sp		USA (NM)	2744	N/A	HM062665	HM062758	HM062686	HM062699
Schizophora									
Acalyptratae									
Conopoidea									
Conopidae									
Conopinae	<i>Physocephala marginata</i>	Say, 1823	Canada (QC)	1680	HM062719	HM062651	HM062744	HM062674	HM062716
	<i>Leopoldius coronatus</i>	(Rondani, 1857)	Germany	2481	HM062720	N/A	HM062745	HM062679	HM062707
Dalmaniinae	<i>Dalmanina nigriceps</i>	Loew, 1866	Canada (ON)	2259	HM062725	HM062656	N/A	HM062676	HM062702
	<i>Dalmanina vitiosa</i>	Coquillett, 1892	Canada (QC)	2469	HM062726	N/A	N/A	HM062678	HM062697
Myopinae	<i>Myopa vesiculosa</i>	Say, 1823	Canada (QC)	2460	HM062721	HM062652	HM062746	HM062677	HM062714
	<i>Thecophora occidentalis</i>	(Walker, 1849)	Canada (ON)	2731	HM062722	HM062653	HM062747	N/A	N/A
Stylogastriinae	<i>Stylogaster neglecta</i>	Williston, 1883	USA (NM)	2202	N/A	N/A	HM062749	HM062675	HM062713
	<i>Stylogaster stylata</i>	Fabricius, 1805	French Guiana	2606	N/A	N/A	HM062750	HM062681	HM062705
Zodioninae	<i>Zodion fulvifrons</i>	Say, 1823	Canada (QC)	2457	HM062723	HM062654	N/A	N/A	HM062710
	<i>Zodion cinereum</i>	(Fabricius, 1794)	Italy	2492	HM062724	HM062655	HM062748	HM062680	HM062703
Nerioidea									
Micropezidae	<i>Taeniaptera trivittata</i>	Macquart, 1835	USA (SC)	2758	HM062732	HM062662	HM062755	HM062693	HM062709
Diopsoidea									
Psilidae	<i>Chyliza scrobiculata</i>	Melander, 1920	Canada (BC)	2719	HM062738	HM062668	N/A	N/A	HM062711
Strongylophthalmyiidae	<i>Strongylophthalmyia angustipennis</i>	Melander, 1920	Canada (ON)	2741	HM062741	HM062671	N/A	HM062683	HM062698
Tephritoidea									
Platystomatidae	<i>Lamprogaster nigripes</i>	Macquart, 1851	Australia (QD)	2743	HM062737	HM062667	HM062760	HM062685	HM062715
Tephritidae	<i>Campiglossa pygmaea</i>	(Novak, 1974)	USA (OR)	2745	HM062743	HM062673	HM062763	N/A	N/A
Pyrgotidae	<i>Pyrgota undata</i>	Wiedemann, 1830	Canada (ON)	1527	HM062739	HM062669	HM062761	N/A	HM062696
Pallopidae	<i>Toxoneura superba</i>	(Loew, 1861)	Canada (ON)	2751	HM062734	HM062663	HM062756	N/A	HM062712
Lauxanioidae									
Lauxaniidae	<i>Minettia lupulina</i>	(Fabricius, 1787)	USA (OR)	2746	HM062729	HM062659	HM062753	N/A	HM062706
Lauxaniidae	<i>Melanina</i> sp		Australia (QD)	495	HM062730	HM062660	N/A	HM062694	HM062708
Sphaeroceroidae									
Sphaeroceridae	<i>Rachispoda</i> sp		Canada (ON)	2750	HM062740	HM062670	N/A	HM062689	HM062695
Ephydroidea									
Drosophilidae	<i>Drosophila</i> sp		Chile	2742	HM062727	HM062657	HM062751	HM062684	HM062700
Calypttratae									
Muscoidea									
Muscidae	<i>Spilogona</i> sp		USA (OR)	2756	HM062733	N/A	N/A	HM062692	HM062717

N/A – gene region not successfully sequenced.

Table 3.2. Primer oligonucleotides used for PCR amplification of selected gene segments in Chapter 3, including original reference for primers and type of polymerase used. Reprinted from Gibson et al., 2010 with permission of Elsevier.

Gene Locus	Primer	Sequence	Reference	Polymerase
12S	12Sai	AAACTAGGATTAGATACCTATTAT	Simon et al 1994	Taq
	12Sbi	AAGAGCGACGGCGATGTGT	Simon et al 1994	Taq
COI	Pat	TCCAATGCACTAATCTGCCATATTA	Simon et al 1994	Taq
	Jerry	CAACATTTATTTTGATTTTTTGG	Simon et al 1994	Taq
	hebF (LCO1490)	GGTCAACAAATCATAAAGATATTGG	Folmer et al 1994	Taq
	hebR (HCO2198)	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al 1994	Taq
	MLepF	GCTTTCCACGAATAAATAATA	Hajibabaei et al 2006	Taq
	MLepR	CCTGTCCAGCTCCATTTTC	Hajibabaei et al 2006	Taq
CytB	10933F	TATGTTTTACCTTGAGGACAAATATC	Simon et al 1994	ExTaq
	11683R	AAATTCTATCTTATGTTTTCAAAC	Simon et al 1994	ExTaq
AATS	A1x40F	GNATGAAYCARTTYAARCCNAT	Feng-Yi Su et al 2008	ExTaq
	rA1x244	CATNCCRCARTCNATRTGYTT	Feng-Yi Su et al 2008	ExTaq
EF-1a	M44-1	GCTGAGCGYGARCGTGGTATCAC	Cho et al 1995	ExTaq
	rcM4	ACAGCVACKGYTGYCTCATRTC	Cho et al 1995	ExTaq
	2477-2495 (S)	CTTGCTTTTCACTTGGGGTG	Baker et al 2001	ExTaq
	2934-2954 (A)	CTTCGTGATGCATTTCACCGG	Baker et al 2001	ExTaq
white	11404-11426 (S)	TGYGCNTATGTNCAACARGAYGA	Baker et al 2001	ExTaq
	11975-11997 (A)	ACYTGNACRTAAAARTCNCGNGG	Baker et al 2001	ExTaq
wingless	LepWG1F	GARTGYAARTGYCAYGGYATGTCTGG	Brower & DeSalle 1998	ExTaq
	PompWG2R	ACTGCGCAGCACCAGTGGAATGTGCA	Pilgrm et al 2008	ExTaq
TPI	tpi111FBb	GGNAAYTGGAATGAAAYGG	Bertone et al 2008	ExTaq
	tpi275R	GCCCANACNGGYTCRTANGC	Bertone et al 2008	ExTaq
PGD	pgd2F	GATATHGARTAYGGNGAYATG	Bertone et al 2008	ExTaq
	pgd3R	GTRTNGCNCRCRAARTARTC	Bertone et al 2008	ExTaq
	pgd4R	CCNGTCCARTTNGTRTG	Bertone et al 2008	ExTaq
28S	rc28AB	ACTACCCCTGAATTTAAGCA	Bertone et al 2008	Taq
	28C	GCTATCCTGAGGGAACTTCGG	Bertone et al 2008	Taq
	rc28B	CCCGTCTTGAAACACGGACC	Bertone et al 2008	Taq
	28E	CCTTATCCCGAAGTTACG	Wiegmann et al 2000	Taq
	rc28D	CCGCAGCTGGTCTCCAAG	Wiegmann et al 2000	Taq
	28I	GGGTCTTCTTTCCCGCT	Lonsdale et al , 2010	Taq
	rc28F	GTGATTTCTGCCAGTGCTCTG	Lonsdale et al 2010	Taq
	28Q	AACTCCCTACCTGGCAAT	Collins & Wiegmann 2002a	Taq
	28K	GAAGAGCCGACATCGAAG	Wiegmann et al 2000	Taq
	rc28Q	GGACATTGCCAGGTAGGGAGTT	Wiegmann et al 2000	Taq
	28ZC	TGGATCGCAGTATGCGAGCT	Bertone et al 2008	Taq
CAD	54F	GTNGTNTTYCARACNGGNATGGT	Moulton & Wiegmann 2004	ExTaq
	364R	TCNCANGCRAANCCRTGRTTYTG	Moulton & Wiegmann 2004	ExTaq
	405R	GCNGTRTGYTCNNGRTGRAAYTG	Moulton & Wiegmann 2004	ExTaq
	338F	ATGAARTAYGGYAATCGTGGHCAYAA	Moulton & Wiegmann 2004	ExTaq
	680R	AANGCRTNCGNACMACYTCTAYTC	Moulton & Wiegmann 2004	ExTaq
	581F2	GGWGGWCAACWGCWYTMAYTYGG	Moulton & Wiegmann 2004	ExTaq
	843R	GCYTTYTGRAANGCYTCYTCRAA	Moulton & Wiegmann 2004	ExTaq
	787F	GGDGTNACNACNGCNTGYTTYGARCC	Moulton & Wiegmann 2004	ExTaq
	1098R	TTNNGGNAGYTGNCNCCCAT	Moulton & Wiegmann 2004	ExTaq
	1057F	GTNTCNACNGAYTAYGAYATGTG	Moulton & Wiegmann 2004	ExTaq
	1278R	TCRTTNTTYTTWGCRATYAAATGCAT	Moulton & Wiegmann 2004	ExTaq
	1436R	CCRTGYTCNGCRTARAARTC	Moulton & Wiegmann 2004	ExTaq

Table 3.3. Summary of results of Chapter 3 analysis for individual and concatenated gene partitions. Reprinted from Gibson et al., 2010 with permission of Elsevier.

	Individual Gene Regions									
	COI	cytB	12S	28S	AATS	CAD	EF1a	PGD	TPI	white
# taxa included	26	22	28	28	25	25	23	20	21	24
# characters analyzed	1495	718	374	3361	553	3824	827	731	453	462
% characters constant	50.9	44.2	39.5	69.9	46.1	48.0	58.6	30.4	33.8	49.1
% characters informative	40.7	46.8	42.7	17.4	47.7	44.6	33.4	62.9	57.6	44.9
Average nucleotide frequencies										
A	29.5	32.0	37.4	30.8	28.3	29.6	29.4	28.0	29.4	24.8
C	16.6	16.4	8.0	17.5	16.1	20.2	21.3	21.1	18.7	24.7
G	15.3	11.6	15.1	23.6	25.7	25.6	27.0	25.1	29.2	23.3
T	38.5	40.0	39.5	28.1	29.9	24.6	22.2	25.8	22.7	27.2
alpha	0.233	0.839	0.601	0.447	0.253	0.858	0.443	0.436	0.579	0.750
# most parsimonious trees	18	16	10	2	1	1	56	7	4	1
length of shortest tree(s)	908	637	797	3158	382	2170	213	784	549	238
Consistency Index (CI)	0.414	0.440	0.425	0.493	0.487	0.504	0.563	0.533	0.463	0.475
Retention Index (RI)	0.369	0.380	0.384	0.385	0.556	0.430	0.581	0.468	0.419	0.481
Support for nodes (PBS/JKS)										
1	-3/-	3/-	8/100	25/100	5/84	0/68	0/-	8/100	11/100	1/68
2	16/100	14/100	9/97	66/100	18/100	0/<50	0/-	-1/-	12/100	9/97
3	4/<50	3/-	0/-	-3/-	-1/-	2/<50	-1/-	0/-	2/-	1/-
4	0/-	0/-	7/89	13/87	0/-	6/77	2/-	3/89	0/-	0/-
5	0/-	-5/-	0/74	51/100	0/-	0/100	0/93	4/-	-6/-	4/-
6	-2/61 *	1/-	1/-	12/-	0/-	-2/63	4/-	3/66 *	-8/-	0/-
7	0/<50	-2/-	0/-	8/67	1/67 *	0/56	0/52 *	0/-	1/-	1/-
8	6/100	0/-	21/98	23/100	17/98	0/-	3/-	10/98	15/99	1/99
9	-5/-	12/59 *	2/<50	5/<50	8/-	0/56 *	0/52 *	-2/-	-5/-	4/-
10	11/-	2/-	2/-	2/-	0/-	1/-	2/-	-2/-	-8/-	0/-
11	-4/-	2/-	-1/-	19/-	-7/-	2/-	-3/-	0/-	3/-	-4/-
12	6/78	4/53	6/<50	25/100	-5/-	11/100	-1/76	4/-	0/-	10/81
13	-4/-	2/-	-1/-	19/<50	-7/-	2/<50	-3/-	0/-	3/-	-4/-
14	1/-	1/-	1/-	2/-	-2/-	-3/-	2/-	2/-	-2/-	0/-
15	2/-	-3/-	-5/-	19/71	-6/-	6/<50	0/-	-2/-	0/-	1/-
16	-4/-	2/-	-1/-	19/-	-7/-	2/<50	-3/-	0/-	3/-	-4/-
17	5/-	8/79	3/-	11/-	-5/-	13/58	1/-	0/100	-5/-	1/-
18	4/-	-3/-	0/-	5/93	-2/-	7/<50	1/-	-2/-	0/-	-1/-
19	-4/-	2/-	-1/-	19/-	-7/-	2/<50	-3/-	0/-	3/-	-4/-
20	1/-	5/-	3/-	5/<50	0/-	-6/-	-2/<50	5/-	0/-	-2/-
21	-3/-	0/-	6/-	6/<50	6/-	0/-	3/<50	0/<50	6/77 *	-4/-
22	0/-	0/-	2/-	10/62	0/-	0/-	1/-	-1/-	1/-	-3/-
23	2/-	0/<50 *	4/-	10/80	0/-	0/-	-1/-	-2/-	-3/-	1/-
24	2/-	2/-	-7/-	29/94	2/-	1/91	2/<50	-9/-	-2/-	0/-
25	-2/-	0/-	0/-	17/81	4/-	-7/-	-1/-	-4/-	6/<50	3/-
TBS (overall/within Conopidae)	29/16	50/26	59/48	417/200	12/48	37/6	3/8	14/25	27/22	11/21

Table 3.3. Continued.

	Subsets				Total Evidence			
	mtDNA	nrDNA	rDNA	PCG	Equal/5th	Equal/missing	nt3=0/missing	nt3=0/5th
# taxa included	28	28	28	28	28	28	28	28
# characters analyzed	2587	10211	3735	9063	12798	12798	12798	12798
% characters constant	47.4	54.1	66.8	47.0	52.8	54.5	54.5	52.8
% characters informative	42.7	36.8	20.0	45.4	38.0	37.1	37.1	38.0
Average nucleotide frequencies								
A	27.1	30.0	31.6	28.1	29.4	29.4	29.4	29.4
C	17.3	18.8	16.4	19.8	18.5	18.5	18.5	18.5
G	18.5	24.8	22.6	22.0	23.5	23.5	23.5	23.5
T	37.1	26.3	29.4	30.1	28.6	28.6	28.6	28.6
alpha	0.557	0.538	0.524	0.549				
# most parsimonious trees	1	3	1	1	1	1	2	1
length of shortest tree(s)	2436	7713	4009	6136	27194	26213	9262	10204
Consistency Index (CI)	0.408	0.485	0.473	0.463	0.388	0.385	0.460	0.464
Retention Index (RI)	0.334	0.394	0.369	0.386	0.317	0.316	0.372	0.373
Support for nodes (PBS/JKS)								
1	8/100	50/100	33/100	25/100	100	100	100	58/100
2	39/99	84/100	75/100	68/100	100	100	100	143/100
3	7/<50	0/-	-3/-	10/89	100	99	61	7/57
4	7/88	24/100	20/100	11/95	100	100	100	31/100
5	-5/64	53/100	51/100	-3/98	100	100	100	48/100
6	0/-	9/74	13/-	-4/-	68	-	73	9/82
7	-2/-	11/93	8/57	1/-	100	94	63	9/68
8	27/100	69/100	44/100	52/100	100	100	100	96/100
9	9/73	10/56	7/67	12/100	65	53	94	19/95
10	15/-	-5/-	4/-	6/<50	-	-	73	10/74
11	-3/-	10/-	18/-	-11/-	-	-	-	7/<50
12	16/87	44/100	31/100	29/100	100	100	100	60/100
13	-3/-	10/<50	18/55	-11/-	63	-	-	7/<50
14	3/-	-1/-	3/-	-1/-	-	-	-	2/<50
15	-6/-	18/88	14/85	-2/-	-	-	<50	12/87
16	-3/-	10/-	18/-	-11/-	<50	-	-	7/<50
17	16/-	16/100	14/-	18/99	100	99	99	32/100
18	1/-	8/80	5/89	4/-	58	<50	57	9/72
19	-3/-	10/-	18/-	-11/-	<50	-	-	7/54
20	9/-	0/<50	8/<50	1/55	-	-	<50	9/65
21	3/-	17/98	12/75	8/81	65	<50	73	20/99
22	2/-	8/70	12/80	-2/-	<50	-	-	10/83
23	6/-	5/83	14/79	-3/-	-	-	-	11/85
24	-3/-	23/98	22/99	-2/54	<50	-	73	20/93
25	-2/-	18/91	17/79	-1/-	54	-	-	16/79
TBS (overall/within Conopidae)	138/90	501/310	476/248	183/172				

Equal - equal weighting; nt3=0 - nt3 weighted to 0; missing - gaps treated as missing; 5th - gaps treated as a fifth state; alpha - Shape parameter of the gamma distribution (as calculated by ModelTest3.7); PBS - Partitioned Bremer support; TBS - total Bremer support; JKS - jackknife support values (36% exclusion); nodes not recovered indicated as -; nodes depicting relationships within Conopidae are in bold. * denotes nodes for which JKS are above 50%, but for which all taxa included in that node for the full dataset are not available for that gene

Table 4.1. List of taxa included in Chapter 4 analysis with GenBank Accession numbers. Previously proposed tribal classification not included. Genus, subgenus, and subfamily classifications listed according to valid status and current catalogues prior to this analysis.

Taxa	Species	Author	Geographic origin	Vouch. #	COI	CytB	12S	28S	AATS
Conopidae	<i>Atrichopara</i> sp. A		Australia (QLD)	2230	JN664799	JN664849	JN664598	JN664667	JN664738
Conopinae	<i>Atrichopara</i> sp. B		Australia (NSW)	2320	JN664803	JN664853	JN664602	JN664671	JN664742
	<i>Atrichopara</i> sp. B		Australia (NSW)	2326	JN664806	JN664856	JN664604	JN664674	JN664744
	<i>Australoconops phaeomeros</i>	Schneider, 2010	Australia (QLD)	3097	HM398240	JN664881	JN664631	JN664702	JN664770
	<i>Camrasiconops ater</i>	Camras, 1961	Australia (QLD)	2217	JN664797	JN664847	JN664596	JN664665	JN664736
	<i>Conops (Asiconops) australianus</i>	Camras, 1961	Australia (QLD)	502	JN664790	JN664838	JN664585	JN664654	JN664725
	<i>Conops (Asiconops) chinensis</i>	Camras, 1960	Japan	1768	JN664793	N/A	JN664591	JN664660	JN664731
	<i>Conops (Conops) flavipes</i>	Linnaeus, 1758	Germany, Italy	2477	JN664810	JN664863	JN664613	JN664682	JN664751
	<i>Conops (Conops) vesiculans</i>	Linnaeus, 1761	Germany, Italy, South Korea	2479	JN664811	JN664864	JN664614	JN664683	JN664752
	<i>Conops (Smithiconops) rondanii</i>	Bezzi, 1901	South Africa, Tanzania	4149	JN664828	JN664890	JN664642	JN664713	JN664780
	<i>Euconops bellus</i>	Krober, 1915g	South Africa	3113	HM398242	JN664885	JN664635	JN664706	JN664774
	<i>Heteroconops sp</i>		Australia (QLD)	2233	JN664800	JN664850	JN664599	JN664668	JN664739
	<i>Leopoldius coronatus</i>	(Rondani, 1857)	Germany, Italy	2481	JN664812	JN664865	JN664615	JN664684	JN664753
	<i>Microconops ornatus</i>	Krober, 1915g	Australia (QLD)	2227	JN664798	JN664848	JN664597	JN664666	JN664737
	<i>Microconops ornatus</i>	Krober, 1915g	Australia (ACT)	162	JN664788	JN664834	JN664581	JN664650	JN664721
	<i>Microconops tasmaniensis</i>	Krober, 1940a	Australia (VIC)	2329	JN664807	JN664857	JN664605	JN664675	***
	<i>Physocephala maculipes</i>	(Bigot, 1887)	Tanzania, Tunisia, Uganda	3110	HQ559806	JN664884	JN664634	JN664705	JN664773
	<i>Physocephala madagascariensis</i>	Krober, 1915d	Madagascar	3119	HQ559799	JN664886	JN664636	JN664707	JN664775
	<i>Physocephala marginata</i>	Say, 1823	Canada (ON, QC)	1680	HM398216	N/A	JN664590	JN664659	JN664730
	<i>Physocephala rufipes</i>	(Fabricius, 1782)	Germany, Italy, Serbia	3905	HM398245	JN664889	JN664641	JN664712	N/A
	<i>Physocephala tibialis</i>	(Say, 1829)	Canada (ON), USA (VA)	2723	JN664820	JN664876	JN664625	JN664696	JN664765
	<i>Physoconops (Pachyconops) brachyrhynchus</i>	(Macquart, 1843)	Canada (ON), USA (MD, MI)	2729	JN664821	JN664877	JN664626	JN664697	N/A
	<i>Physoconops (Pachyconops) guranicus</i>	(Curran, 1934)	Costa Rica, Venezuela	2840	HM398248	JN664879	JN664628	JN664699	JN664767
	<i>Physoconops (Physoconops) discalis</i>	(Williston, 1892)	Brazil, Mexico, Venezuela, USA (AZ)	3095	JN664824	JN664880	JN664630	JN664701	JN664769
	<i>Pleurocerina brevis</i>	Schneider, 2010	Australia (QLD)	457	JN664789	JN664837	JN664584	JN664653	JN664724
	<i>Pleurocerina longicornis</i>	(Krober, 1915g)	Australia (NT)	2324	JN664804	JN664854	***	JN664672	JN664743
	<i>Pleurocerina vespiformis</i>	Schneider, 2010	Australia (QLD)	456	HM398246	JN664836	JN664583	JN664652	JN664723
	<i>Smartiomyia arena</i>	Schneider, 2010	Australia (QLD)	533	JN664791	JN664839	JN664586	JN664655	JN664726
	<i>Smartiomyia arena</i>	Schneider, 2010	Australia (QLD)	3102	HM398249	JN664882	JN664632	JN664703	JN664771

Table 4.1. Continued.

Taxa	Species	Author	Geographic origin	Vouch. #	COI	CytB	12S	28S	AATS
Dalmanniinae	<i>Dalmannia aculeata</i>	(Linnaeus, 1761)	Italy, Spain	2524	HM398251	JN664870	JN664609	JN664689	JN664758
	<i>Dalmannia nigriceps</i>	Loew, 1866	Canada (BC, ON, QC)	2259	JN664802	JN664852	JN664601	JN664670	JN664741
	<i>Dalmannia vitiosa</i>	Coquiliet, 1892	Canada (AB, ON, QC)	2469	JN664809	JN664862	JN664612	JN664681	JN664750
	<i>Parazodion schmidt</i>	Krober, 1927a	Brazil, Guyana, Fr Guiana	2642	JN664819	JN664874	JN664624	JN664694	JN664763
	<i>Parazodion schmidt</i>	Krober, 1927a	Brazil, Guyana, Fr Guiana	2644	HM398262	JN664875	N/A	JN664695	JN664764
	<i>Myopinae</i>								
Myopinae	<i>Myopa buccata</i>	(Linnaeus, 1758)	England, Israel, Germany	2482	JN664813	JN664866	JN664616	JN664685	JN664754
	<i>Myopa clausa</i>	Loew, 1866	Canada (BC, QC, NS, SK)	2196	JN664795	JN664845	JN664594	JN664663	JN664734
	<i>Myopa occulta</i>	Wiedemann, 1824	Czech Rep, Germany, Italy, Spain	2567	HM398252	JN664871	JN664620	JN664690	JN664759
	<i>Myopa vesiculosa</i>	Say, 1823	Canada (BC, ON, QC)	2460	HM398217	JN664861	JN664611	JN664680	JN664749
	<i>Myopa</i> sp		Australia (NSW)	2325	JN664805	JN664855	JN664603	JN664673	N/A
	<i>Pseudoconops antennatus</i>	Camras, 1962a	Madagascar	3508	JN664825	JN664887	JN664637	JN664708	JN664776
	<i>Sicus ferrugineus</i>	(Linnaeus, 1761)	France, Sweden	2252	JN664801	JN664851	JN664600	JN664669	JN664740
	<i>Thecophora africana</i>	(Brunetti, 1925b)	Madagascar	1816	JN664794	JN664844	JN664593	JN664662	JN664733
	<i>Thecophora atra</i>	(Fabricius, 1775)	England, Czech Rep, Germany, Spain	2516	JN664816	JN664869	JN664619	JN664688	JN664757
	<i>Thecophora australiana</i>	(Camras, 1955a)	Australia (NSW, QLD)	395	HM398253	JN664835	JN664582	JN664651	JN664722
	<i>Thecophora metallica</i>	Camras, 1962a	Madagascar	3520	JN664826	JN664888	JN664638	JN664709	JN664777
	<i>Thecophora modesta</i>	(Williston, 1883)	Canada (AB, BC, YT), USA (OR)	1059	HM398291	JN664841	JN664588	JN664657	JN664728
	<i>Thecophora occidentalis</i>	(Walker, 1849)	Canada (ON, QC, SK)	2731	JN664822	JN664878	JN664627	JN664698	JN664766
	<i>Zodion cinereum</i>	(Fabricius, 1794)	Italy, Turkey	2492	JN664814	JN664867	JN664617	JN664686	JN664755
	<i>Zodion erythrum</i>	Rondani, 1865	Israel, Italy	2493	HQ559803	JN664868	JN664618	JN664687	JN664756
	<i>Zodion fulvifrons</i>	Say, 1823	Canada (ON, QC), USA (TX)	2457	JN664808	JN664860	JN664610	JN664679	JN664748
	<i>Zodion intermedium</i>	Banks, 1916	Canada (ON, QC), USA (MS)	1503	JN664792	JN664842	JN664589	JN664658	JN664729
	<i>Zodion pictum</i>	Schiner, 1868	Argentina, Ecuador, Mexico	3069	JN664823	N/A	JN664629	JN664700	JN664768
Stylogastrinae	<i>Stylogaster biannulata</i>	(Say, 1823)	Canada (ON), USA (MS, TX)	3572	HM398255	N/A	JN664639	JN664710	JN664778
	<i>Stylogaster breviventris</i>	Aldrich, 1930	Ecuador, Guyana, Peru	2445	HM398256	N/A	JN664606	JN664676	JN664745
	<i>Stylogaster decorata</i>	Aldrich, 1930	Ecuador, Guyana, Peru	2448	HM398257	JN664858	JN664607	JN664677	JN664746
	<i>Stylogaster frauci</i>	Smith, 1979	Australia (QLD)	551	HM398258	JN664840	JN664587	JN664656	JN664727
	<i>Stylogaster frauci</i>	Smith, 1979	Australia (QLD)	3109	HM398259	JN664883	JN664633	JN664704	JN664772
	<i>Stylogaster inca</i>	Camras and Parillo, 1985	French Guiana	2621	JN664818	JN664873	JN664623	JN664693	JN664762
	<i>Stylogaster neglecta</i>	Williston, 1883	Canada (ON), USA (MD, NM)	2202	JN664796	JN664846	JN664595	JN664664	JN664735

Table 4.1. Continued.

Taxa	Species	Author	Geographic origin	Vouch. #	COI	CytB	12S	28S	AATS
Stylogastrinae	<i>Stylogaster pauliani</i>	Camras, 1962a	Madagascar	1814	HM398260	JN664843	JN664592	JN664661	JN664732
	<i>Stylogaster rectinervis</i>	Aldrich, 1930	Brazil, Ecuador, French Guiana	2618	JN664817	JN664872	JN664622	JN664692	JN664761
	<i>Stylogaster stylata</i>	Fabricius, 1805	Brazil, Ecuador, French Guiana	2606	JN664815	N/A	JN664621	JN664691	JN664760
	<i>Stylogaster westwoodi</i>	Smith, 1967	Congo, Kenya, Nigeria, Tanzania, Zambia	3575	JN664827	N/A	JN664640	JN664711	JN664779
	<i>Stylogaster</i> sp		Madagascar	2450	HM398261	JN664859	JN664608	JN664678	JN664747
Outgroups									
Lonchopteridae	<i>Lonchoptera tristis</i>	Meigen, 1824	Czech Rep., Denmark, England	2747	JN664832	JN664895	JN664647	JN664718	JN664785
Phoridae	<i>Conicera (Conicera) dauci</i>	Meigen, 1830	Canada (QC), USA (AZ)	2748	HM398219	JN664896	JN664648	JN664719	JN664786
Syrphidae	<i>Toxomerus marginatus</i>	(Say, 1823)	Canada (ON, QC)	2752	JN664833	JN664897	JN664649	JN664720	JN664787
Lauxaniidae	<i>Minettia lupulina</i>	(Fabricius, 1787)	Canada (QC), USA (OR)	2746	JN664831	JN664894	JN664646	JN664717	JN664784
Psilidae	<i>Chyliza scrobiculata</i>	Melander, 1920	Canada (BC)	2719	JN664830	JN664892	JN664644	JN664715	JN664782
Pyrgotidae	<i>Pyrgota undata</i>	Wiedemann, 1830	Canada (ON, QC)	1527	JN664829	JN664891	JN664643	JN664714	JN664781
Strongylophthalmyidae	<i>Strongylophthalmyia angustipennis</i>	Melander, 1920	Canada (BC, ON, QC)	2741	HM398221	JN664893	JN664645	JN664716	JN664783

N/A – gene region not successfully sequenced.

*** - sequence length is less than 200bp and could not be submitted to GenBank.

Accession numbers beginning with HM or HQ were generated from BOLD sequences.

Table 4.2. Primer oligonucleotides used for PCR amplification of selected gene segments in Chapter 4, including original reference for primers and type of polymerase used.

Gene Locus	Primer	Sequence	Reference	Polymerase
12S	12Sai	AACTAGGATTAGATACCCTATTAT	Simon et al 1994	Taq
	12Sbi	AAGAGCGACGGGCGATGTGT	Simon et al 1994	Taq
	12Sh	GACCAAATTGGTGCCAGCAGT	Simon et al 1994	Taq
COI	12S-Dipt-14525F	CGGTATTTTAKTCTDTYCAGAGG	Gibson et al 2011	Taq
	hebF (LCO1490)	GGTCAACAAATCATAAAGATATTGG	Folmer et al 1994	Taq
	hebR (HCO2198)	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al 1994	Taq
	MLepF	GCTTTCCACGAATAAATAATA	Hajibabaei et al 2006	Taq
	MLepR	CCTGTTCCAGCTCCATTTTC	Hajibabaei et al 2006	Taq
	Uni Minibar F	TCCACTAATCACAARGATATTGGTAC	Meusnier et al 2008	Taq
	COI-Dipt-1703F	CCHRTHATRATYGGWGGNTTYGG	Gibson et al 2011	Taq
	COI-Dipt-2183F	CAACAYTTATTTTGATTTTTTGG	Gibson et al 2011	Taq
CytB	K699R	GGGGGTAAACTGTTTCATCC	Wahlberg 2010	Taq
	10933F	TATGTTTTACCTTGAGGACAAATATC	Simon et al 1994	ExTaq
	11683R	AAATTCTATCTTATGTTTTCAAAAC	Simon et al 1994	ExTaq
	CytB-Dipt-11389R	ACNCCCHCWARYTTRTTNGG	Gibson et al 2011	ExTaq
	CytB-Dipt-11545R	ACDGGDCGDCGYCCRATTC	Gibson et al 2011	ExTaq
AATS	CytB-Dipt-11035F	GGNTTYKCNGTNGAYAYAGC	Gibson et al 2011	ExTaq
	A1x40F	GNATGAAYCARTTYAARCCNAT	Feng-Yi Su et al 2008	ExTaq
	rA1x244	CATNCCRCARTCNATRTGYTT	Feng-Yi Su et al 2008	ExTaq
	AATS-Dipt-828R	CCCATYTCCCARAARTTRTC	Gibson et al 2011	ExTaq
28S	AATS-Dipt-962R	CGATTWAYTGWRTRAANACHARRTTCC	Gibson et al 2011	ExTaq
	AATS-Dipt-562F	CGNGCHGGHGGHAARCAAYAYGA	Gibson et al 2011	ExTaq
	rc28AB	ACTACCCCTGAATTTAAGCA	Bertone et al 2008	Taq
	28S-Dipt-3385F	GGATTTTCTTAGTAGCGGCG	Gibson et al 2011	Taq
	28C	GCTATCCTGAGGGAACTTCGG	Bertone et al 2008	Taq
	rc28B	CCCGTCTTGAAACACGGACC	Bertone et al 2008	Taq
	28E	CCTTATCCCGAAGTTACG	Wiegmann et al 2000	Taq
	A28F	TGGAACCGTATTCCTTTTCG	Han et al 2002	Taq
	rc28D	CCGCAGCTGGTCTCCAAG	Wiegmann et al 2000	Taq
	28I	GGGTCTTCTTTCCCGCT	Lonsdale et al, 2010	Taq
	rc28F	GTGATTTCTGCCCAGTGCTCTG	Lonsdale et al 2010	Taq
	28Q	AACTCCCTACCTGGCAAT	Collins & Wiegmann 2002a	Taq
	28K	GAAGAGCCGACATCGAAG	Wiegmann et al 2000	Taq
	rc28Q	GGACATTGCCAGGTAGGGAGTT	Wiegmann et al 2000	Taq
	28ZC	TGGATCGCAGTATGGCAGCT	Bertone et al 2008	Taq
	28S-Dipt-4997F	GGAGGACTGAAGTGAGAAGG	Gibson et al, 2011	Taq
	rc28C	CCGAAGTTTCCCTCAGGATAGC	Wiegmann et al 2000	Taq
	rc28P	TGGTATGCGTAGAAGTGTTTGGC	Wiegmann et al 2000	Taq
	28S-Dipt-4534F	CCTATTCTCAAACTTAAATGGG	Gibson et al 2011	Taq
	28S-Dipt-6834F	GCGTAGTACGAGAGGAACCG	Gibson et al 2011	Taq
	28S-Dipt-5532R	CTCAATCTTCAGAGCCAATCC	Gibson et al 2011	Taq
	28S-Dipt-6647R	CGTCGCTATGAACGCTTGCC	Gibson et al 2011	Taq
	28S-Dipt-6018R	GCCCGTTCCCTTGCTGTGG	Gibson et al 2011	Taq
	28S-Dipt-5497F	GGAAGTCGGCAAATTAGATCCG	Gibson et al 2011	Taq
	28S-Dipt-4632R	GGTTCATCCACAGCGCC	Gibson et al 2011	Taq
	28S-Dipt-6565F	CGGCCTATCGATCCTTTTGG	Gibson et al 2011	Taq
	28S-Dipt-6916R	GAGGCGTTTCAGGCATAATCC	Gibson et al 2011	Taq
	28S-Dipt-7176R	CCACTTACAACACCTTGCC	Gibson et al 2011	Taq

Table 4.3. Character state matrix used for morphological analysis in Chapter 4.
Characters 1-23.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Atrichoparia</i> sp. A	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Atrichoparia</i> sp. B	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Atrichoparia</i> sp. B	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Australoconops phaeomeros</i>	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Camrasiconops ater</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	1
<i>Conops (Asiconops) australianus</i>	1	1	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Conops (Asiconops) chinensis</i>	1	1	1	1	1	0	1	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Conops (Conops) flavipes</i>	1	1	1	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Conops (Conops) vesicularis</i>	1	1	1	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Conops (Smithiconops) rondanii</i>	1	1	1	1	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Euconops bellus</i>	1	1	1	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	0
<i>Heteroconops</i> sp.	1	1	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Leopoldius coronatus</i>	1	1	1	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Microconops ornatus</i>	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	0
<i>Microconops ornatus</i>	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	0
<i>Microconops tasmaniensis</i>	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	1	0
<i>Physocephala maculipes</i>	1	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physocephala madagascariensis</i>	1	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physocephala marginata</i>	1	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physocephala rufipes</i>	1	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physocephala tibialis</i>	1	1	1	1	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physoconops (Pachyconops) brachyrhynchus</i>	1	1	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physoconops (Pachyconops) guianicus</i>	1	1	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Physoconops (Physoconops) discalis</i>	1	1	0	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	1	0	1	1	0
<i>Pleurocerina brevis</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	1
<i>Pleurocerina longicornis</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	1
<i>Pleurocerina vespiformis</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	0	1	1	1
<i>Smartiomyia arena</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Smartiomyia arena</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>Dalmannia aculeata</i>	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0
<i>Dalmannia nigriceps</i>	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0
<i>Dalmannia vitiosa</i>	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0
<i>Parazodion schmidt</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Parazodion schmidt</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Myopa buccata</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	1
<i>Myopa clausa</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	1
<i>Myopa occulta</i>	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	1	0
<i>Myopa vesiculosa</i>	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	1	0
<i>Myopa</i> sp.	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	1	0
<i>Pseudoconops antennatus</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	1	0
<i>Sicus ferrugineus</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Thecophora africana</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Thecophora atra</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Thecophora australiana</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Thecophora metallica</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Thecophora modesta</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Thecophora occidentalis</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Stylogaster biannulata</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster breviventris</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster decorata</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster frauci</i>	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster frauci</i>	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster inca</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster neglecta</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster pauliani</i>	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster rectinervis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster stylata</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster westwoodi</i>	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Stylogaster</i> sp.	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	1	0
<i>Zodion cinereum</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Zodion erythrurum</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Zodion fulvifrons</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Zodion intermedium</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Zodion pictum</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Lonchoptera tristis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conicera (Conicera) dauci</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Toxomerus marginata</i>	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Minettia lupulina</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
<i>Chyliza scrobiculata</i>	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0
<i>Pyrgota undata</i>	1	1	1	1	1	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	0	1	0
<i>Strongylophthalmyia angustipennis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0

Table 4.3. Continued. Characters 47-69.

Species	4 7	4 8	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8	5 9	6 0	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9
<i>Atrichoparia</i> sp. A	0	0	1	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0
<i>Atrichoparia</i> sp. B	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0
<i>Atrichoparia</i> sp. B	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	0
<i>Australoconops phaeomeros</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Camrasiconops ater</i>	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Conops</i> (<i>Asiconops</i>) <i>australianus</i>	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Conops</i> (<i>Asiconops</i>) <i>chinensis</i>	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	?
<i>Conops</i> (<i>Conops</i>) <i>flavipes</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Conops</i> (<i>Conops</i>) <i>vesicularis</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Conops</i> (<i>Smithiconops</i>) <i>rondanii</i>	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Euconops bellus</i>	1	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Heteroconops</i> sp.	0	0	1	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0
<i>Leopoldius coronatus</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Microconops ornatus</i>	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Microconops ornatus</i>	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	1	0
<i>Microconops tasmaniensis</i>	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	1	1	?
<i>Physocephala maculipes</i>	1	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physocephala madagascariensis</i>	1	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physocephala marginata</i>	1	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physocephala rufipes</i>	1	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physocephala tibialis</i>	1	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physoconops</i> (<i>Pachyconops</i>) <i>brachyrhynchus</i>	0	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physoconops</i> (<i>Pachyconops</i>) <i>guianicus</i>	0	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Physoconops</i> (<i>Physoconops</i>) <i>discaelis</i>	0	0	1	0	0	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Pleurocenna brevis</i>	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Pleurocenna longicornis</i>	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Pleurocenna vespiformis</i>	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0
<i>Smartiomys arena</i>	0	0	1	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0
<i>Smartiomys arena</i>	0	0	1	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0
<i>Dalmanella aculeata</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
<i>Dalmanella nigriceps</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
<i>Dalmanella vitosa</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
<i>Parazodion schmidt</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Parazodion schmidt</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Myopa buccata</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Myopa clausa</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Myopa occulta</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Myopa vesiculosa</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Myopa</i> sp.	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Pseudoconops antennatus</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Sicus ferrugineus</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	0
<i>Thecophora africana</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Thecophora atra</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Thecophora australiana</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Thecophora metallica</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Thecophora modesta</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Thecophora occidentalis</i>	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0
<i>Stylogaster biannulata</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster breviventr</i>	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster decorata</i>	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster frauci</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster frauci</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster inca</i>	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster neglecta</i>	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster pauliani</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster rectinervis</i>	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster stylata</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster westwoodi</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1
<i>Stylogaster</i> sp.	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	?
<i>Zodion cinereum</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Zodion erythrurum</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Zodion fulvifrons</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Zodion intermedium</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Zodion pictum</i>	0	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	0
<i>Lonchoptera tristis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conicera</i> (<i>Conicera</i>) <i>dauci</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Toxomerus marginata</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Minettia lupulina</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Chyliza scrobiculata</i>	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Pyrgota undata</i>	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
<i>Strongylophthalmyia angustipennis</i>	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Table 4.3. Continued. Characters 70-92.

Species	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	
<i>Atrichoparia</i> sp. A	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	0	1	
<i>Atrichoparia</i> sp. B	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	1	0	0	1	1	1	1	0	1
<i>Atrichoparia</i> sp. B	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Australoconops phaeomeros</i>	1	0	1	1	1	0	1	0	2	2	2	2	2	2	0	0	0	1	1	1	1	1	0	1
<i>Camrasiconops ater</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Conops (Asiconops) australianus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	2	2	2
<i>Conops (Asiconops) chinensis</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	1	1	1	1	1	0	1
<i>Conops (Conops) flavipes</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1
<i>Conops (Conops) vesicularis</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	0	1
<i>Conops (Smithiconops) rondanii</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Euconops bellus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Heteroconops</i> sp.	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Leopoldius coronatus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	1	0	1	1	1	1	1	0	1
<i>Microconops ornatus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	1	1	0	1
<i>Microconops ornatus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Microconops tasmaniensis</i>	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	1	1	1	1	1	0	1
<i>Physocephala maculipes</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physocephala madagascariensis</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physocephala marginata</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physocephala rufipes</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physocephala tibialis</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physoconops (Pachyconops) brachyrhynchus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physoconops (Pachyconops) guianicus</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Physoconops (Pachyconops) discalis</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1
<i>Pleurocerna brevis</i>	1	0	1	1	1	0	1	0	2	2	2	2	2	2	2	0	0	0	1	1	1	1	0	1
<i>Pleurocerna longicornis</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	2	2	2
<i>Pleurocerna vespiformis</i>	1	0	1	1	1	0	1	0	2	2	2	2	2	2	0	0	0	1	1	1	1	1	0	1
<i>Smartomyia arena</i>	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Smartomyia arena</i>	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Dalmannia aculeata</i>	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
<i>Dalmannia nigriceps</i>	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
<i>Dalmannia vitiosa</i>	0	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
<i>Parazodion schmidt</i>	1	0	1	0	1	0	1	2	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Parazodion schmidt</i>	1	0	1	0	1	0	1	2	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Myopa buccata</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Myopa clausa</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Myopa occulta</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Myopa vesiculosa</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Myopa</i> sp.	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	1	2	2	2	2	2	2	2	2
<i>Pseudoconops antennatus</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	1	2	2	2	2	2	2	2	2
<i>Sicus ferrugineus</i>	0	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Thecophora africana</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	2	2	2
<i>Thecophora atra</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Thecophora australiana</i>	0	0	1	1	1	0	1	0	2	2	2	2	2	2	0	0	0	1	1	1	1	1	0	0
<i>Thecophora metallica</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	1	2	2	2	2	2	2	2	2
<i>Thecophora modesta</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Thecophora occidentis</i>	0	0	1	1	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0
<i>Stylogaster biannulata</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0
<i>Stylogaster breviventris</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0
<i>Stylogaster decorata</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0
<i>Stylogaster frauci</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0
<i>Stylogaster frauci</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0
<i>Stylogaster inca</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	2	2	2	2	2	2	2	2	2
<i>Stylogaster neglecta</i>	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0
<i>Stylogaster pauliani</i>	0	1	1	0	0	0	0	0	2	2	2	2	2	2	0	0	0	0	1	1	0	1	0	0
<i>Stylogaster rectinervis</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0
<i>Stylogaster stylata</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0
<i>Stylogaster westwoodi</i>	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0
<i>Stylogaster</i> sp.	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	1	1	0	1	0	0
<i>Zodion cinereum</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Zodion erythrurum</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Zodion fulvifrons</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Zodion intermedium</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Zodion pictum</i>	1	0	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	1
<i>Lonchoptera tristis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conicera (Conicera) dauci</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				

Table 4.3. Continued. Characters 93-113.

	9	9	9	9	9	9	9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Species	3	4	5	6	7	8	9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3
Atrichoparia sp. A	1	0	2	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Atrichoparia sp. B	1	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Atrichoparia sp. B	1	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Australoconops phaeomeros	1	0	2	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	
Camrasiconops ater	1	0	2	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Conops (Asiconops) australianus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Conops (Asiconops) chinensis	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Conops (Conops) flavipes	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Conops (Conops) vesicularis	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Conops (Smithiconops) rondanii	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Euconops bellus	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Heteroconops sp	1	0	2	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Leopoldius coronatus	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Microconops ornatus	1	0	2	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	
Microconops ornatus	1	0	2	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	
Microconops tasmaniensis	1	0	2	1	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	
Physocephala maculipes	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physocephala madagascariensis	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physocephala marginata	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physocephala rufipes	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physocephala tibialis	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physoconops (Pachyconops) brachyrhynchus	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physoconops (Pachyconops) guianicus	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Physoconops (Physoconops) discalis	1	0	2	1	0	2	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	
Pleurocenna brevis	1	0	2	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	
Pleurocenna longicornis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Pleurocenna vespiformis	1	0	2	1	0	2	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	
Smartomyia arena	1	0	2	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	
Smartomyia arena	1	0	2	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	
Dalmannia aculeata	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	
Dalmannia nigriceps	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	
Dalmannia vitiosa	0	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	
Parazodion schmidt	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Parazodion schmidt	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Myopa buccata	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Myopa clausa	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Myopa occulta	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Myopa vesiculosa	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Myopa sp	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Pseudoconops antennatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Sicus ferrugineus	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Thecophora africana	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Thecophora atra	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Thecophora australiana	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Thecophora metallica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Thecophora modesta	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Thecophora occidentalis	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	
Stylogaster biannulata	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster breviventr	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster decorata	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster frauci	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster frauci	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster inca	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Stylogaster neglecta	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster pauliani	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster rectinervis	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster stylata	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster westwoodi	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Stylogaster sp	0	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	
Zodion cinereum	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Zodion erythrurum	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Zodion fulvifrons	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Zodion intermedium	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Zodion pictum	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Lonchoptera tristis	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Conicera (Conicera) dauci	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Toxomerus marginata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Minettia lupulina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Chyliza scrobiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Pyrgota undata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	
Strongylophthalmyia angustipennis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	

See text for description of characters and states. ? – character state unknown.

Table 4.4. Summary of results for data subsets and total evidence data set.

	Data Subsets						Total Evidence			
	morph	allDNA	mtDNA	nrDNA	rDNA	PCG	Equal/ 5th	Equal/ missing	nt3=0/ missing	nt3=0/ 5th
# characters analyzed	113	6824	1625	5199	5120	1704	6937	6937	6937	6937
% characters constant	0 0	59 4	40 2	52 2	51 0	43 7	48 4	48 4	48 4	48 4
% characters informative	100 0	32 6	53 6	32 7	33 1	51 8	38 8	38 8	38 8	38 8
# most parsimonious trees	4	1	1	2	14	94	1	2	3	1
Length of shortest tree(s)	193	12770	3717	8957	10139	2534	21261	18542	10309	12985
Consistency Index (CI)	0 611	0 372	0 265	0 420	0 404	0 259	0 286	0 259	0 349	0 375
Retention Index (RI)	0 951	0 635	0 571	0 667	0 649	0 604	0 565	0 553	0 653	0 655
Support for nodes (PBS/JKS)										
1	8/61	106/100	34/100	72/100	84/100	22/100	100	100	100	114/100
2	-3/-	8/81	7/50	1/50	32/63	3/50	64	>50	86	5/84
3	0/50	50/100	21/100	29/100	32/100	18/99	100	100	100	50/100
4	2/78	1/50	0/-	1/70	1/70	0/50	0	0	93	3/66
5	2/52	8/94	4/50	4/88	4/91	4/50	99	97	100	10/98
6	1/67	59/100	15/100	44/100	42/100	17/100	100	100	100	60/100
7	3/97	29/100	26/55	3/100	-3/100	32/72	100	98	100	32/100
8	0/-	2/54	3/50	-1/50	1/50	1/50	57	>50	>50	2/50
9	1/54	8/84	0/50	8/50	5/61	3/50	74	>50	64	9/94
10	0/50	4/86	2/75	2/51	4/-	0/63	97	64	0	4/84
11	2/81	53/100	13/98	40/100	40/100	13/100	100	100	100	55/100
12	4/83	37/100	15/94	22/100	16/98	21/99	100	100	100	41/100
13	1/50	1/50	8/50	-7/50	-8/50	9/50	>50	0	>50	2/50
14	1/-	1/50	5/50	-4/50	-4/50	5/50	>50	>50	>50	2/50
15	0/50	26/100	17/100	9/100	13/100	13/100	100	100	100	26/100
16	0/50	16/100	6/91	10/95	10/94	6/94	91	84	100	16/100
17	0/50	14/100	18/96	-4/85	-3/92	17/97	83	91	99	14/99
18	3/94	43/100	4/87	39/100	40/100	3/67	100	100	100	46/100
19	0/50	20/100	1/62	19/100	17/100	3/82	99	100	100	20/100
20	3/81	7/75	1/50	6/87	3/79	4/50	0	0	65	10/90
21	4/85	4/74	2/50	2/99	3/79	1/50	0	0	62	8/93
22	1/78	1/50	6/50	-5/50	-6/50	7/50	0	0	>50	2/50
23	0/-	5/50	13/50	-8/50	-10/50	15/50	0	0	>50	5/60
24	1/66	20/100	11/100	9/100	11/100	9/99	100	100	100	21/100
25	-1/-	2/-	7/50	-5/-	-5/-	7/50	0	0	0	1/-
26	0/-	7/50	18/50	-11/-	-7/50	14/-	0	0	>50	7/69
27	4/63	26/100	12/50	14/100	14/100	12/-	100	100	100	30/100
28 - Conopinae	17/100	71/100	36/97	35/100	49/100	22/83	100	100	100	88/100
29	3/97	35/100	12/100	23/100	17/100	18/100	100	100	100	38/100
30	0/50	9/77	6/88	3/-	2/85	7/-	70	72	96	9/94
31	0/50	1/-	0/50	1/-	0/-	1/50	0	56	70	1/50
32	0/50	30/100	12/100	18/100	17/100	13/100	100	100	100	30/100
33	0/50	9/96	7/91	2/90	3/68	6/81	100	100	93	9/95
34 - Zodioninae	6/100	105/100	23/100	82/100	86/100	19/100	100	100	100	111/100
35 - Conopinae+Zodioninae	7/100	6/71	17/50	-11/-	-10/50	16/-	95	81	77	13/95
36 - Conopinae+Zodioninae+Sicus	3/94	4/50	0/50	4/-	6/50	-2/50	>50	0	60	7/79
37	1/50	11/100	15/99	-4/93	4/100	7/71	99	99	100	12/100
38	1/50	27/100	6/50	21/100	16/100	11/95	100	100	100	28/100
39	0/50	13/98	8/90	5/80	9/94	4/75	100	89	85	13/98
40	1/61	1/-	8/86	-7/-	-6/-	7/89	69	92	62	2/50
41	0/50	1/62	3/-	-2/-	-3/-	4/-	0	0	0	1/56
42	0/50	52/100	-11/-	63/100	56/100	-4/-	100	0	0	52/100
43	0/50	3/89	-1/-	4/100	3/100	0/-	95	0	0	3/90
44	0/50	24/100	5/99	19/100	16/100	8/100	100	100	100	24/100
45	1/50	20/100	18/100	2/99	7/100	13/84	100	100	100	21/100
46	3/89	147/100	25/100	122/100	124/100	23/100	100	100	100	150/100
47 - Myopinae	4/92	30/100	11/65	19/100	16/100	14/-	100	100	100	34/100
48 - Conopinae+Zodioninae+Sicus+Myopinae	11/100	7/59	-2/50	9/-	13/62	-6/50	>50	0	77	18/99
49	0/50	4/72	-4/-	8/97	5/76	-1/-	60	0	0	4/79
50 - Dalmanninae	9/100	145/100	25/100	120/100	124/100	21/100	100	100	100	154/100
51- Conopidae excl. Stylogaster	5/99	8/84	-1/50	9/92	6/61	2/50	62	91	99	13/98
52	3/66	55/100	11/95	44/100	50/100	5/82	100	100	100	58/100
53	1/74	31/100	14/100	17/96	36/100	-5/-	100	100	100	32/100
54	0/-	52/100	5/96	47/100	52/100	0/-	100	100	100	52/100
55	2/55	169/100	11/56	158/100	150/100	19/100	100	100	100	171/100
56	1/72	16/81	6/50	10/65	10/50	6/57	59	73	89	17/94
57	2/-	22/93	7/51	15/85	9/58	13/55	93	100	99	24/97

Table 4.4. Continued.

	Data Subsets						Total Evidence			
	morph	alIDNA	mtDNA	nrDNA	rDNA	PCG	Equal/ 5th	Equal/ missing	nt3=0/ missing	nt3=0/ 5th
Support for nodes (PBS/JKS)										
58	0/>50	134/100	31/100	103/100	114/100	20/93	100	100	100	134/100
59	0/>50	6/68	3/58	3/57	1/-	5/>50	52	62	72	6/80
60	>50	15/96	5/85	10/78	17/93	-2/-	89	91	100	15/97
61	3/90	15/100	0/>50	15/89	13/95	2/83	100	100	99	18/100
62 – Stylogastrinae	17/100	155/100	28/100	127/100	132/100	23/100	100	100	100	172/100
63 – Conopidae	8/91	24/95	17/74	7/61	6/80	18/92	81	79	98	32/99
64	-1/-	9/90	5/>50	4/68	12/90	-3/>50	65	>50	>50	8/91
65	-1/-	17/94	-7/-	24/83	26/91	-9/-	75	>50	>50	16/98
66	1/-	12/93	-1/>50	13/70	18/88	-6/-	64	>50	55	13/98
67 – Schizophora	5/99	42/100	0/-	42/100	42/100	0/-	100	100	100	47/100
68	1/74	52/100	5/-	47/100	51/100	1/66	100	100	100	53/100
Combined Bremer support of partition	151	2147	627	1520	1598	549				
% overall Bremer support	6.6	93.4	27.3	66.1	69.5	23.9				

Equal - equal weighting; nt3=0 - nt3 weighted to 0; missing - gaps treated as missing; 5th - gaps treated as a fifth state; PBS - partitioned Bremer support; JKS - jackknife support values (36% exclusion); nodes not recovered indicated as -; nodes depicting important clades are in bold with classification to the left.

Table 5.1. Past tribal classifications for genera of Conopidae.

Zimina 1960
Conopidae of USSR

Conopinae
 Brachyceraeini
 Brachyceraea
 Neobrachyceraea
 Conopini
 Abrachyglossum
 Conops
 Brachyglossum (now *Leopoldius*)
 Physocephala
 Tropidomyiini
 Tropidomyia
 Myopinae
 Myopini
 Melanosoma
 Myopa
 Occeomyia (now *Thecophora*)
 Sicini
 Sicus
 Carbonosicus
 Zodionini
 Zodion
 Dalmanniini
 Dalmannia

Smith 1980
Afrotropical Conopidae

Conopinae
 Conopini
 Anticonops
 Archiconops
 Caenoconops
 Conops (2 subgenera)
 Dacops
 Euconops
 Physocephalini
 Physocephala
 Physoconops
 Pleurocennella
 Pseudophysocephala
 Tropidomyia
 Myopinae
 Paramyopa
 Pseudoconops
 Thecophora
 Zodion
 Stylogasterinae
 Stylogaster

Camras 1965
Nearctic Conopidae

Conopinae
 Conopini
 Conops (1 subgenus)
 Physoconops (3 subgenera)
 Physocephalini
 Physocephala
 Myopinae
 Myopa
 Robertsonomyia
 Thecophora
 Zodion
 Dalmanniinae
 Dalmannia
 Stylogasterinae
 Stylogaster

Chvála and Smith 1988
Palaeartic Conopidae

Conopinae
 Brachyceraeini
 Brachyceraea
 Neobrachyceraea
 Conopini
 Abrachyglossum
 Archiconops
 Conops (2 subgenera)
 Leopoldius
 Macroconops
 Neobrachyglossum
 Physocephala
 Siniconops
 Pleurocennellini
 Pleurocennella
 Tropidomyiini
 Tropidomyia
 Myopinae
 Myopini
 Melanosoma
 Myopa
 Myopotta
 Thecophora
 Sicini
 Carbonosicus
 Sicus
 Zodionini
 Zodion
 Dalmanniinae
 Dalmannia

Papavero 1971
Neotropical Conopidae

Conopinae
 Conopini
 Conops (5 subgenera)
 Mallachoconops
 Physoconops (3 subgenera)
 Physocephalini
 Physocephala
 Tropidomyiini
 Tropidomyia
 Myopinae
 Myopa
 Neozodion
 Robertsonomyia
 Scatocemyia
 Thecophora
 Zodion
 Dalmanniinae
 Baruerizodion
 Parazodion
 Stylogasterinae
 Stylogaster

Camras 2000, 2001
Afrotropical Conopinae

Conopinae
 Conopini
 Anticonops
 Caenoconops
 Conops (3 subgenera)
 Euconops
 Physoconops
 Physocephalini
 Dacops
 Physocephala
 Pleurocennella
 Pseudophysocephala
 Tropidomyia

Table 5.2. List of taxa included in Chapter 5 analysis. Proposed tribal classification not included. Genus, subgenus, and subfamily classifications listed according to current catalogues prior to this analysis.

Taxa	Species	Author	Geographic origin	Specimens examined	Notes
Conopidae					
Conopinae	<i>Abrazyglossum capitatum</i>	Loew, 1847	Switzerland	2M, 1F	TSP
	<i>Anticonops abdominalis</i>	Krober, 1936b	Zaire	lit only	TSP, F only
	<i>Archiconops insularis</i>	Krober, 1936b	Madagascar	2M	TSP, M only
	<i>Archiconops pseudoerythrocephalus</i>	Stuke, 2004c	Tanzania	1M, 1F	
	<i>Atrichoparia curticornis</i>	(Krober, 1940a)	Australia (SA, WA)	2M, 2F	TSP
	<i>Atrichoparia</i> sp A		Australia (QLD)	2M, 3F	
	<i>Atrichoparia</i> sp B		Australia (NSW)	2M, 2F	
	<i>Australoconops perbellum</i>	(Krober, 1939d)	Australia (WA)	2M, 1F	
	<i>Australoconops phaeomeros</i>	Schneider, 2010	Australia (QLD)	1M	
	<i>Australoconops uncinatus</i>	(Krober, 1939d)	Australia (ACT, NSW, QLD, WA)	2M, 1F	
	<i>Brachyceraea brevicornis</i>	Loew, 1847	Iran, Lebanon	1M, F	TSP
	<i>Caenoconops bicolor</i>	(Krober, 1931)	South Africa	1M, 1F	TSP
	<i>Caenoconops clarpennisi</i>	(Camras, 1962b)	Nigeria	1F, HT	F only
	<i>Caenoconops fredbergi</i>	Camras, 2000	Kenya	1M, HT	M only
	<i>Camrasiconops ater</i>	(Camras, 1961)	Australia (NSW, QLD)	1M, 1F	TSP
	<i>Chrysiomyia hirsuta</i>	(Krober, 1940a)	Australia (WA)	1M	
	<i>Chrysiomyia rufa</i>	Krober, 1940a	Australia (WA)	1M	TSP
	<i>Chrysiomyia rugifrons</i>	Schneider, 2010	Australia (WA)	1M	
	<i>Conops (Asiconops) ater</i>	Macquart, 1843	Kenya	1M, 1F	
	<i>Conops (Asiconops) aureomaculatus</i>	Krober, 1933	China	1M	TSP
	<i>Conops (Asiconops) australianus</i>	Camras, 1961	Australia (QLD)	1M, 2F	
	<i>Conops (Asiconops) chinensis</i>	Camras, 1960	Japan	1M	M only
	<i>Conops (Asiconops) nubeculosus</i>	Bigot, 1887	Indonesia (W Java)	1M, 1F	
	<i>Conops (Ceratoconops) ornatus</i>	Williston, 1892a	Brazil	1M, HT	TSP, M only
	<i>Conops (Conops) flavipes</i>	Linnaeus, 1758	Germany, Italy	3M, 2F	TSP
	<i>Conops (Conops) nigripes</i>	Krober, 1913	Taiwan	2M, 2F	
	<i>Conops (Conops) verus</i>	Camras, 1955b	Brazil	1M, HT	M only
	<i>Conops (Conops) vesicularis</i>	Linnaeus, 1761	Germany, Italy, South Korea	3M, 2F	
	<i>Conops (Diconops) geminatus</i>	Camras, 1957a	Costa Rica, Peru	2F	F only
	<i>Conops (Diconops) trichus</i>	Camras, 1957a	Brazil	1F, PT	TSP, F only
	<i>Conops (Smithiconops) guineensis</i>	Krober, 1915f	Kenya	1M	M only
	<i>Conops (Smithiconops) rondani</i>	Bezzi, 1901	South Africa, Tanzania	3M, 2F	TSP
	<i>Conops (Sphenconops) brunneosericeus</i>	Krober, 1937	Brazil	1F	
	<i>Conops (Sphenconops) nobilis</i>	Williston, 1892a	Argentina, Brazil	1M, 1F	TSP
	<i>Dacops abdominalis</i>	Krober, 1915g	Kenya, Mozambique, South Africa	1M, 2F	TSP
	<i>Dacops kaplanae</i>	Camras, 2001	Ethiopia	1M, 1F, AT, PT	
	<i>Delkeskampomyia fasciata</i>	Krober, 1940a	Australia (WA)	lit only	TSP, M only
	<i>Euconops bellus</i>	Krober, 1915g	South Africa	3M, 2F	TSP
	<i>Heteroconops antennatus</i>	Krober, 1940a	Australia (WA)	2M, 2F	
	<i>Heteroconops gracilis</i>	Krober, 1915g	Australia (NT)	2M, 1F	TSP
	<i>Heteroconops</i> sp		Australia (QLD)	3M, 2F	
	<i>Jelte neotropica</i>	(Camras, 2008)	Bolivia	1F, PT	TSP, F only
	<i>Leopoldius coronatus</i>	(Rondani, 1857)	Germany, Italy	3M, 2F	
	<i>Leopoldius signatus</i>	(Wiedemann, 1824)	England, Italy	2M, 2F	TSP
	<i>Macroconops helleri</i>	Krober, 1927a	China	lit only	TSP, M only
	<i>Mallachoconops atratulus</i>	(Malloch, 1933)	Chile	1M HT	TSP, M only
	<i>Microbrachyceraea pendleburyi</i>	(Brunetti, 1927)	Malaysia	lit only	TSP, M only
	<i>Microconops nigrithorax</i>	Krober, 1940a	Australia (WA)	4M, 1F	
	<i>Microconops ornatus</i>	Krober, 1915g	Australia (ACT, QLD, WA)	3M, 2F	TSP
	<i>Microconops similis</i>	Krober, 1940a	Australia (SA)	2M, 2F	
	<i>Microconops tasmaniensis</i>	Krober, 1940a	Australia (NSW, TAS, VIC)	2M, 1F	
	<i>Neobrachyceraea elongata</i>	Stuke & Clements, 2005	Thailand	1F	
	<i>Neobrachyceraea obscuripennis</i>	(Krober, 1913)	China	1M	
	<i>Neobrachyglossum punctatum</i>	Krober, 1915g	Turkey?	lit only	TSP, M only
	<i>Neobrachyceraea obscuripennis</i>	(Krober, 1913)	China	1M	
	<i>Neoconops brevistylus</i>	Schneider, 2010	Australia (QLD)	1M	

Table 5.2. Continued.

Taxa	Species	Author	Geographic origin	Specimens examined	Notes
Conopidae					
Conopinae	<i>Neoconops longicornis</i>	Krober, 1915g	Australia (NSW, WA)	1M, 1F	TSP
	<i>Neozodion pruinosum</i>	Szlady, 1926	Peru	lit only	TSP, F only
	<i>Physocephala bimarginipennis</i>	Karsch, 1887	Angola, Congo, Tanzania	1M, 2F	
	<i>Physocephala maculipes</i>	(Bigot, 1887)	Tanzania, Tunisia, Uganda	4M, 1F	
	<i>Physocephala madagascariensis</i>	Krober, 1915d	Madagascar	3M, 2F	
	<i>Physocephala marginata</i>	(Say, 1823)	Canada (ON, QC)	3M, 1F	
	<i>Physocephala rufipes</i>	(Fabricius, 1781)	Germany, Italy, Serbia	2M, 3F	TSP
	<i>Physocephala tibialis</i>	(Say, 1829)	Canada (ON), USA (VA)	3M, 2F	
	<i>Physoconops (Aconops) antennatus</i>	(Krober, 1915j)	Argentina, Brazil	1M, 2F	TSP
	<i>Physoconops (Aconops) costatus</i>	(Fabricius, 1805)	Argentina, Venezuela	2M, 2F	
	<i>Physoconops (Aureoconops) aureolus</i>	Camras, 2004	Peru	1M, HT	TSP, M only
	<i>Physoconops (Gyroconops) abbreviatus</i>	Camras, 1955b	Mexico	1M, 1F	
	<i>Physoconops (Gyroconops) parvus</i>	(Williston, 1892a)	Brazil, Costa Rica, Mexico	2M, 1F	
	<i>Physoconops (Gyroconops) sylvius</i>	(Williston, 1882)	Mexico, USA (AL, UT)	2M, 2F	TSP
	<i>Physoconops (Kroeberoconops) argentinus</i>	Camras, 2004	Argentina	1M, HT	
	<i>Physoconops (Kroeberoconops) hermanni</i>	(Krober, 1915j)	Brazil	1F	TSP
	<i>Physoconops (Kroeberoconops) rufipennis</i>	(Macquart, 1843)	Argentina	1M, 1F	
	<i>Physoconops (Pachyconops) brachyrhynchus</i>	(Macquart, 1843)	Canada (ON), USA (MD, MI)	3M, 2F	
	<i>Physoconops (Pachyconops) bulbirostris</i>	(Loew, 1853)	Guatemala, USA (AL, MS, SC)	2M, 2F	TSP
	<i>Physoconops (Pachyconops) guianicus</i>	(Curran, 1934)	Costa Rica, Venezuela	2M, 1F	
	<i>Physoconops (Physoconops) discalis</i>	(Williston, 1892a)	Brazil, Mexico, Venezuela, USA (AZ)	3M, 2F	
	<i>Physoconops (Physoconops) fronto</i>	(Williston, 1885)	Canada (MB), USA (IA, MI, NM)	2M, 2F	
	<i>Physoconops (Physoconops) microvalvus</i>	(Krober, 1930)	Indonesia (W Java)	3M, 2F	
	<i>Physoconops (Physoconops) obscuripennis</i>	(Williston, 1882)	Canada (BC), USA (AL, DE)	2M, 2F	TSP
	<i>Physoconops (Physoconops) sepulchralis</i>	(Brunetti, 1912)	India	1M	
	<i>Physoconops (Shannonconops) apicalis</i>	Camras, 1955b	Brazil	1M	TSP
	<i>Physoconops notatifrons</i>	Camras, 1962b	Kenya, Zambia	1F	F only
	<i>Physoconops quadripunctatus</i>	(Krober, 1915f)	South Africa	1M	
	<i>Physoconops rhodesiensis</i>	(Brunetti, 1925a)	South Africa	1M, 1F	
	<i>Pleurocerina brevis</i>	Schneider, 2010	Australia (QLD)	1M	
	<i>Pleurocerina fasciata</i>	Macquart, 1851	Australia (NSW)	1M, 1F	TSP
	<i>Pleurocerina longicornis</i>	(Krober, 1915g)	Australia (NT)	1M, 1F	
	<i>Pleurocerina luteiceps</i>	Schneider, 2010	Australia (WA)	2M, 2F	
	<i>Pleurocerina turneri</i>	(Camras, 1961)	Australia (WA)	2M, 2F	
	<i>Pleurocerina vespiformis</i>	Schneider, 2010	Australia (NSW, QLD)	1M, 1F	
	<i>Pleurocerinella albobalterata</i>	Smith, 1960	Botswana, South Africa	1M, 1F	
	<i>Pleurocerinella copelandi</i>	Stuke, 2009	Botswana	1M, HT	M only
	<i>Pleurocerinella srilankai</i>	Stuke & Camras, 2009 *	Sri Lanka	1M, HT	M only
	<i>Pleurocerinella tibialis</i>	Chen, 1939	China	1F	
	<i>Pleurocerinella sp</i>		Nepal	3M	
	<i>Pseudophysocephala constricta</i>	(Krober, 1915d)	Lesotho, South Africa	1M, 2F	
	<i>Pseudophysocephala platycephala</i>	(Loew, 1853)	South Africa	1M	TSP
	<i>Setosiconops epixanthus</i>	Schneider, 2010	Australia (WA)	1M	M only
	<i>Setosiconops robustus</i>	(Krober, 1940a)	Australia (WA)	1F	TSP
	<i>Siniconops elegans</i>	Chen, 1939	China	1M, 1F	TSP
	<i>Smartomyia arena</i>	Schneider, 2010	Australia (QLD)	3M, 1F	
	<i>Smartomyia obscura</i>	Krober, 1940a	Australia (WA)	2M	TSP

Table 5.2. Continued.

Taxa	Species	Author	Geographic origin	Specimens examined	Notes
Conopidae					
Conopinae	<i>Stenoconops niger</i>	Krober, 1939d	Australia (WA)	lit only	TSP, F only
	<i>Tammo rufa</i>	(Camras, 1955a)	Mozambique	1M	TSP
	<i>Tanyconops longicaudus</i>	Schneider, 2010	Australia (SA)	1F	TSP
	<i>Tropidomyia alexanderi</i>	Camras, 1955a	Argentina, Brazil	2M, 1F	
	<i>Tropidomyia aureifacies</i>	Krober, 1915g	Lebanon	1M	
	<i>Tropidomyia bimaculata</i>	Williston, 1888	Costa Rica	3M, 3F, CTs	TSP
	<i>Tropidomyia ornata</i>	Krober, 1915g	Côte D'Ivoire, Malawi, Namibia, South Africa	2M, 2F	
Dalmanniinae	<i>Tropidomyia</i> sp		Brazil	1M, 1F	
	<i>Baruerizodion steyskali</i>	Papavero, 1970	Brazil	1F	TSP, F only
	<i>Dalmannia aculeata</i>	(Linnaeus, 1761)	Italy, Spain	4M, 1F	
	<i>Dalmannia nigriceps</i>	Loew, 1866	Canada (BC, ON, QC)	3M, 3F	
	<i>Dalmannia vitosa</i>	Coquillett, 1892	Canada (AB, ON, QC)	2M, 2F	
	<i>Parazodion schmidtii</i>	Krober, 1927a	Brazil, Guyana, French Guiana	1M, 5F	TSP
	<i>Parazodion</i> sp		Brazil	1F	
Myopinae	<i>Pseudomyopa camrasi</i>	Pearson, 1974	Brazil	1M, PT	TSP, M only
	<i>Carbonosicus carbonarius</i>	(Krober, 1915g)	China	1M, 1F, CTs	TSP
	<i>Melanosoma bicolor</i>	(Meigen, 1824)	Italy, Syria	2M, 1F	
	<i>Melanosoma hyalipenne</i>	Krober, 1915b	Israel	1M, 1F	
	<i>Myopa buccata</i>	(Linnaeus, 1758)	England, Israel, Germany	2M, 3F	TSP
	<i>Myopa clausa</i>	Loew, 1866	Canada (BC, QC, NS, SK)	4M, 3F	
	<i>Myopa occulta</i>	Wiedemann, 1824	Czech Rep., Germany, Italy, Spain	3M, 2F	
	<i>Myopa vesiculosa</i>	Say, 1823	Canada (BC, ON, QC)	3M, 2F	
	<i>Myopa</i> sp		Australia (NSW)	2F	
	<i>Myopotta pallipes</i>	(Wiedemann, 1824)	England?	1M, 2F	TSP
	<i>Myopotta rubripes</i>	(Villeneuve, 1909)	Germany	2M, 1F	
	<i>Paramyopa oestracea</i>	(Loew, 1863)	Lesotho, South Africa	2M, 2F	
	<i>Pseudoconops antennatus</i>	Camras, 1962a	Madagascar	3F	F only
	<i>Robertsonomyia mexicana</i>	Camras, 1979	Mexico	2M	
	<i>Robertsonomyia palpalis</i>	(Robertson, 1901)	Canada (AB), USA (GA, MS, NC)	2M, 2F	TSP
	<i>Robertsonomyia parva</i>	(Adams, 1903)	Mexico, USA (CA, UT)	2M, 2F	
	<i>Robertsonomyia pearsoni</i>	(Camras, 1976)	Brazil	1M, 1F, PT	
	<i>Scatocemyia plaumanni</i>	Camras, 1957a	Brazil	1M, HT	TSP, M only
	<i>Sicus abdominalis</i>	Krober, 1915g	Italy, Japan, Russia	2M, 2F	
	<i>Sicus ferrugineus</i>	(Linnaeus, 1761)	France, Sweden	2M, 3F	TSP
	<i>Thecophora africana</i>	(Brunetti, 1925b)	Madagascar	1F	
	<i>Thecophora atra</i>	(Fabricius, 1775)	England, Czech Rep., Germany, Spain	3M, 2F	TSP
	<i>Thecophora australiana</i>	(Camras, 1955a)	Australia (NSW, QLD)	3M	
	<i>Thecophora metallica</i>	Camras, 1962a	Madagascar	1F	F only
	<i>Thecophora modesta</i>	(Williston, 1883)	Canada (AB, BC, YT), USA (OR)	3M, 2F	
	<i>Thecophora occidensis</i>	(Walker, 1849)	Canada (ON, QC, SK)	5M, 2F	
	<i>Zodiomyia sumbaensis</i>	Camras, 1957c	India, Sri Lanka	2F	TSP, F only
	<i>Zodion cinereum</i>	(Fabricius, 1794)	Italy, Turkey	2M, 2F	TSP
	<i>Zodion erythrurum</i>	Rondani, 1865	Israel, Italy	2M, 1F	
	<i>Zodion fulvifrons</i>	Say, 1823	Canada (ON, QC), USA (TX)	3M, 2F	
	<i>Zodion gneseum</i>	Brunetti, 1923	India	1M, 1F	
	<i>Zodion intermedium</i>	Banks, 1916	Canada (ON, QC), USA (MS)	2M, 3F	
	<i>Zodion pictum</i>	Schiner, 1868	Argentina, Ecuador, Mexico	1M, 3F	
Notoconopinae	<i>Notoconops alexanderi</i>	Schneider, 2010	Australia (NSW)	1M	TSP
Palaeomyopinae	<i>Palaeomyopa tertiana</i>	Meunier, 1912	Baltic Amber fossil	lit only	TSP, F only
Conopidae					
Stylogastrinae	<i>Stylogaster biannulata</i>	(Say, 1823)	Canada (ON), USA (MS, TX)	2M, 3F	
	<i>Stylogaster breviventris</i>	Aldrich, 1930	Ecuador, Guyana, Peru	3M, 2F	
	<i>Stylogaster decorata</i>	Aldrich, 1930	Ecuador, Guyana, Peru	2M, 2F	
	<i>Stylogaster frauci</i>	Smith, 1979	Australia (QLD)	4M, 2F	

Table 5.2. Continued.

Taxa	Species	Author	Geographic origin	Genders examined	Notes
Conopidae	<i>Stylogaster inca</i>	Camras and Parillo, 1985	French Guiana	1F	F only
Stylogastrinae	<i>Stylogaster neglecta</i>	Williston, 1883	Canada (ON), USA (MD, NM)	3M, 3F	
	<i>Stylogaster pauliani</i>	Camras, 1962a	Madagascar	2M	
	<i>Stylogaster rectinervis</i>	Aldrich, 1930	Brazil, Ecuador, French Guiana	2M, 3F	
	<i>Stylogaster stylata</i>	Fabricius, 1805	Brazil, Ecuador, French Guiana	3M, 1F	TSP
	<i>Stylogaster westwoodi</i>	Smith, 1967a	Congo, Kenya, Nigeria, Tanzania, Zambia	2M, 3F	
	<i>Stylogaster</i> sp		Madagascar	2M	
Subfam unknown	<i>Hoffeinsia baltica</i>	Stuke, 2005b	Baltic Amber fossil	lit only	TSP, M only
Outgroups					
Lonchopteridae	<i>Lonchoptera tristis</i>	Meigen, 1824	Czech Rep , Denmark, England	2M, 2F	
Phoridae	<i>Conicera (Conicera) dauci</i>	Meigen, 1830	Canada (QC), USA (AZ)	2M, 2F	
Syrphidae	<i>Toxomerus marginatus</i>	(Say, 1823)	Canada (ON, QC)	2M, 2F	
Lauxaniidae	<i>Minettia lupulina</i>	(Fabricius, 1787)	Canada (QC), USA (OR)	2M, 2F	
Psilidae	<i>Chyliza scrobiculata</i>	Melander, 1920	Canada (BC)	2M, 2F	
Pyrgotidae	<i>Pyrgota undata</i>	Wiedemann, 1830	Canada (ON, QC)	2M, 2F	
Strongylophthalmyidae	<i>Strongylophthalmyia angustipennis</i>	Melander, 1920	Canada (BC, ON, QC)	2M, 2F	

TSP - type species of genus or subgenus; M only - only males have been described for this species; F only - only females have been described for this species; HT – holotype; PT – paratype; AT – allotype; CTs – co-types; lit. only - only the literature description(s) were examined. * in Stuke, 2009.

Table 5.3. Character state matrix used for phylogenetic analysis in Chapter 5. Characters 1-23. Genus names according to previous classifications.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Abrachyglossum capitatum</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Archiconops insularis</i>	1	1	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Archiconops pseudoerythrocephalus</i>	1	1	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Atrichoparia curticornis</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Atrichoparia</i> sp A	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Atrichoparia</i> sp B	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	0
<i>Australoconops perbellum</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Australoconops phaeomeros</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Australoconops uncinatus</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Brachyceraea brevicornis</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	
<i>Caenococonops bicolor</i>	1	1	1	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Caenococonops claripennis</i>	1	1	1	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Caenococonops fredbergi</i>	1	1	1	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Camrasiconops ater</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	0	
<i>Chrysidiomyia hirsuta</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Chrysidiomyia rufa</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Chrysidiomyia rugifrons</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Conops (Asiconops) ater</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Asiconops) aureomaculatus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Asiconops) australianus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Asiconops) chinensis</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Asiconops) nubeculosus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Ceratococonops) ornatus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Conops) flavipes</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Conops (Conops) nigripes</i>	1	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Conops) verus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Conops) vesicularis</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Conops (Diconops) geminatus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Diconops) trichus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Smithiconops) guineensis</i>	1	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Smithiconops) rondani</i>	1	1	1	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Sphenococonops) brunneosericeus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Conops (Sphenococonops) nobilis</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Dacops abdominalis</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Dacops kaplanae</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Euconops bellus</i>	1	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	0	1	0
<i>Heterococonops antennatus</i>	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Heterococonops gracilis</i>	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Heterococonops</i> sp	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Jelte neotropica</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Leopoldius coronatus</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Leopoldius signatus</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Mallachoconops atratulus</i>	1	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	0	1	0
<i>Microconops nignthorax</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Microconops ornatus</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Microconops similis</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Microconops tasmaniensis</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Neobrachyceraea elongata</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Neobrachyceraea obscuripennis</i>	1	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Neoconops brevistylus</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Neoconops longicornis</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Physocephala bimarginipennis</i>	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Physocephala maculipes</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physocephala madagascariensis</i>	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	1	1	0
<i>Physocephala marginata</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physocephala rufipes</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physocephala tibialis</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Aconops) antennatus</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Aconops) costatus</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Aureococonops) aureolus</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Gyroconops) abbreviatus</i>	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Gyroconops) parvus</i>	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Gyroconops) sylvosus</i>	1	0	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Kroeberoconops) argentinus</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Kroeberoconops) hermanni</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0
<i>Physococonops (Kroeberoconops) rufipennis</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1	0	1	1	0

Table 5.3. Continued. Characters 1-23.

Species	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	2	2	2	2
<i>Physoconops (Pachyconops) brachyrhynchus</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops (Pachyconops) bulbirostris</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops (Pachyconops) guianicus</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops (Physoconops) discalis</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops (Physoconops) fronto</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops (Physoconops) microvalvus</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Physoconops (Physoconops) obscuripennis</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops (Physoconops) sepulchralis</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Physoconops (Shannonconops) apicalis</i>	1	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops notatifrons</i>	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	0
<i>Physoconops quadripunctatus</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1
<i>Physoconops rhodesiensis</i>	1	1	1	0	1	0	0	1	0	0	1	1	0	1	1	1	0	0	1	0	1	1
<i>Pleurocerina brevis</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0
<i>Pleurocerina fasciata</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0
<i>Pleurocerina longicornis</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0
<i>Pleurocerina luteiceps</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0
<i>Pleurocerina turneri</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0
<i>Pleurocerina vespiformis</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0
<i>Pleurocernella albobalterata</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Pleurocernella copelandi</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Pleurocernella srilankai</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Pleurocernella tibialis</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Pleurocernella sp</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Pseudophysocephala constricta</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1
<i>Pseudophysocephala platycephala</i>	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	0	1	1
<i>Setosiconops epixanthus</i>	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1
<i>Setosiconops robustus</i>	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1
<i>Siniconops elegans</i>	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Smartomyia arena</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1
<i>Smartomyia obscura</i>	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1
<i>Tammo rufa</i>	1	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0
<i>Tanyconops longicaudus</i>	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	1	0	0	1	0	0	1
<i>Tropidomyia alexanderi</i>	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1
<i>Tropidomyia aureifacies</i>	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1
<i>Tropidomyia bimaculata</i>	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1
<i>Tropidomyia ornata</i>	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1
<i>Tropidomyia sp</i>	1	1	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0	1	1	1	1
<i>Baruerizodion steyskali</i>	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	0
<i>Dalmanina aculeata</i>	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	0
<i>Dalmanina nigriceps</i>	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	0	0	1	0
<i>Dalmanina vitosa</i>	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	0	0	1	0
<i>Parazodion schmidtii</i>	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Parazodion sp</i>	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Pseudomyopa camrasi</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
<i>Carbonosicus carbonarius</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Melanosoma bicolor</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
<i>Melanosoma hyalipenne</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
<i>Myopa buccata</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Myopa clausa</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Myopa occulta</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Myopa vesiculosa</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Myopa sp</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Myopotta pallipes</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Myopotta rubripes</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0
<i>Paramyopa oestracea</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
<i>Pseudoconops antennatus</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Robertsonomyia mexicana</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Robertsonomyia palpalis</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Robertsonomyia parva</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Robertsonomyia pearsoni</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Scatocernomyia plumannii</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Sicus abdominalis</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Sicus ferrugineus</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Thecophora africana</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Thecophora atra</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Thecophora australiana</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Thecophora metallica</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Thecophora modesta</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Thecophora occidensis</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Zodiomyia sumbaensis</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0

Table 5.3. Continued. Characters 1-23.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>Zodion cinereum</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Zodion erythrurum</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Zodion fulvifrons</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Zodion griseum</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Zodion intermedium</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Zodion pictum</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0
<i>Notoconops alexanderi</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Stylogaster biannulata</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Stylogaster breviventris</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Stylogaster decorata</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Stylogaster frauci</i>	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1
<i>Stylogaster inca</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Stylogaster neglecta</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Stylogaster pauliani</i>	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1
<i>Stylogaster rectinervis</i>	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Stylogaster stylata</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Stylogaster westwoodi</i>	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1
<i>Stylogaster</i> sp	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1
<i>Lonchoptera tristis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conicera (Conicera) dauci</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Toxomerus marginata</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Minettia lupulina</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Chyliza scrobiculata</i>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0
<i>Pyrgota undata</i>	1	1	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	0	1	0
<i>Strongylophthalmyia angustipennis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

Table 5.3. Continued. Characters 24-46.

Species	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4
	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
<i>Abrachyglossum capitatum</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	1	0	1
<i>Archiconops insulans</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Archiconops pseudoerythrocephalus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Atrichopana curticornis</i>	1	1	0	1	1	0	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Atrichopana</i> sp. A	1	1	0	1	1	0	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Atrichopana</i> sp. B	1	1	0	1	1	0	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Australoconops perbellum</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Australoconops phaeomeros</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Australoconops uncinatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Brachyceraea brevicornis</i>	1	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Caenoconops bicolor</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Caenoconops clarpennisi</i>	1	0	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	1	1	0	0	0	0
<i>Caenoconops friedbergi</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Camrasiconops ater</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Chrysiomyia hirsuta</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Chrysiomyia rufa</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Chrysiomyia rufifrons</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Asiconops) ater</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Asiconops) aureomaculatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Asiconops) australianus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Asiconops) chinensis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Asiconops) nubeculosus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Ceratoconops) ornatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Conops) flavipes</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Conops (Conops) nigripes</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Conops (Conops) verus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Conops) vesicularis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Conops (Diconops) geminatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Diconops) trichus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Smithiconops) guineensis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Smithiconops) rondani</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Spheniconops) brunneosentens</i>	1	0	0	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	1	1	0	0	0	0
<i>Conops (Spheniconops) nobilis</i>	1	0	0	1	1	0	0	0	0	1	1	0	0	1	0	1	1	0	1	1	1	0	0	0	0
<i>Dacops abdominalis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Dacops kaplanae</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Euconops bellus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Heteroconops antennatus</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	0
<i>Heteroconops gracilis</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	0
<i>Heteroconops</i> sp.	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	0	0
<i>Jelte neotropica</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Leopoldius coronatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	1	0	1
<i>Leopoldius signatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	1	0	1
<i>Mallachocnops atratulus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Microconops nigrithorax</i>	1	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Microconops ornatus</i>	1	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Microconops similis</i>	1	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Microconops tasmaniensis</i>	1	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Neobrachyceraea elongata</i>	1	0	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Neobrachyceraea obscuripennis</i>	1	0	0	0	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Neoconops brevistylus</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0
<i>Neoconops longicornis</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0
<i>Physocephala bimarginipennis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physocephala maculipes</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physocephala madagascariensis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physocephala marginata</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physocephala rufipes</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physocephala tibialis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Aconops) antennatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Aconops) costatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Aureoconops) aureolus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Gyroconops) abbreviatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Gyroconops) parvus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Physoconops (Gyroconops) sylvestris</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Physoconops (Kroeberoconops) argentinus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Kroeberoconops) hermanni</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0
<i>Physoconops (Kroeberoconops) rufipennis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0

Table 5.3. Continued. Characters 24-46.

Species	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	
	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	
<i>Physoconops (Pachyconops) brachyrhynchus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops (Pachyconops) bulbirostris</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	1	1	0	0	
<i>Physoconops (Pachyconops) guianicus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops (Physoconops) discalis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops (Physoconops) fronto</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops (Physoconops) microvalvus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	
<i>Physoconops (Physoconops) obscuripennis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops (Physoconops) sepulchralis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	
<i>Physoconops (Shannonconops) apicalis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops notatifrons</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops quadripunctatus</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Physoconops rhodesiensis</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	
<i>Pleurocerina brevis</i>	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pleurocerina fasciata</i>	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pleurocerina longicornis</i>	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pleurocerina luteiceps</i>	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pleurocerina turneri</i>	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pleurocerina vespiformis</i>	1	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pleurocennella albohalterata</i>	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	
<i>Pleurocennella copelandi</i>	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	
<i>Pleurocennella srilankai</i>	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	
<i>Pleurocennella tibialis</i>	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	
<i>Pleurocennella sp</i>	1	0	1	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	
<i>Pseudophysocephala constricta</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Pseudophysocephala platycephala</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Setosiconops epixanthus</i>	1	1	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	
<i>Setosiconops robustus</i>	1	1	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	
<i>Siniconops elegans</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	1	1	0	0	
<i>Smartomyia arena</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	
<i>Smartomyia obscura</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	
<i>Tamno rufa</i>	1	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	
<i>Tanyconops longicaudus</i>	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	0	
<i>Tropidomyia alexanderi</i>	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	1	1	0	0	
<i>Tropidomyia aureifacies</i>	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Tropidomyia bimaculata</i>	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Tropidomyia ornata</i>	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Tropidomyia sp</i>	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	
<i>Baruerzodion steyskali</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	
<i>Dalmanina aculeata</i>	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	
<i>Dalmanina nigriceps</i>	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Dalmanina vitiosa</i>	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Parazodion schmidt</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	
<i>Parazodion sp</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	
<i>Pseudomyopa camrasi</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	
<i>Carbonosicus carbonarius</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Melanosoma bicolor</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Melanosoma hyalipenne</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Myopa buccata</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	
<i>Myopa clausa</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Myopa occulta</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	
<i>Myopa vesiculosa</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Myopa sp</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Myopotta pallipes</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Myopotta rubripes</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Paramyopa oestracea</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Pseudoconops antennatus</i>	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	
<i>Robertsonomyia mexicana</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
<i>Robertsonomyia palpalis</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
<i>Robertsonomyia parva</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
<i>Robertsonomyia pearsoni</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
<i>Scatocemyia plaurmanni</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Sicus abdominalis</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Sicus ferrugineus</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Thecophora africana</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Thecophora atra</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Thecophora australiana</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Thecophora metallica</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Thecophora modesta</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Thecophora occidentalis</i>	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
<i>Zodiomyia sumba</i>																								

Table 5.3. Continued. Characters 24-46.

[illegible]

Table 5.3. Continued. Characters 47-69.

Species	4 7	4 8	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8	5 9	6 0	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9
<i>Abrachyglossum capitatum</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Archiconops insularis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Archiconops pseudoerythrocephalus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Atrichopana curticornis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Atrichopana</i> sp A	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Atrichopana</i> sp B	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Australoconops perbellum</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Australoconops phaeomeros</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Australoconops uncinatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Brachyceraea brevicornis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Caenoconops bicolor</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Caenoconops claripennis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Caenoconops fredbergi</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Camrasiconops ater</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Chrysiomyia hirsuta</i>	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1
<i>Chrysiomyia rufa</i>	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1
<i>Chrysiomyia rugifrons</i>	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1
<i>Conops (Asiconops) ater</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Asiconops) aureomaculatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Asiconops) australianus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Asiconops) chinensis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Asiconops) nubeculosus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Ceratoconops) ornatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Conops) flavipes</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Conops (Conops) nigripes</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Conops (Conops) verus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Conops) vesicularis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Conops (Diconops) geminatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Diconops) trichus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Smithiconops) guineensis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Smithiconops) rondanii</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Sphenococonops) brunneosenceus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Conops (Sphenococonops) nobilis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Dacops abdominalis</i>	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Dacops kaplanae</i>	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Euconops bellus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Heteroconops antennatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Heteroconops gracilis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Heteroconops</i> sp	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Jelte neotropica</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Leopoldius coronatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Leopoldius signatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Mallachoconops atratulus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Microconops nigrithorax</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Microconops ornatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Microconops similis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Microconops tasmaniensis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Neobrachyceraea elongata</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Neobrachyceraea obscuripennis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Neoconops brevistylus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Neoconops longicornis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Physocephala bimarginipennis</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Physocephala maculipes</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Physocephala madagascanensis</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Physocephala marginata</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Physocephala rufipes</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Physocephala tibialis</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Physoconops (Aconops) antennatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Aconops) costatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Aureoconops) aureolus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Gyroconops) abbreviatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Physoconops (Gyroconops) parvus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Physoconops (Gyroconops) sylvosus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Physoconops (Kroeberoconops) argentinus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Kroeberoconops) hermanni</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Kroeberoconops) rufipennis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1

Table 5.3. Continued. Characters 47-69.

Species	4 7	4 8	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8	5 9	6 0	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9
<i>Physoconops (Pachyconops) brachyrhynchus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Pachyconops) bulbirostris</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Pachyconops) guianicus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Physoconops) discalis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Physoconops) fronto</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Physoconops) microvalvus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Physoconops (Physoconops) obscuripennis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops (Physoconops) sepulchralis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Physoconops (Shannonconops) apicalis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops notatifrons</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Physoconops quadripunctatus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Physoconops rhodesiensis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Pleurocerina brevis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Pleurocerina fasciata</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Pleurocerina longicornis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Pleurocerina luteiceps</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Pleurocerina turneri</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Pleurocerina vespiformis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
<i>Pleurocernella albohalterata</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Pleurocernella copelandi</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Pleurocernella srilankai</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Pleurocernella tibialis</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Pleurocernella sp</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Pseudophysocephala constricta</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1
<i>Pseudophysocephala platycephala</i>	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	1
<i>Setosiconops epixanthus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Setosiconops robustus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Siniconops elegans</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Smartomyia arena</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Smartomyia obscura</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Tammo rufa</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1
<i>Tanyconops longicaudus</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Tropidomyia alexanderi</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Tropidomyia aureifacies</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Tropidomyia bimaculata</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Tropidomyia ornata</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Tropidomyia sp</i>	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1
<i>Baruerizodion steyskali</i>	0	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1
<i>Dalmanina aculeata</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Dalmanina nigriceps</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Dalmanina vitiosa</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Parazodion schmidtii</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Parazodion sp</i>	2	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Pseudomyopa camrasi</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Carbonosicus carbonarius</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Melanosoma bicolor</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Melanosoma hyalipenne</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopa buccata</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopa clausa</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopa occulta</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopa vesiculosa</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopa sp</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopotta pallipes</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Myopotta rubripes</i>	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Paramyopa oestracea</i>	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Pseudoconops antennatus</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Robertsonomyia mexicana</i>	2	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Robertsonomyia palpalis</i>	2	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Robertsonomyia parva</i>	2	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Robertsonomyia pearsoni</i>	2	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Scatocernomyia plaumanni</i>	1	1	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1
<i>Sicus abdominalis</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Sicus ferrugineus</i>	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
<i>Thecophora africana</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Thecophora atra</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Thecophora australiana</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Thecophora metallica</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Thecophora modesta</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Thecophora occidensis</i>	1	1	1	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1
<i>Zodiomyia sumbaensis</i>	2	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1

Table 5.3. Continued. Characters 47-69.

Species	4 7	4 8	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8	5 9	6 0	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9
<i>Zodion cinereum</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Zodion erythrurum</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Zodion fulvifrons</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Zodion griseum</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Zodion intermedium</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Zodion pictum</i>	2	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1
<i>Notoconops alexanderi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Stylogaster biannulata</i>	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Stylogaster breviventrīs</i>	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>Stylogaster decorata</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1
<i>Stylogaster frauci</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Stylogaster inca</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1
<i>Stylogaster neglecta</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1
<i>Stylogaster pauliani</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Stylogaster rectinervis</i>	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1
<i>Stylogaster stylata</i>	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Stylogaster westwoodi</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Stylogaster sp</i>	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Lonchoptera tristis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conicera (Conicera) dauci</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Toxomerus marginata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
<i>Minettia lupulina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Chyliza scrobiculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
<i>Pyrgota undata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0
<i>Strongylophthalmyia angustipennis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0

Table 5.3. Continued. Characters 70-92.

Species	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9	
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
<i>Abrachyglossum capitatum</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Archiconops insularis</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	1	?	?	?	?	?	?	?	?	
<i>Archiconops pseudoerythrocephalus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	1	0	0	0	1	1	1	1	0	
<i>Atrichopana curticornis</i>	1	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Atrichopana</i> sp A	1	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Atrichopana</i> sp B	0	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Australoconops perbellum</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	1	0	0	1	1	1	1	0	
<i>Australoconops phaeomeros</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	1	0	0	1	1	1	1	0	
<i>Australoconops uncinatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	1	0	0	1	1	1	1	0	
<i>Brachyceraea brevicornis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Caenoconops bicolor</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Caenoconops claripennis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Caenoconops friedbergi</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Camrasiconops ater</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Chrysiatomyia hirsuta</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Chrysiatomyia rufa</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Chrysiatomyia rugifrons</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Asiconops) ater</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Asiconops) aureomaculatus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Asiconops) australianus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Asiconops) chinensis</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Conops (Asiconops) nubeculosus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Ceratconops) ornatus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Conops (Conops) flavipes</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Conops) nigripes</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Conops) verus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Conops (Conops) vesicularis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Diconops) geminatus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Diconops) trichus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Smithiconops) guineensis</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Conops (Smithiconops) rondanii</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Sphenconops) brunneosensceus</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Conops (Sphenconops) nobilis</i>	0	1	1	0	0	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Dacops abdominalis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Dacops kaplanae</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Euconops bellus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Heteroconops antennatus</i>	1	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	
<i>Heteroconops gracilis</i>	1	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	
<i>Heteroconops</i> sp	1	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	
<i>Jelte neotropica</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Leopoldius coronatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Leopoldius signatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Mallachoconops atratulus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Microconops nigrithorax</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Microconops ornatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Microconops similis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Microconops tasmaniensis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Neobrachyceraea elongata</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Neobrachyceraea obscuripennis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	?	?	?	?	?	
<i>Neoconops brevistylus</i>	0	1	1	0	0	1	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	?	
<i>Neoconops longicornis</i>	0	1	1	0	0	1	1	0	1	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Physocephala bimarginipennis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physocephala maculipes</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physocephala madagascariensis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physocephala marginata</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physocephala rufipes</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physocephala tibialis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Aconops) antennatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Aconops) costatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Aureoconops) aureolus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Physoconops (Gyroconops) abbreviatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Gyroconops) parvus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Gyroconops) sylvosus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Kroeberoconops) argentinus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?	?	
<i>Physoconops (Kroeberoconops) hermanni</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	
<i>Physoconops (Kroeberoconops) rufipennis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	0	

Table 5.3. Continued. Characters 70-92.

Species	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	9	9	9
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
<i>Physoconops (Pachyconops) brachyrhynchus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Pachyconops) bulbirostris</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Pachyconops) guianicus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Physoconops) discalis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Physoconops) fronto</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Physoconops) microvalvus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Physoconops) obscuripennis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops (Physoconops) sepulchralis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?
<i>Physoconops (Shannonconops) apicalis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops notatifrons</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Physoconops quadripunctatus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	?	?	?	?	?
<i>Physoconops rhodesiensis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocerina brevis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocerina fasciata</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocerina longicornis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocerina luteiceps</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocerina turneri</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocerina vespiformis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocennella albohalterata</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocennella copelandi</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?
<i>Pleurocennella srilankai</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?
<i>Pleurocennella tibialis</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pleurocennella sp</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?
<i>Pseudophysocephala constricta</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Pseudophysocephala platycephala</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Setosiconops epixanthus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	?	?	?	?	?	?	?
<i>Setosiconops robustus</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Siniconops elegans</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Smartiomyia arena</i>	1	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Smartiomyia obscura</i>	1	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tamno rufa</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tanyconops longicaudus</i>	1	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tropidomyia alexanderi</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tropidomyia aureifacies</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tropidomyia bimaculata</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tropidomyia ornata</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Tropidomyia sp</i>	0	1	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1
<i>Baruerizodion steyskali</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dalmannia aculeata</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dalmannia nigriceps</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dalmannia vitiosa</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Parazodion schmidtii</i>	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0
<i>Parazodion sp</i>	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0
<i>Pseudomyopa camrasi</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	?	?	?	?	?	?	?
<i>Carbonosicus carbonarius</i>	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1
<i>Melanosoma bicolor</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Melanosoma hyalipenne</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Myopa buccata</i>	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1
<i>Myopa clausa</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Myopa occulta</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Myopa vesiculosa</i>	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1
<i>Myopa sp</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Myopotta pallipes</i>	0	1	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Myopotta rubripes</i>	0	1	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Paramyopa oestracea</i>	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Pseudoconops antennatus</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Robertsonomyia mexicana</i>	0	1	1	0	0	1	1	0	1	1	1	0	1	0	0	0	0	1	1	?	?
<i>Robertsonomyia palpalis</i>	0	1	1	0	0	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1
<i>Robertsonomyia parva</i>	0	1	1	0	0	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1
<i>Robertsonomyia pearsoni</i>	0	1	1	0	0	1	1	0	1	1	1	0	1	0	0	0	0	1	1	1	1
<i>Scatocermomyia plaumanni</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	?	?	?	?	?	?	?
<i>Sicus abdominalis</i>	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Sicus ferrugineus</i>	0	1	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Thecophora africana</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Thecophora atra</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Thecophora australiana</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Thecophora metallica</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Thecophora modesta</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Thecophora occidensis</i>	0	1	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>Zodiomyia sumbaensis</i>	0	1	1	0	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1

Table 5.3. Continued. Characters 93-117.

Species	9	9	9	9	9	9	9	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	
<i>Abrachyglossum capitatum</i>	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Archiconops insularis</i>	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	1	0	1	0	0	1	1	0	1	
<i>Archiconops pseudoerythrocephalus</i>	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	1	
<i>Atrichopana curticornis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Atrichopana</i> sp A	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Atrichopana</i> sp B	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Australoconops perbellum</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Australoconops phaeomeros</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Australoconops uninctus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Brachyceraea brevicornis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Caenoconops bicolor</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1
<i>Caenoconops claripennis</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Caenoconops friedbergi</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1
<i>Camrasiconops ater</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Chrysiomyia hirsuta</i>	0	0	0	1	0	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Chrysiomyia rufa</i>	0	0	0	1	0	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Chrysiomyia rugifrons</i>	0	0	0	1	0	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Conops (Asiconops) ater</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Asiconops) aureomaculatus</i>	0	0	?	1	0	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Asiconops) australianus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Asiconops) chinensis</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Asiconops) nubeculosus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Ceratoconops) ornatus</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Conops) flavipes</i>	0	0	0	1	0	1	0	1	0	1	1	1	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Conops) nigripes</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	1	0	0	0	1	1	0	1	
<i>Conops (Conops) verus</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Conops) vesicularis</i>	0	0	0	1	0	1	0	1	0	1	1	1	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Diconops) geminatus</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Conops (Diconops) trichus</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Conops (Smithiconops) guineensis</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1
<i>Conops (Smithiconops) rondanii</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Conops (Sphenconops) brunneosericeus</i>	0	0	0	1	0	1	0	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Conops (Sphenconops) nobilis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Dacops abdominalis</i>	0	1	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Dacops kaplanae</i>	0	1	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Euconops bellus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Heteroconops antennatus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Heteroconops gracilis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Heteroconops</i> sp	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0	
<i>Jelte neotropica</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Leopoldius coronatus</i>	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Leopoldius signatus</i>	1	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Mallachoconops atratulus</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Microconops nigrithorax</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Microconops ornatus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Microconops similis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Microconops tasmaniensis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	
<i>Neobrachyceraea elongata</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Neobrachyceraea obscuripennis</i>	?	?	?	1	0	?	?	?	?	?	?	0	0	1	1	0	1	0	1	0	0	1	1	0	1	
<i>Neoconops brevistylus</i>	0	0	0	1	0	?	?	?	?	?	?	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0
<i>Neoconops longicornis</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	1	0	1	0	0	1	1	0	0
<i>Physocephala bimarginipennis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physocephala maculipes</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physocephala madagascariensis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physocephala marginata</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physocephala rufipes</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physocephala tibialis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physoconops (Aconops) antennatus</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physoconops (Aconops) costatus</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physoconops (Aureoconops) aureolus</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1
<i>Physoconops (Gyroconops) abbreviatus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physoconops (Gyroconops) parvus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physoconops (Gyroconops) sylvosus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	0	1	0	0	1	1	0	1	
<i>Physoconops (Kroeberoconops) argentinus</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1
<i>Physoconops (K</i>																										

Table 5.3. Continued. Characters 93-117.

Species	9 3	9 4	9 5	9 6	9 7	9 8	9 9	0 0	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9
<i>Physoconops (Pachyconops) brachyrhynchus</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	1	0
<i>Physoconops (Pachyconops) bulbirostris</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	1	1	0	1	0	1	0
<i>Physoconops (Pachyconops) guianicus</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Physoconops (Physoconops) discalis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	1	0	1	0	1	1	0	1
<i>Physoconops (Physoconops) fronto</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Physoconops (Physoconops) microvalvus</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1
<i>Physoconops (Physoconops) obscuripennis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	1	1	0	1
<i>Physoconops (Physoconops) sepulchralis</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	1	1	0	0	1	0	0	1	1	0	1
<i>Physoconops (Shannonconops) apicalis</i>	?	0	0	?	?	?	?	?	?	?	0	0	1	1	0	1	1	0	1	0	0	0	1	1	0	1	0
<i>Physoconops notatitrons</i>	0	0	0	1	0	1	0	1	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Physoconops quadripunctatus</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0
<i>Physoconops rhodesiensis</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Pleurocerina brevis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0
<i>Pleurocerina fasciata</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Pleurocerina longicornis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Pleurocerina luteiceps</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Pleurocenna turneri</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Pleurocenna vesiformis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Pleurocennella albohalterata</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Pleurocennella copelandi</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	1	1	0	1	0	1
<i>Pleurocennella snlankai</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Pleurocennella tibialis</i>	0	0	0	1	0	1	0	1	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pleurocennella sp</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	1	1	0	1	0	1
<i>Pseudophysocephala constricta</i>	0	0	1	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Pseudophysocephala platycephala</i>	0	0	1	1	0	?	?	?	?	?	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Setosiconops epixanthus</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	1	1	0	0	1	0
<i>Setosiconops robustus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?
<i>Siniconops elegans</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0
<i>Smartomyia arena</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Smartomyia obscura</i>	0	0	0	1	0	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
<i>Tamno rufa</i>	0	0	0	1	0	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Tanyconops longicaudus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	?	?	?	?	?	?
<i>Tropidomyia alexanderi</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	1
<i>Tropidomyia aureifacies</i>	0	0	0	1	0	?	?	?	?	?	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Tropidomyia bimaculata</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Tropidomyia ornata</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Tropidomyia sp</i>	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>Baruerizodion steyskali</i>	0	0	0	1	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dalmannia aculeata</i>	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dalmannia nigriceps</i>	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dalmannia vitiosa</i>	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Parazodion schmidtii</i>	0	0	0	1	2	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Parazodion sp</i>	0	0	0	1	2	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Pseudomyopa camrasi</i>	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Carbonosiscus carbonarius</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Melanosoma bicolor</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Melanosoma hyalipenne</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Myopa buccata</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Myopa clausa</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Myopa occulta</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Myopa vesiculosa</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Myopa sp</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Myopotta pallipes</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Myopotta rubripes</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Paramyopa oestracea</i>	0	0	0	1	3	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Pseudoconops antennatus</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Robertsonomyia mexicana</i>	?	?	?	0	1	0	?	?	?	?	?	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
<i>Robertsonomyia palpalis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Robertsonomyia parva</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Robertsonomyia pearsoni</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0
<i>Scatocernyia plaumanni</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Sicus abdominalis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Sicus ferrugineus</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
<i>Thecophora africana</i>	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Thecophora atra</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Thecophora australiana</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Thecophora metallica</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Table 5.3. Continued. Characters 93-117.

	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1															
Species	9 3	9 4	9 5	9 6	9 7	9 8	9 9	0 0	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8
<i>Thecophora modesta</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Thecophora occidentis</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Zodiomyia sumbaensis</i>	0	0	0	1	0	1	0	1	0	1	?	?	?	?	?	?
<i>Zodion cinereum</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Zodion erythrurum</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Zodion fulvifrons</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Zodion gnseum</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Zodion intermedium</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Zodion pictum</i>	0	0	0	1	0	1	0	1	0	1	0	0	0	1	0	1
<i>Notoconops alexanderi</i>	?	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0
<i>Stylogaster biannulata</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Stylogaster breviventris</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Stylogaster decorata</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Stylogaster frauci</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Stylogaster inca</i>	0	0	0	0	0	1	1	0	1	0	?	?	?	?	?	?
<i>Stylogaster neglecta</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Stylogaster pauliani</i>	0	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0
<i>Stylogaster rectinervis</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Stylogaster stylata</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Stylogaster westwoodi</i>	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Stylogaster sp</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Lonchoptera tristis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Conicera (Conicera) dauci</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Toxomerus marginata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Minettia lupulina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chyliza scrobiculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pyrgota undata</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Strongylophthalmyia angustipennis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

See text for description of characters and states. ? – character state unknown.

Figures

Fig. 3.1. Phylogenetic hypotheses of schizophoran relationships including examples of Conopidae. ** Syrphidae is not classified under Schizophora although it was recovered as such in Han et al., 2002.

Fig. 3.2. Single most parsimonious cladogram generated from combined COI, cytB, 12S, 28S, AATS, CAD, EF1a, PGD, TPI, and *white* DNA sequence data (treelength=10,204, CI=0.464, RI=0.373). nt3 weighted to zero and gaps coded as a fifth base. Numbers above nodes represent - number of node. Total Bremer support/jackknife support value. Taxon labels include superfamily:family classifications according to McAlpine, 1989. ** indicates the sole representative of Calyptratae included, remaining schizophoran taxa are classified under Acalyptratae (McAlpine, 1989).

Fig. 3.3. Majority rule consensus cladogram of Bayesian Markov Chain Monte Carlo analysis (20,000,000 generations) of combined COI, cytB, 12S, 28S, AATS, CAD, EF1a, PGD, TPI, and *white* DNA sequence data, including branch lengths. Numbers at each node represent posterior probabilities. Taxon labels include superfamily:family classifications according to McAlpine, 1989. ** indicates the sole representative of Calyptratae included; remaining schizophoran taxa are classified under Acalyptratae (McAlpine, 1989).

Fig. 3.4. Congruent topological information (CTI) of data subset most parsimonious tree compared to total evidence most parsimonious tree (See section 3.2.5. for CTI calculation). CTI calculated for: "All nodes" - all nodes in total evidence tree (nodes 1-25). "Within Conopidae" - nodes containing only Conopidae (nodes 1-9). "Outside Conopidae" - nodes not containing only Conopidae (nodes 10-25).

Fig. 4.1. *Camrasiconops ater* (A) female abdomen and terminalia, lateral view; (B) male abdomen and terminalia, lateral view; (C) dissected male internal terminalia, ventral view. Abbreviations: dbr hypd – dorsal bridge of hypandrium; epand – epandrium; hypd arm – hypandrial arm; pgt – postgonite; phapod – phallapodeme; sgt – segment; st – sternite; syntrgst – syntergosternite; tg – tergite; vgp – ventral genital plate. Scale bars 500 microns.

Fig. 4.2. *Stylogaster biannulata*. (A) female abdomen and terminalia, lateral view; (B) male abdomen and terminalia, lateral view; (C) dissected male internal terminalia, lateral view. Abbreviations: ej apod – ejaculatory apodeme; epand – epandrium; hypd – hypandrium; llb – lateral lobes; pregt – pregonite; phapod – phallapodeme; pos sur – posterior surstyli; sgt – segment; spm dt – sperm duct; st – sternite; syntrgst – syntergosternite. Scale bars 500 microns.

Fig. 4.3. *Dalmannia nigriceps*. (A) female abdomen and terminalia, lateral view; (B) male abdomen and terminalia, lateral view. Abbreviations: epand – epandrium; hypd – hypandrium; phapod – phallapodeme; sgt – segment; st – sternite; syntg – syntergite; syntrgst – syntergosternite. Scale bars 500 microns.

Fig. 4.4. *Parazodion schmidtii*. (A) female abdomen and terminalia, lateral view; (B) male abdomen and terminalia, lateral view; (C) dissected male internal terminalia, ventral view. Abbreviations: epand – epandrium; hypd arm – hypandrial arm; hyprct – hypoproct; phapod – phallapodeme; pos sur – posterior surstyli; sgt – segment; st – sternite; syntg – syntergite. Scale bar for (A) 500 microns. Other scale bars 200 microns.

Fig. 4.5. *Thecophora modesta* (A) female abdomen and terminalia, lateral view; (B) male abdomen and terminalia, lateral view; (C) dissected male internal terminalia, ventral view. Abbreviations: epand – epandrium; hypd – hypd – hypandrium; hypd plt – hypandrial plate; pgt – postgonite; phapod – phallapodeme; sgt – segment; st – sternite – syntg – syntergite; syntrgst – syntergosternite; tg – tergite. All scale bars 500 microns.

Fig. 4.6. Single most parsimonious cladogram generated from combined 28S, 12S, COI, CytB, and AATS sequence data and 113 morphological characters, nt3 weighted to zero, gaps coded as a fifth base (length 12,985; CI - 0.375; RI - 0.655). Numbers above nodes represent the node number corresponding to node support data in Table 4.3. A large 'X' represents nodes recovered with JKS >64% and TBS >3. Black boxes represent morphological autapomorphies, with character number above and state below.

Fig. 5.1A. One of 47 most parsimonious cladograms (length - 218, CI - 0.550, RI - 0.957).

Support values for each node are given (boot above; TBS below; boot >50% and TBS >1 are depicted as -). Taxon names are depicted in their previously accepted combinations. Character state transformation illustrated. Boxes depicted have character number above and state below. Black boxes represent uniquely derived states, white boxes represent homoplasious states and subsequent transformations. Character states for individual outgroup taxa not depicted. Newly proposed subfamily and tribal classifications given at top. Continued in Fig. 5.1B on next page.

Fig. 5.1B. Continued.

Fig. 5.2. Stylogastrinae – *Stylogaster rectinervis* ♀ (A) lateral habitus ; (B) head; (C) wing. Abbreviations: am sbrcav – anterior margin of subcranial cavity; ar – arista; fcar – facial carina; lbl – labella; premnt – prementum; st 8 lb – lateral lobes on sternite 8; sgt – segment.

Fig. 5.3. Sicinae – *Sicus ferrugineus* ♂ (A) lateral habitus; (B) wing; (C) head; (D) lateral postabdomen; (E) lateral pleural sclerites. Abbreviations: anepm – anepimeron; anepst – anepisternum; ffov – facial fovea; kepst – katepisternum; plp – maxillary palpus; prepm – proepimeron; prepst – proepisternum; st 8 – sternite 8.

Fig. 5.4. Sicinae – *Carbonosicus carbonarius* ♂ (A) lateral habitus; (B) head.

Fig. 5.5. Dalmanniinae – *Baruerizodion steyskali* ♀ (A) lateral habitus; (B) lateral postabdomen; (C) ventral head and thorax.

Fig. 5.6. Dalmanniinae – *Dalmannia nigriceps* ♀ (A) lateral habitus; (B) wing; (C) head.

Fig. 5.7. Myopinae – Myopini - *Paramyopa oestracea* ♀ (A) lateral habitus; (B) postabdomen.

Fig. 5.8. Myopinae – Myopini - *Melanosoma bicolor* ♀ (A) lateral habitus; (B) head.

Fig. 5.9. Myopinae – Myopini - *Pseudomyopa camrasi* ♂ (A) lateral habitus; (B) wing.

Fig. 5.10. Myopinae – Myopini - *Myopa vesiculosa* ♂ (A) lateral habitus; (B) head; (C) lateral postabdomen; (D) wing.

Fig. 5.11. Myopinae – Myopini - *Myopotta rubripes* ♂ (A) lateral habitus; (B) head; (C) lateral postabdomen. Abbreviation: frfac sp – fronto-facial spot.

Fig. 5.12. Myopinae – Thecophorini - *Pseudoconops antennatus* ♀ lateral habitus. Abbreviations: plp – maxillary palp; tg 2 – tergite 2.

Fig. 5.13. Myopinae – Thecophorini – *Scatoccemyia plaumanni* ♂ (A) lateral habitus; (B) lateral postabdomen.

Fig. 5.14. Myopinae – Thecophorini – *Thecophora occidentis* ♂ (A) lateral habitus; (B) lateral postabdomen; (C) wing.

Fig. 5.15. Zodioninae - *Parazodion schmidtii* ♀ (A) lateral habitus; (B) head.

Fig. 5.16. Zodioninae - *Zodion cinereum* ♀ (A) lateral habitus; (B) head; (C) wing.

Fig. 5.17. Zotioninae – *Robertsonomyia pearsoni* ♀ (A) lateral habitus; (B) head.

Fig. 5.18. Zotioninae – *Zodiomyia sumbaensis* ♀ (A) lateral habitus; (B) head.

Fig. 5.19. Conopinae – *Euconops bellus* ♀ (A) lateral habitus; (B) dorsal head and thorax.

Fig. 5.20. Conopinae – Asiconopini – *Archiconops insularis* ♂ (A) lateral habitus; (B) ventral head and thorax; (C) wing.

Fig. 5.21. Conopinae – Asiconopini – *Smithiconops rondanii* ♀ (A) lateral habitus; 8mm

Fig. 5.22. Conopinae – Asiconopini – *Asiconops (Aegloconops) quadripunctatus* ♂ (A) lateral habitus; (B) head 9mm

Fig. 5.23. Conopinae – Pleurocerini - *Pleurocerina fasciata* ♀ (A) lateral habitus; (B) head; (C) wing.

Fig. 5.24. Conopinae – Pleurocerini – *Camrasiconops ater* ♂ (A) lateral habitus.

Fig. 5.25. Conopinae – Pleurocerini – *Callosiconops rugifrons* ♂ (A) lateral habitus; (B) lateral thorax.

Fig. 5.26. Conopinae – Pleurocerini – *Atrichoparia* sp. A ♂ lateral habitus.

Fig. 5.27. Conopinae – Pleurocerini – *Neoconops brevistylus* ♂ (A) lateral habitus; (B) face.

Fig. 5.28. Conopinae – Pleurocerini – *Smartiomyia obscura* ♂ (A) lateral habitus; (B) dorsal head.

Fig. 5.29. Conopinae – Pleurocerini – *Setosiconops robustus* ♀ (A) lateral habitus; (B) head.

Fig. 5.30. Conopinae – Pleurocerini - *Tanyconops longicaudus* ♀ lateral habitus.

Fig. 5.31. Conopinae – Pleurocerini – *Heteroconops gracilis* ♀ lateral habitus.

Fig. 5.32. Conopinae – *Mallachoconops atratulus* ♀ (A) lateral habitus; (B) dorsal head.

Fig. 5.33. Conopinae – Siniconopini – *Siniconops nigripes* ♂ (A) lateral habitus; (B) dorsal head.

Fig. 5.34. Conopinae – Brachyceraeini – *Neobrachyceraea elongata* ♀ (A) lateral habitus; (B) face; (C) dorsal head.

Fig. 5.35. Conopinae – Brachyceraeini – *Brachyceraea brevicornis* ♀ (A) lateral habitus; (B) dorsal head.

Fig. 5.36. Conopinae – Caenoconopini – *Caenoconops bicolor* ♂ (A) lateral habitus; (B) dorsal head.

Fig. 5.37. Conopinae – Physocephalini – *Dacops abdominalis* ♀ (A) lateral habitus; (B) lateral abdomen.

Fig. 5.38. Conopinae – Physocephalini – *Pseudophysocephala constricta* ♀ (A) lateral habitus; (B) dorsal abdomen.

Fig. 5.39. Conopinae – Physocephalini – *Physocephala marginata* ♂ (A) lateral habitus; (B) head.

Fig. 5.40. Conopinae – Tropidomyiini – *Tropidomyia ornata* ♂ (A) lateral habitus; (B) lateral head; (C) wing.

Fig. 5.41. Conopinae – Tropidomyiini – *Schedophysoconops notatifrons* ♀ (A) lateral habitus; (B) head; (C) wing.

Fig. 5.42. Conopinae – Tropicomyiini – *Physoconops (Aconops) costatus* ♀ (A) lateral habitus; (B) dorsal head.

Fig. 5.43. Conopinae – Conopini – *Conops vesicularis* ♂ (A) lateral habitus; (B) dorsal abdomen; (C) dorsal head.

Fig. 5.44. Conopinae – Conopini – *Abrachyglossum capitatum* ♂ (A) lateral habitus; (B) head.

Fig. 5.45. Conopinae – Conopini – *Leopoldius signatus* ♀ (A) lateral habitus; (B) head; (C) ventral abdomen.

Fig. 5.46. Conopinae –
Pleurocerinellini – *Tammo rufus* ♂
lateral habitus.

Fig. 5.47. Conopinae –
Pleurocerinellini – *Pleurocerinella*
albohalterata ♂ lateral habitus.

Fig. 5.48. Conopinae – Gyroconopini – *Gyroconops parvus* ♀ (A) lateral habitus; (B)
dorsal head; (C) wing.

Fig. 5.49. Conopinae – Microconopini – *Microconops ornatus* ♂ (A) lateral habitus; (B) head.

Fig. 5.50. Conopinae – Microconopini – *Australoconops perbellum* ♀ (A) lateral habitus; (B) wing.