

Phylogeny of Polycentropodidae Ulmer, 1903 (Trichoptera : Annulipalpia : Psychomyioidea) inferred from larval, pupal and adult characters

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Abstract. Phylogeny of Polycentropodidae Ulmer is inferred based on data from immature and adult stages. Larval information is unknown for 61% of the taxa included in this study. To understand the effects of including characters with large sets of missing data, three alternative datasets were analysed using parsimony and Bayesian methods. Five outgroup taxa, including the four families in Psychomyioidea and the single family in Hydropsychoidea, were used in all datasets. Monophyly of Polycentropodidae, as currently defined, was rejected and the monophyly of the three largest cosmopolitan genera, *Polycentropus*, *Polyplectropus* and *Nyctiophylax*, was not confirmed. Monophyly of Pseudoneureclipsinae, including the genera *Antillopsyche* and *Pseudoneureclipsis*, was supported in all analyses. The placement of *Pseudoneureclipsis* within Dipseudopsidae was rejected. Monophyly of Kambaitipsychinae was supported, but its placement within Polycentropodidae was not confirmed. Analyses were sensitive to either inclusion or exclusion of characters from immature stages. Based on the results of these analyses, the following taxonomic changes are established: Kambaitipsychidae, **stat. nov.** and Pseudoneureclipsidae, **stat. nov.** are elevated to family status. North American *Polycentropus* species originally described in either *Plectrocnemia* or *Holocentropus* are returned to their original combinations and North American species described in *Polycentropus* post-1944 are transferred to either *Holocentropus* or *Plectrocnemia*. The following new or reinstated combinations are proposed: *Plectrocnemia albipuncta* Banks, **comb. rev.**; *Plectrocnemia aureola* Banks, **comb. rev.**; *Plectrocnemia cinerea* (Hagen), **comb. rev.**; *Plectrocnemia clinei* Milne, **comb. rev.**; *Plectrocnemia crassicornis* (Walker), **comb. rev.**; *Plectrocnemia jenula* (Denning) **comb. nov.**; *Plectrocnemia icula* (Ross), **comb. nov.**; *Plectrocnemia nascotia* (Ross), **comb. nov.**; *Plectrocnemia remota* (Banks), **comb. rev.**; *Plectrocnemia sabulosa* (Leonard & Leonard), **comb. nov.**; *Plectrocnemia smithae* (Denning), **comb. nov.**; *Plectrocnemia vigilatrix* Navás, **comb. rev.**; *Plectrocnemia weedi* (Blickle & Morse), **comb. nov.**; *Holocentropus chellus* (Denning), **comb. nov.**; *Holocentropus flavus* Banks, **comb. nov.**; *Holocentropus glacialis* Ross, **comb. rev.**; *Holocentropus grellus* Milne, **comb. rev.**; *Holocentropus interruptus* Banks, **comb. rev.**; *Holocentropus melanae* Ross, **comb. rev.**; *Holocentropus milaca* (Etnier), **comb. nov.**; and *Holocentropus picicornis* (Stephens), **comb. rev.**

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Introduction

The cosmopolitan caddisfly family Polycentropodidae Ulmer, 1903b is one of the most diverse in the suborder Annulipalpia, with more than 650 species in 16 genera (Holzenthal *et al.* 2007b). The family has three subfamilies, Polycentropodinae Ulmer, 1903b, Pseudoneureclipsinae Ulmer, 1951 and Kambaitipsychinae Malicky, 1992 (Gibbs 1973; Malicky 1990; Malicky and Chantaramongkol 1993; Morse 1997). Traditional classification has been modified recently with the

transfer of Pseudoneureclipsinae to Dipseudopsidae Ulmer, 1904 (Li *et al.* 2001). However, this change in classification is not universally accepted (e.g. Mey 2006; Malicky 2007). Further, the establishment of Kambaitipsychinae within the family to accommodate the genus *Kambaitipsyche* Malicky, 1992 was tentative since it was first described (Malicky 1992). Additionally, monophyly of several cosmopolitan genera is uncertain (e.g. *Polyplectropus* Ulmer, 1903a, see Chamorro and Holzenthal 2010). Two genera, *Tasmanoplegas* Neboiss,

1977 and *Eodipseudopsis* Marlier, 1959, were recently synonymised with *Plectrocnemia* Stephens, 1836 and *Polyplectropus*, respectively (Oláh and Johanson 2010).

Like other annulipalpans, Polycentropodinae larvae construct silken retreats and are either filter-feeders (e.g. *Neureclipsis* McLachlan, 1864) or predators (e.g. *Polyplectropus*). Generally, polycentropodid larvae are found in flowing bodies of water where they attach their retreats in areas where the current is moderate to slow (Ross 1944; Wiggins 1996, 2004). Polycentropodinae larvae build silken retreats with variously shaped capture nets. For example, *Plectrocnemia* species build nets in the shape of a sac with a small tubular dwelling chamber, while species of *Neureclipsis* build funnel-shaped retreats with the posterior end becoming narrow and curved (Lepneva 1964, 1970). Other polycentropodids build fixed tubular retreats and use associated silk strands to detect vibrations of their prey, as in *Polyplectropus* and *Nyctiophylax* Brauer, 1865 (Flint 1964b; Wiggins 1996).

Pseudoneureclipsinae larvae are grazers (Flint 1964a, 1964b; Vieira-Lanero 2000; Tachet *et al.* 2001). *Pseudoneureclipsis* Ulmer, 1913 retreats resemble the branching tube-dwellings constructed by Dipseudopsidae with incorporated large sand grains and an inner reddish silk-coated wall (Vieira-Lanero 2000; Tachet *et al.* 2001). Larval feeding and retreat-making behaviours differ only slightly from species in the pseudoneureclipsine genus *Antillopsyche* Banks, 1941 (Flint, 1964b), whose behaviours mostly resemble those of the Psychomyiidae Walker, 1852. Polycentropodid larval biology has been reviewed by Lepneva (1964, 1970), Flint (1964a, 1964b), Wiggins (1996) and Tachet *et al.* (2001, for *Pseudoneureclipsis*). Immature stages remain unknown for Kambaitipsychinae and an additional six of the 16 polycentropodid genera. This information also remains unknown for all but a few species within each genus; therefore sets of characters are uncoded in this study for a large subset of taxa.

More than 30% of characters (36 immature characters) are missing for 29 (61%) exemplar taxa. Studies have shown that including all available data from as many character systems as possible improves the chances of inferring an accurate hypothesis of relationships, even when large amounts of missing data exist (Novacek 1992; Wiens 1998, 2003, 2006; Kearney 2002; Kearney and Clark 2003; Wiens *et al.* 2005). However, simulation studies also suggest that including highly incomplete data, that is, including taxa with numerous unknown characters or including features unknown for several taxa, may lead to poorly resolved trees and decreased accuracy (Wiens 2003). Including an abundance of missing data may not be problematic when the overall number of characters is high (e.g. thousands of base pairs); however, this may not hold true when the dataset combines an abundance of missing entries and an overall low number of informative characters (Wiens and Moen 2008); as in some morphological datasets. Accordingly, three partitions of the data were analysed under parsimony and Bayesian inference to understand how missing information influenced results.

We present the first thorough morphological assessment of the phylogeny of polycentropodid caddisflies based on 122

larval, pupal and adult characters across 54 taxa representing all traditionally recognised genera from all biogeographic regions. This study, particularly the character analysis and associated illustrations, will facilitate future studies in this and related families of caddisflies and will provide independent data and a starting point for molecular studies that are sure to follow.

Taxonomic history and phylogeny of Polycentropodidae

Taxonomic history

Polycentropodinae (as Polycentropinae) was first proposed by Ulmer (1903b) to include several genera described originally in Hydropsychidae Curtis, 1835. The subfamily included six genera with tricalcarate protibiae (three tibial spurs) described in the mid- to late 1800s from the West Palearctic region. Ulmer (1906) elevated Polycentropodinae to family-status and Brues and Melander (1915, not Tillyard 1926) emended the name Polycentropidae to Polycentropodidae. Traditionally, however, taxa with tricalcarate protibiae (Dipseudopsidae; Ecnomidae Ulmer, 1903b; Hyalopsychinae Lestage, 1925; Polycentropodidae; and Psychomyiidae) were placed under a single, broadly defined Psychomyiidae (Ross 1944; Riek 1970; Flint 1980, 1981, 1991). Lepneva (1956) presented evidence, based on larval, pupal and adult characters, in support of treating Polycentropodidae, Ecnomidae and Psychomyiidae as separate and mutually exclusive families. Several of the characters identified by Lepneva (1956) as separating psychomyiids and polycentropodids included differences in retreat construction (long and tubular 'fixed' cases in psychomyiids v. nets at the end of short silk tubes in polycentropodids), presence of secondary chaetotaxy and of 'special tracheal gills' in polycentropodid larvae, as well as differences in the overall organisation of the pupal body, especially mouthparts, breathing organs and anal appendages. Larval chaetotaxy was cited by Lepneva (1956) to be particularly different between ecnomids and polycentropodids. Treatment of Polycentropodidae as a separate family from Psychomyiidae and Ecnomidae is now broadly accepted (Ulmer 1951; Mosely and Kimmins 1953; Fischer 1962; Lepneva 1964, 1970; Ross 1967; Flint *et al.* 1999; Holzenthal *et al.* 2007a, 2007b).

Pseudoneureclipsinae was established in Polycentropodidae by Ulmer (1951) to include the Old World genus *Pseudoneureclipsis* (Fischer 1972). In 2001, Li *et al.* transferred *Pseudoneureclipsis* to Dipseudopsidae based on the results of their cladistic analysis. Pseudoneureclipsinae includes the Old World genus *Pseudoneureclipsis* and the Greater Antilles endemic *Antillopsyche* (Flint 1964b; Holzenthal *et al.* 2007b, Morse 2011), both having nearly identical immature stages. The placement of *Pseudoneureclipsis* in Dipseudopsidae has not been fully accepted (Malicky 2001, 2007; Malicky and Prommi 2006; Mey 2006) and is not corroborated by higher-level phylogenetic studies (Kjer *et al.* 2001, 2002; Holzenthal *et al.* 2007a). Recently, Johanson and Espeland (2010) found *Pseudoneureclipsis* to be more closely related to Ecnomidae and suggested elevating the subfamily to family status.

The latest subfamily included in Polycentropodidae is Kambaitipsychinae from South-east Asia, and includes a single genus, *Kambaitipsyche*. Malicky (1992) expressed

considerable difficulty placing the genus due to the presence of characters also found in several annulipalpi families. Among polycentropodids, the genus is unique in having a two-segmented male inferior appendage, cylindrical maxillary palpomere two, and a distal insertion of maxillary palpomere three into palpomere two (rather than preapically) among other characters.

The following 16 genera are currently recognised in Polycentropodidae (Holzenthal *et al.* 2007b): *Adeptophylax* Neboiss, 1982; *Cernotina* Ross, 1938; *Cyrnellus* Banks, 1913; *Cyrnodes* Ulmer, 1910; *Cyrnopsis* Martynov, 1935; *Cyrnus* Stephens, 1836; *Holocentropus* McLachlan, 1878; *Kambaitipsyche*; *Neucentropus* Martynov, 1907; *Neureclipsis*; *Neurocentropus* Navás, 1918 [*nomen dubium* (Malicky 2005) and not included in this study]; *Nyctiophylax*; *Pahamunaya* Schmid, 1958; *Plectrocnemia*; *Polycentropus* Curtis, 1835; and *Polyplectropus*. *Paranyctiophylax* Tsuda, 1942 is treated as a valid genus (Neboiss 1993, 1994; Malicky 2007) or as a subgenus of *Nyctiophylax* (Holzenthal *et al.* 2007b; Oláh and Johanson 2010; Morse 2011). Herein we treat *Paranyctiophylax* as a subgenus of *Nyctiophylax*. Finally, Ross (1944) synonymised *Holocentropus* and *Plectrocnemia* with *Polycentropus*; however, only American workers recognise this classification.

Extinct taxa

Polycentropodids are well represented in the fossil record with nine extinct genera and numerous fossil species in extant genera (e.g. *Holocentropus*, *Nyctiophylax*) (Fischer 1962, 1972; Oláh and Johanson 2010; Morse 2011). The oldest fossils attributed to Polycentropodidae were found in Late Jurassic and Early Cretaceous deposits from Russia, Mongolia and England (Sukatcheva 1993, 1999). Most fossil polycentropodid genera are from Tertiary deposits in the USA (Scudder 1890).

Hypothesised phylogenetic relationships of Polycentropodidae within Annulipalpia

Most of the taxa once considered subfamilies of either Hydropsychidae (*sensu* Ulmer 1903a), Polycentropodidae (*sensu* Ulmer 1903b, 1906), or Psychomyiidae (*sensu* Ross 1944) have been elevated to family status and classified, until recently, in the superfamily Hydropsychoidea Curtis, 1835 (i.e. Dipseudopsidae, Ecnomidae, Psychomyiidae, Polycentropodidae and Xiphocentronidae, in addition to Hydropsychidae). Recent studies find these families, exclusive of Hydropsychidae, to constitute a monophyletic group (Holzenthal *et al.* 2007a; Kjer *et al.* 2001, 2002), the Psychomyioidea Ivanov, 2002. In recent years, several hypotheses have been proposed regarding the relationships among the major families in Psychomyioidea (Ross and Gibbs 1973; Weaver and Malicky 1994; Frania and Wiggins 1997; Li and Morse 1997; Kjer *et al.* 2001, 2002; Ivanov 2002; Holzenthal *et al.* 2007a). Nonetheless, relative placement of Polycentropodidae within the superfamily has not been firmly established.

A sister relationship was proposed between dipseudopsids and polycentropodids by Ross and Gibbs (1973) based on the

possession of fused larval foretrochantins, one-segmented male inferior appendages and 'several similarities in the larvae.' Ross and Gibbs chose to retain Dipseudopsinae as a subfamily of Polycentropodidae to best express phylogenetic relationship and 'amount of evolutionary divergence' (Ross and Gibbs 1973: 315).

More recently, Weaver and Malicky (1994) inferred Dipseudopsidae phylogeny by analysing 24 morphological characters of larvae, males and females (Fig. 1A). Taxon sampling consisted of a generalised concept (groundplan) of each of the six dipseudopsid genera and for Ecnomidae, Polycentropodidae, Psychomyiidae, Xiphocentronidae and Hydropsychidae. The consensus of three equally parsimonious trees is shown in Fig. 1A.

Frانيا and Wiggins (1997) analysed 70 morphological characters across a representative sample of the order to determine the relationships among caddisfly suborders. Based on their results, ecnomids, xiphocentronids, psychomyiids and monophyletic polycentropodids + dipseudopsids formed a polytomy (Fig. 1B).

Ivanov (2002) included fossil psychomyioid †Dysoneuridae Sukatcheva, 1968 and †Electralbertidae Botosaneanu & Wichard, 1983 and several other fossil caddisfly species in extant genera in his study of Trichoptera phylogeny. Polycentropodidae formed a tritomy with Ecnomidae and †Electralbertidae, with monophyletic psychomyiids + xiphocentronids the sister group to this clade (Fig. 1E). The sister group to this large clade was either †Dysoneuridae or Dipseudopsidae.

Higher-level studies based on combined morphological and molecular data continue to place polycentropodids within Psychomyioidea; however, sister group relationships remain weakly supported and uncorroborated (Kjer *et al.* 2001, 2002; Holzenthal *et al.* 2007a). Holzenthal *et al.* (2007a) found Pseudoneureclipsinae to be the sister taxon to Polycentropodidae, with Xiphocentronidae + Psychomyiidae, Dipseudopsidae and Ecnomidae as successive sister taxa (Fig. 1D). Results of Kjer *et al.* (2002) and Holzenthal *et al.* (2007a) counter the transfer by Li *et al.* (2001) of Pseudoneureclipsinae to Dipseudopsidae.

Hypothesised phylogenetic relationships of genera within Polycentropodidae

Only one study of relationships among polycentropodid genera has been carried out to date. Neboiss (1993) conducted a phylogenetic analysis of polycentropodid genera with 3, 4, 4 tibial spur formula and lack of fork I in the forewing: *Adeptophylax*, *Cyrnellus*, *Cyrnodes*, *Cyrnopsis*, *Cyrnus*, *Nyctiophylax*, *Pahamunaya* and *Paranyctiophylax*. Generic concepts instead of actual species constituted terminal taxa in this analysis, thus determining monophyly *a priori*. Furthermore, all genera lacking fork I in the forewing having 3, 4, 4 tibial spur formula were assumed to be collectively monophyletic. His hypothesis of relationship was based on a subset of wing venation characters. Neboiss (1993) inferred the following relationships among taxa included in his analysis:

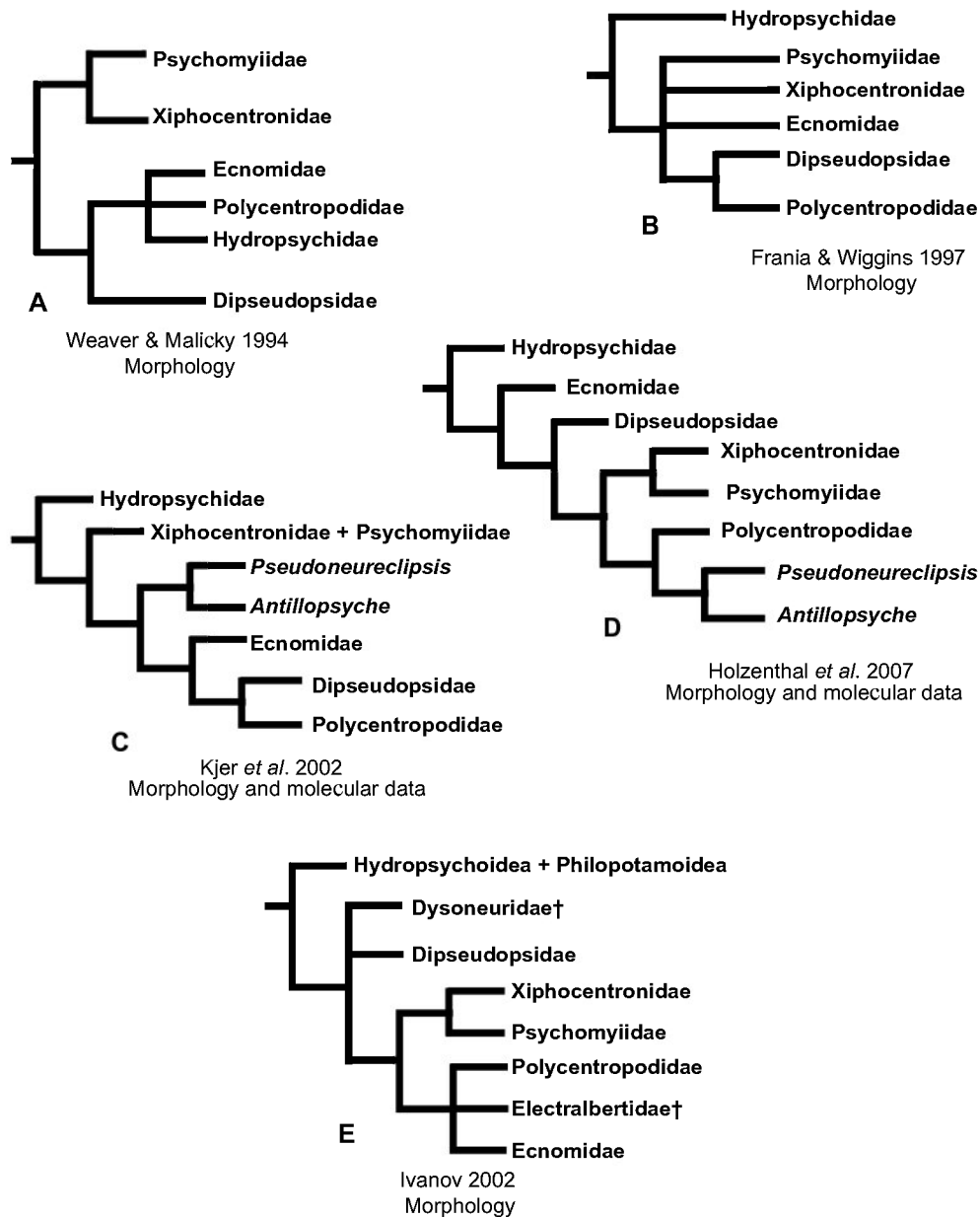


Fig. 1. Diagrammatic summary of previously published phylogenetic hypotheses of Psychomyioidea, including Polycentropodidae and related families.

Cyrnellus + ((*Pahamunaya* + *Cyrnodes*) + (*Adectophylax* ((*Nyctiophylax* + *Paranyctiophylax*) + (*Cyrnopsis* + *Cyrmus*))))).

Materials and methods

Specimen preparation

To observe male and female genitalic structures obscured by muscles and other soft tissues, abdomens were cleared using standard methods as outlined by Ross (1944) and expanded and explained in detail by Holzenthal and Andersen (2004). Protocols for clearing genitalic structures were slightly modified during the course of this research, having started with KOH and subsequently changing to hot 85% lactic acid (Blahnik *et al.*

2007). Lactic acid treatment was preferred because it almost always caused the phallic endothelial membranes to evert, rendering otherwise obscure structures more visible. Several specimens, particularly females, were stained with Chlorazole Black E (Fischer Scientific) to observe membranes and lightly sclerotised structures. Wing preparations followed standard protocols as outlined by Prather (2003) and Blahnik and Holzenthal (2004).

Morphological terminology

Terminology for head and thoracic setal warts follows Ivanov (1990) (Fig. 4.4). Terminology for male and female genitalia

follows Chamorro and Holzenthal (2010). Terminology for wing venation follows the Comstock–Needham system as interpreted for Trichoptera by Mosely and Kimmins (1953). Paired structures in the discussion below are referred to in singular form.

Taxon sampling

Exemplar species were coded for this study following the recommendations of Prendini (2001). However, since immature stages have been unequivocally associated with adults for only a handful of species within each genus, characters of the immature stages for a particular exemplar species may not reflect observations of that species' semaphoront, but of a closely related species from the same biogeographic region (Appendix 3, *Polycentropus zaneta* Denning, 1948 for *P. flavomaculatus* Pictet, 1834 and *Pseudoneureclipsis lusitanicus* Malicky, 1980 for *P. saccheda* Schmid & Denning, 1979). Immature stages are known for 70% of genera included in this study (16 of 23): *Antillopsyche*, *Cernotina*, *Cyrnellus*, *Cyrnus*, *Ecnomus* McLachlan, 1864, *Holocentropus*, *Hydropsyche* Pictet, 1834, *Neureclipsis*, *Nyctiophylax* (*Paranyctiophylax*), *Phylocentropus* Banks, 1907, *Plectrocnemia*, *Polycentropus*, *Polyplectropus*, *Pseudoneureclipsis*, *Psychomyia* Latreille, 1829 and *Xiphocentron* Brauer, 1870.

Ingroup taxa

The ingroup (Polycentropodidae in the traditional sense including Pseudoneureclipsinae) consisted of 49 taxa in three subfamilies and 17 genera (Appendix 4). Three new species from Brazil with uncertain generic affinities were included in this analysis to determine their proper placement within the family: Genus A, sp. 1; Genus A, sp. 2; and Genus B, sp. 1. Species-rich genera were sampled more intensively to include 10 *Polyplectropus*, 9 *Polycentropus* and 6 *Nyctiophylax* species from their entire distribution range. Characters were coded from published accounts rather than direct observation for *Cyrnopsis palpalis* (Martynov 1935), *Polyplectropus tomensis* (Marlier, 1959) (Marlier 1959, 1962), *Cyrnodes scotti* Ulmer, 1910 (Kjaerandsen and Netland 1997) and *Nyctiophylax sinensis* Brauer, 1865 (Neboiss 1994). As a result, the above-mentioned taxa and those with unknown immature stages had a high percentage of missing data. Fossil taxa were not included.

Outgroup taxa

The outgroup consisted of five taxa representing all four families in the Psychomyioidea and Hydropsychidae (Hydropsychoidea) (Appendix 4). Exemplars were chosen to infer Polycentropodidae phylogeny.

Depositories

Material examined is deposited at MVM, Museum Victoria, Melbourne, Australia (P. Lillywhite); NMNH, National Museum of Natural History, Washington, DC (O. Flint); UMSP, University of Minnesota Insect Collection, Saint Paul, MN (P. Clausen, P. Tinerella); and Swedish Museum of Natural History, Stockholm, Sweden (K. Johanson). Specimens were generously donated to UMSP for this study by T. Andersen,

Museum of Zoology, University of Bergen; H. Malicky, Lunz am See, Austria; B. Smith, National Institute of Water and Atmospheric Research, NIWA, New Zealand; J. Weaver, Charleston, South Carolina. Specimens examined housed at UMSP have an associated unique alphanumeric barcode label (starting with UMSP) linked to the BIOTA database maintained by UMSP, which can be accessed from <http://www.entomology.umn.edu/museum/databases/BIOTAdatabase.html>, verified October 2011.

Character sources and observations

Most of the 122 characters included in this analysis are new. However, the following earlier works were consulted, particularly for coding larval characters: Trichoptera higher-level phylogeny (Frانيا and Wiggins 1997); Calamoceratidae phylogeny (Integripalpia) (Prather 2002); placement of Pseudoneureclipsinae (Li *et al.* 2001); and *Dipseudopsis* Walker, 1852 phylogeny (Weaver and Malicky 1994). Characters were modified and coded to address the objectives of this study (when applicable indicated by stating 'in part' in Appendix 1). A reference to the publication where the character first appeared and the character number as it appeared in the original text is indicated where applicable (e.g. F&W18 = Frانيا and Wiggins (1997), character 18; P24 = Prather (2002), character 24; LMT9 = Li *et al.* (2001), character 9; W&M3 = Weaver and Malicky (1994), character 3). Additionally, the pertinent source is cited when coding of the character relied on published observations (i.e. Lepneva 1970). Characters were included in the analysis if: (1) discontinuous variation was clear or could be delimited based on a point of reference (e.g. characters 45, 95); and (2) characters and their states could be observed easily and clearly. When continuous variation could not be discretely delimited, characters were excluded (e.g. wing shape). Additionally, several characters of the female and male genitalia (e.g. subphallic sclerite) were not included since interpretation of internal membranous structures proved difficult. Internal female membranous structures are rarely, if ever, included in phylogenetic studies of Trichoptera.

Approach to coding inapplicable data

Characters were recognised in all taxa included in the analysis based on primary homology and tested through character congruence as a result of cladistic analyses (Patterson 1982). Hypotheses of homology pose no problem when structures in two or more taxa are almost identical or deviate slightly in form and position (e.g. compound eyes). However, in some instances, hypotheses of homology are problematic. For example, when two features on different taxa are similar in form, but differ in position, or conversely when relative position is the same, but the structures differ considerably in form. Coding for characters becomes difficult when structures deemed to be homologous are absent in some taxa (coding for wing veins in apterous or brachypterous taxa v. pterous insects; i.e. inapplicable data).

To account for inapplicable data in this study, a character was coded to address the presence or absence of a feature and a second (or more) character(s) was coded to treat the variation of the condition; inapplicable data were coded as unknown/missing data '-' (dash-coding or reductive-coding) (Hawkins *et al.* 1997;

Strong and Lipscomb 1999). Reductive-coding was preferred for most characters for three primary reasons: (1) characters were based on hypotheses of homology, because there was a clear correspondence of structures across taxa and no ambiguity that they represented the same entities; (2) by coding the inapplicable condition as unknown (with a dash) and not as a separate character state (absence-coding), the absence condition, if optimised as informative when recovering relationships, will not inflate (duplicate) support for taxa lacking the feature; and (3) coding all observations into a single multi-state character (composite coding, Maddison 1993) became unwieldy, particularly when features were complex (e.g. coding for pubescence, size, shape, color, etc., in one character). Under a reductive-coding approach, both the '?' (question mark) for unknown/missing data and '-' (dash) for inapplicable data are optimised as one of the existing states (Strong and Lipscomb 1999); nevertheless, in the data matrix, inapplicable character states are coded with a dash '-' and unknown data with a '?' to conserve character state information. In instances when primary homology assessments were problematic, a composite approach (single, multi-state character) was followed (e.g. character 118) (Maddison 1993; Marshall 2003), thereby retaining information on observed similarity (Schuh 2000) and minimising the possibility that erroneous homologies may conceal reconstructions by true homologies (Kitching *et al.* 1998).

Character treatment

One hundred and twenty-two characters were included in the analysis, including 87 binary characters and 35 multi-state characters, for a total of 298 character states. Eighteen characters were parsimony uninformative. Characters were interpreted from structures of the larvae (32), pupae (4) and adults (head and thorax (24), wings (31), female genitalia (4) and male genitalia (27)). Since uninformative characters may be informative in future higher-level studies, they were incorporated in the character matrix and analysis, but were excluded when calculating tree statistics (Yeates 1992; Bryant 1995). All characters were treated as unordered (non-additive) (Fitch 1971) and equally weighted (Wilkinson 1992). The character matrix (Appendix 2) was constructed and characters mapped with MacClade 4.08 (Maddison and Maddison 2000) to observe character state transformation on a given tree. Character states listed for each group in the discussion are unambiguous character states supporting the same clade under all methods and all applicable datasets (i.e. some taxa were not included in the dataset that included larval, pupal and adult characters).

Missing data and sampling strategy

Three partitions of data were analysed to understand how missing cells in the matrix influenced results. First, all available data, including highly incomplete characters, were analysed for all 49 ingroup taxa, five outgroup taxa and 122 characters (the 'TOTAL' dataset as referred hereafter). Second, the TOTAL dataset was reduced to exclude incomplete taxa (those for which the immature stages are unknown). This dataset, termed 'LPA' (Larval, Pupal, Adult), consisted of 16 ingroup taxa, five outgroup taxa and 122 characters. Third, analysis of 86 characters of male and female adults across all 54 taxa was performed, hereafter referred to as the

'ADULT' dataset. Each dataset was analysed using parsimony and Bayesian methods.

Phylogenetic analyses

Parsimony analysis

Each of the three datasets (TOTAL, LPA, ADULT) was analysed under parsimony with PAUP* 4.0 Beta (Swofford 2003). Heuristic searches were implemented with stepwise taxon addition and 500 random addition sequence replicates, five trees held at each step and tree-bisection-reconnection (TBR) branch swapping algorithm for each of the three datasets. Bootstrapping (Felsenstein 1985) was interpreted to represent nodal support for the preferred topology based on the given dataset. A bootstrap analysis was carried out with 100 pseudoreplicates for each dataset, each with ten random-taxon-addition replicates.

Bayesian inference

As above, each dataset was analysed under Bayesian phylogenetic inference with MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Ronquist *et al.* 2007). Bayesian analyses consisted of the same three datasets analysed under parsimony methods with PAUP*. Once executed in MrBayes, morphological datasets (i.e. standard) are by default assigned the Markov k (Mk) model (Lewis 2001) and the coding parameter for how data are sampled corrected as 'variable' since only non-constant characters were included (Ronquist *et al.* 2007). The Mk model specifies equal rates of character state change.

Analyses of all three sampling strategies involved the inclusion and exclusion of a gamma parameter (Mk and Mk + gamma) to account for different rates of change among characters (e.g. genitalic characters *v.* larval characters or wing characters). The fit of these models to each of the three datasets was tested using Bayes factor, $B_{10} = (\text{harmonic mean Ln likelihood Mk} - \text{harmonic mean Ln likelihood Mk} + \text{gamma}) \times 2$ (Kass and Raftery 1995) to determine if including a gamma parameter was appropriate given the data (Nylander *et al.* 2004; Wiens *et al.* 2005). A value greater than 10 signifies strong support for one model over another (Kass and Raftery 1995; Wiens *et al.* 2005). The harmonic mean was calculated in MrBayes under the *sump* command, *post burn-in* (Ronquist *et al.* 2007). The results for all three datasets strongly favoured the Mk model invoking a gamma parameter (*lset rates = gamma*). Each of the three datasets was executed three times under the preferred model to minimize starting tree bias (A. Simons, pers. comm.; Wiens *et al.* 2005). The number of generations required to reach stationarity differed among the three analyses of the different datasets; however, within two of the three sampling strategies, the resulting consensus trees of all the analyses were the same. The consensus tree with a higher maximum likelihood score in the LPA dataset was more resolved. The results presented and discussed for each of the three datasets reflect the analysis with the highest likelihood score (as expressed by the harmonic mean) implemented under an Mk + gamma model.

Based on earlier test runs, chain mixing was poor (universe of trees was not being thoroughly sampled, numbers in square

brackets were not switching between chains), therefore the default incremental temperature parameter was reduced from 0.2 to 0.075 (*mcmc* temp) (Ronquist *et al.* 2007). Otherwise, default settings were left unchanged. Two parallel Markov Chain Monte Carlo (MCMC) runs, each with one cold chain and three heated chains, were performed with chains sampled every 1000th generation. The datasets were each run for the following number of generations: TOTAL dataset 6 000 000; LPA dataset 4 000 000; and ADULT dataset 4 000 000. The Bayesian analyses were stopped when the convergence diagnostic indicated the analysis had reached stationarity (i.e. average standard deviation of split frequencies was below 0.01, potential scale reduction factor (PSRF) value was 1.00, and plot of the generations against the log probability of the data presented only 'white noise' with no increasing or decreasing trends (Ronquist *et al.* 2007)). Twenty-five per cent of the samples were discarded as *burn-in* under the *sumt* command (Ronquist *et al.* 2007).

Results

Consensus trees summarising results for the given datasets are shown in Figs 11–16. The parsimony analysis of the TOTAL dataset (54 taxa, 122 characters) resulted in 7799 equally parsimonious trees (length: 436; consistency index (CI): 0.349; retention index (RI): 0.632; rescaled consistency index (RC): 0.220) (Fig. 11). In total, 7 equally parsimonious trees of length 257 resulted from analysis of the LPA dataset (21 taxa, 122 characters) (CI: 0.482, RI: 0.576, RC: 0.278) (Fig. 13). The ADULT dataset (54 taxa, 86 characters) resulted in 48 equally parsimonious trees of length 385 (CI: 0.330, RI: 0.636, RC: 0.210) (Fig. 15). Bootstrap percentages (BP) for a given clade are displayed along the internodes.

Branch lengths may be distorted by missing data (Wiens *et al.* 2005), therefore a majority-rule cladogram (50%) is presented for the TOTAL Bayesian analysis (Fig. 12). Phylograms are presented for the LPA and ADULT Bayesian analyses with branch lengths indicating character state changes along each branch (Ronquist *et al.* 2007) (Figs 14, 16). Posterior probability values (PP) for a given clade are displayed above the internodes.

Phylogenetic discussion

Results from both parsimony and Bayesian analyses of the ADULT dataset suggest pseudoneureclipsines are more closely related to polycentropodines than they are to *Phylocentropus* or to any other outgroup taxon (Fig. 17). The ADULT dataset has very few characters with missing data and results mirror traditional classification including Pseudoneureclipsinae within Polycentropodidae. Adult pseudoneureclipsines resemble polycentropodines in having, among other characteristics, ovoid maxillary palpomere two with palpomere three preapically inserted into it, and circular mesoscutal setal warts.

Addition of characters of the immature stages to the matrix, under both methods of analysis, did not find pseudoneureclipsines within polycentropodines or as the sister taxon to *Phylocentropus* (with the exception of results from the TOTAL Bayesian analysis, Fig. 12), suggesting

pseudoneureclipsines are a separate taxon from both polycentropodids and dipseudopsids (Figs 11, 13, 14). It was upon discovery of *Pseudoneureclipsis* larvae that uncertainty arose regarding placement of this taxon within Polycentropodidae (Li *et al.* 2001; Tachet *et al.* 2001). Pseudoneureclipsinae larvae resemble psychomyiid or dipseudopsid larvae in possessing, among other characters, an elongate labial spinneret, which may help in the application of silk to tubular retreats made of mostly sand grains (Tachet *et al.* 2001). As previously discussed in the introduction, this taxon was transferred to Dipseudopsidae based, in large part, on shared possession of certain larval features, yet this classification is not widely followed (Malicky 2001, 2007; Malicky and Prommi 2006; Mey 2006). Furthermore, independent studies based on combined molecular and morphological data (Kjer *et al.* 2001 (represented by *Antillopsyche* in that study), 2002; Holzenthal *et al.* 2007a) or molecular data alone (Johanson and Espeland 2010) failed to recover a sister relationship between Pseudoneureclipsinae and Dipseudopsidae (Fig. 1C, D). In these analyses, Pseudoneureclipsinae was recovered as sister to Polycentropodidae (Holzenthal *et al.* 2007a) or to Ecnomidae (Johanson and Espeland 2010). Therefore, based on independent evidence, we consider estimates of the relationships within Pseudoneureclipsinae including characters of the immature stages to be more accurate (LPA and TOTAL dataset) than estimates based on adult characters alone (ADULT dataset). Characters of immature stages are informative enough to suggest that pseudoneureclipsines are being 'pulled' into the ingroup in the ADULT dataset due to convergent losses of wing veins resulting from an overall reduction in body size (exemplified by the sister relationship in the parsimony analysis between pseudoneureclipsines and a clade containing several small-sized polycentropodines (i.e. *Pahamunaya*, *Cernotina*, *Cyrnellus*)) and due to pleisiomorphies retained by both pseudoneureclipsines and polycentropodines (i.e. ovoid maxillary palpomeres two with palpomere three preapically inserted into it and circular mesoscutal setal warts). The importance of including all available sources of data cannot be overstated, and including data from immature stages is no exception (Wiggins 1981, 1996; Frania and Wiggins 1997).

Under parsimony, results from analysis of the TOTAL dataset (Fig. 11) corroborate many of the relationships found in the LPA dataset analysis (Figs 13, 17). The Bayesian consensus tree based on analysis of the TOTAL dataset was highly unresolved and does not contradict either Bayesian LPA or ADULT topologies (Figs 12, 14, 16, 17), but suggests an inability of the method to handle characters with a large proportion of missing data.

Consensus trees based on parsimony or Bayesian analyses of the TOTAL dataset differed in amount of resolution. Including characters with large sets of missing data under parsimony increased the number of most parsimonious trees from 48 in the ADULT dataset to 7799 in the TOTAL dataset, and resulted in a poorly resolved strict consensus, particularly for the ingroup. The placement of pseudoneureclipsines corroborated results from the LPA parsimony analysis (Fig. 13).

What accounts for the highly unresolved estimate when sets of characters with missing data are included (as in the TOTAL dataset), particularly when analysed under Bayesian methods? In PAUP*, the missing data entry, symbolised by a question mark

‘?’ is ‘interpreted as being one of the existing states. . . and this may affect the placement of taxa for which it is [missing]’ (Strong and Lipscomb 1999: 363; Swofford and Begle 1993; Wiens 1998). Under parsimony, missing data are uninformative, but the coded cells for that character for other taxa may be informative (Wiens 1998). MrBayes treats ‘missing characters as missing data. . . and missing characters will not contribute any phylogenetic information’ (Ronquist *et al.* 2007). How informative are characters with missing cells and how do coded cells affect the placement of incomplete taxa? Simulation studies aimed at trying to determine accuracy of Bayesian methods when missing data are present suggests highly incomplete taxa can be accurately placed in the phylogeny (Wiens and Moen 2008). However, this result may not hold true when the overall number of characters is low; furthermore, the presence of extensive missing data may be even more problematic if the characters without a lot of missing entries are ‘evolving too slowly to be informative or too quickly to be accurate’ (Wiens and Moen 2008: 313).

The Bayesian model for all three datasets included a gamma parameter to account for rate variation among characters. The shape of the gamma distribution can be determined by the alpha (α) parameter under the .p files (Ronquist *et al.* 2007). The alpha parameter for all datasets was below 1 (TOTAL $\alpha = 0.59$, LPA $\alpha = 0.52$, ADULT $\alpha = 0.81$), indicating high variation in rates of change among characters (Swofford *et al.* 1996; Ronquist *et al.* 2007). The gamma distribution for a small α value is L-shaped with a few characters evolving rapidly while most characters are evolving very slowly (i.e. characters are either under low or high selective pressure) (Swofford *et al.* 1996; Ronquist *et al.* 2007). As α becomes larger, variation in rates of evolution between characters diminishes (Ronquist *et al.* 2007). Therefore a combination of factors may account for decreased resolution in estimates of phylogeny: (1) *relatively* large amounts of missing data and (2) non-missing data having high variation in rates of change among characters (Wiens 2006; Wiens and Moen 2008).

Taxonomic conclusions

Family PSEUDONEURECLIPSIDAE Ulmer, *stat. nov.*

Type genus: *Pseudoneureclipsis* Ulmer

Included genera: *Antillopsyche* Banks, 1941: 400 [Type species: *Antillopsyche wrighti* Banks, 1941: 140, original designation by monotypy]; *Pseudoneureclipsis* Ulmer, 1913: 84 [Type species: *Pseudoneureclipsis ramosa* Ulmer, 1913: 85, original designation by monotypy] (2 genera, 2 sampled; 69 species, 4 sampled).

As discussed above, Pseudoneureclipsinae represents a well defined group with family-level ecological and morphological synapomorphies in both the larval and adult forms. The recognition of Pseudoneureclipsinae as a separate family within psychomyioid annulipalpians is appropriate and justified. In previous independent analyses, pseudoneureclipsines have been recovered as sister to Dipseudopsidae (Li *et al.* 2001) and transferred to this family, as sister to Polycentropodidae (Holzenthal *et al.* 2007a) or Ecnomidae (Johanson and Espeland 2010). Nonetheless, a sister

relationship between pseudoneureclipsines and dipseudopsids remains uncorroborated (Li *et al.* 2001), rejecting the notion that pseudoneureclipsines are dipseudopsids. Designation of the family Pseudoneureclipsidae also accurately reflects recent independent total evidence hypotheses of psychomyioid phylogeny (Kjer *et al.* 2002; Holzenthal *et al.* 2007a); raising pseudoneureclipsines to family-level sets them at an ‘even playing field’ when considering higher-level studies. Not recognising Pseudoneureclipsinae as a separate family given our current knowledge of psychomyioid phylogeny would render either Dipseudopsidae or Polycentropodidae polyphyletic.

The pseudoneureclipsid clade is supported minimally by the following characteristics: larvae with metanotal parallel black lines (character 20, synapomorphy); crossvein *a3-a2* in forewing present (character 73, synapomorphy) and tergum IX of the male genitalia sclerotised and fused to sternum IX (character 93). The monophyly of *Antillopsyche*, with extant species restricted to the Greater Antilles (Cuba, Hispaniola and Puerto Rico) and two extinct species known from Dominican (Wichard 1985) and Mexican amber (Wichard *et al.* 2006), is supported by the fused, enlarged and highly sclerotised anterolateral and hypomedial warts (Fig. 5B) (character 47, synapomorphy). *Pseudoneureclipsis*, with an Old World pattern of distribution, but absent from the Australasian region and reaching its greatest diversity in the Oriental region, is monophyletic based on the presence of an inner tooth in the pupal mandible (character 34, synapomorphy) and absence of fork V in the forewing (character 69).

Family KAMBAITIPSYCHIDAE Malicky, *stat. nov.*

Type genus: *Kambaitipsyche* Malicky

Included genera: *Kambaitipsyche* Malicky, 1992: 381 [Type species: *Kambaitipsyche hykriion* Malicky, 1992: 382, original designation] (1 genus, 2 species; 2 species sampled).

Kambaitipsyche has several characters also found in several annulipalpians families, contributing to its uncertain placement in the suborder by Malicky (1992). For example, *Kambaitipsyche* and Dipseudopsidae (*Phylocentropus*) have similar wing venation, small adult labial palps and similar phalli. Similarities between *Kambaitipsyche* and Polycentropodidae lie in the shape of sternum IX of the male genitalia, the presence of rounded mesoscutal setal warts on the adult and similar tentoria of the head.

Only adult male and female characters were included for *Kambaitipsyche* exemplars, since immatures remain unknown. Nonetheless, monophyly of *Kambaitipsyche* is supported, minimally, by the following character states: presence of setae between ommatidia (character 37); anteromedial and hypomedial warts of the head not fused (Fig. 6A) (character 46); sessile fork III of the forewing (character 67); rooted fork I of the hind wing (character 85) (synapomorphy); fork of medial vein sessile with respect to *m-cu* crossvein in the hind wing (character 89); and broad shape of intermediate appendage of the male genitalia (character 97).

Kambaitipsyche forms a polytomy with *Phylocentropus* at the base of the polycentropodines (Figs 11, 16) or as the sister group to a clade containing *Phylocentropus* (polycentropodines [paraphyletic] + pseudoneureclipsines) (Fig. 15). Even though

immatures remain unknown, data on the adult stage alone support recognition of kambaitipsychines as a separate lineage from all other psychomyioid families. Retaining Kambaitipsychinae as a subfamily would render Polycentropodidae polyphyletic and our results do not support transferring the subfamily into any other family. It is therefore necessary and suitable to recognise the family Kambaitipsychidae in Psychomyioidea.

Family **POLYCENTROPODIDAE** (15 genera, 15 sampled; 650 species, 44 sampled)

This study supports a polyphyletic Polycentropodidae as currently constituted. Two of the subfamilies traditionally recognised within Polycentropodidae, Pseudoneureclipsinae and Kambaitipsychinae are each well supported monophyletic groups (Figs 11–16). The monophyly of the largest subfamily,

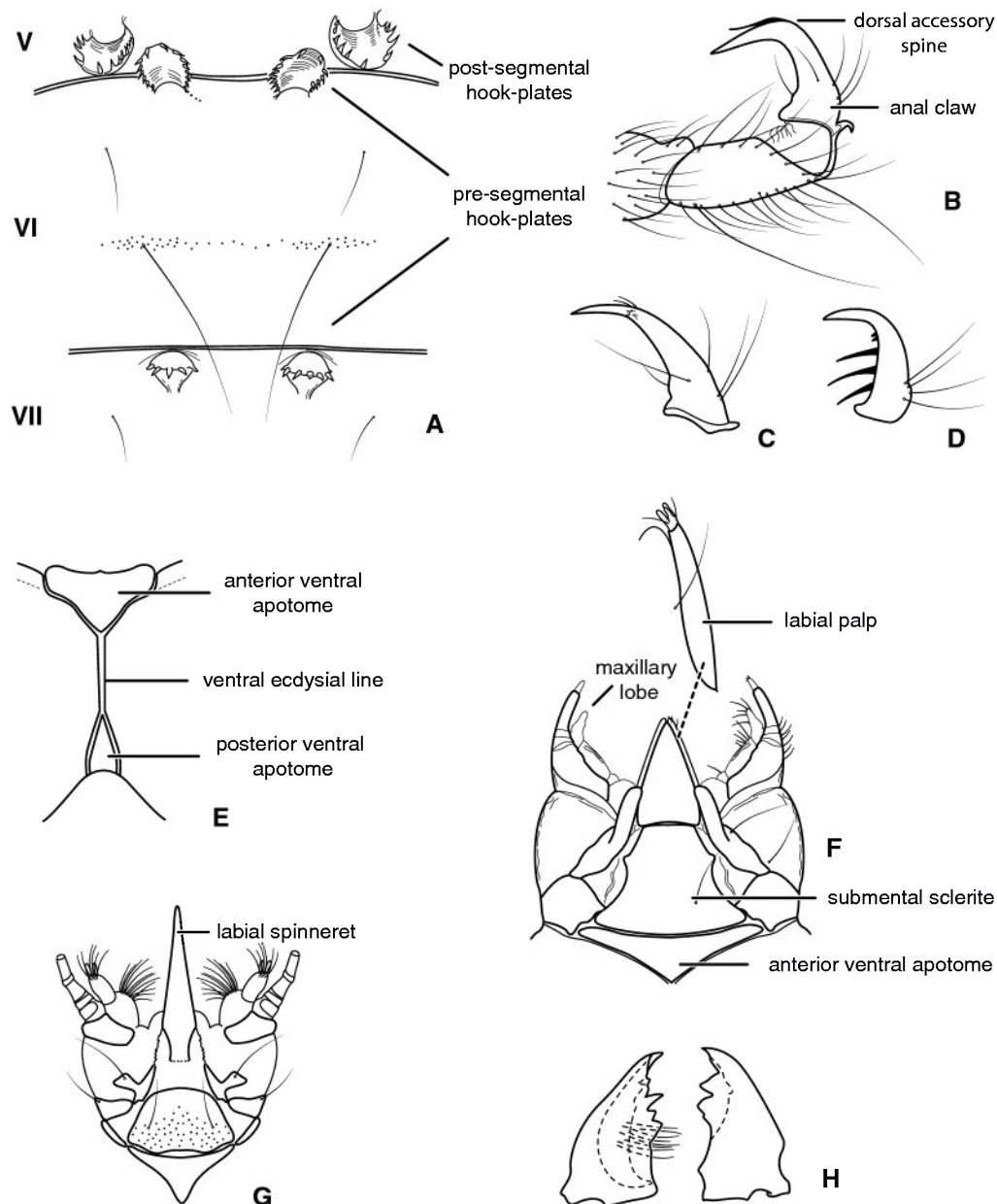


Fig. 2. Larval and pupal characters. (A) *Neureclipsis bimaculata* pupa, abdominal segments V, VI and VII showing dorsal hook plates, dorsal (after Lepneva 1970); (B) *Polycentropus* sp., larva, anal proleg, lateral (after Wiggins 1996); (C) *Plectrocnemia conspersa*, larva, anal claw, lateral (after Lepneva 1970); (D) *Polyplectropus* sp., larva, anal claw, lateral (after Flint 1964a); (E) diplectronine hydropterygine, larva, gular area of head, ventral (after Wiggins 1996); (F) *Polycentropus* sp. larva, maxillae and labium, ventral, labial palp enlarged (after Wiggins 1996); (G) *Antillopsyche tubicola*, larva, maxillae and labium (spinneret), ventral (after Flint 1964b); (H) *Antillopsyche tubicola*, larva, left and right mandibles, ventral (after Flint 1964b).

Polycentropodinae, was supported in some (Figs 11, 13–15), but not all, analyses (Figs 12, 16). Polycentropodidae *sensu stricto* (now excluding Pseudoneureclipsinae and Kambaitipsychinae) can be distinguished from all other families by the following unique combination of character states: larval labial palp appressed to sides of prelabio-hypopharyngeal lobe (Fig. 2F); larval trochantin acute, elongate and fused with episternum and without suture (Fig. 3B, C); larval meso- and metanota

membranous (Fig. 3A); larval secondary setation of the legs present (Fig. 3A); larval anal proleg very prominent, incorporating part of segment IX (Fig. 3A); pupae with presegmental hook plates on segments III–VIII and postsegmental hook plates on segment V (Fig. 2A); adults without ocelli; adults with antennae stout, never longer than wings; preapical insertion of maxillary palpomere three into two (Figs 4B, 6C, D); maxillary palpi five-segmented, with first

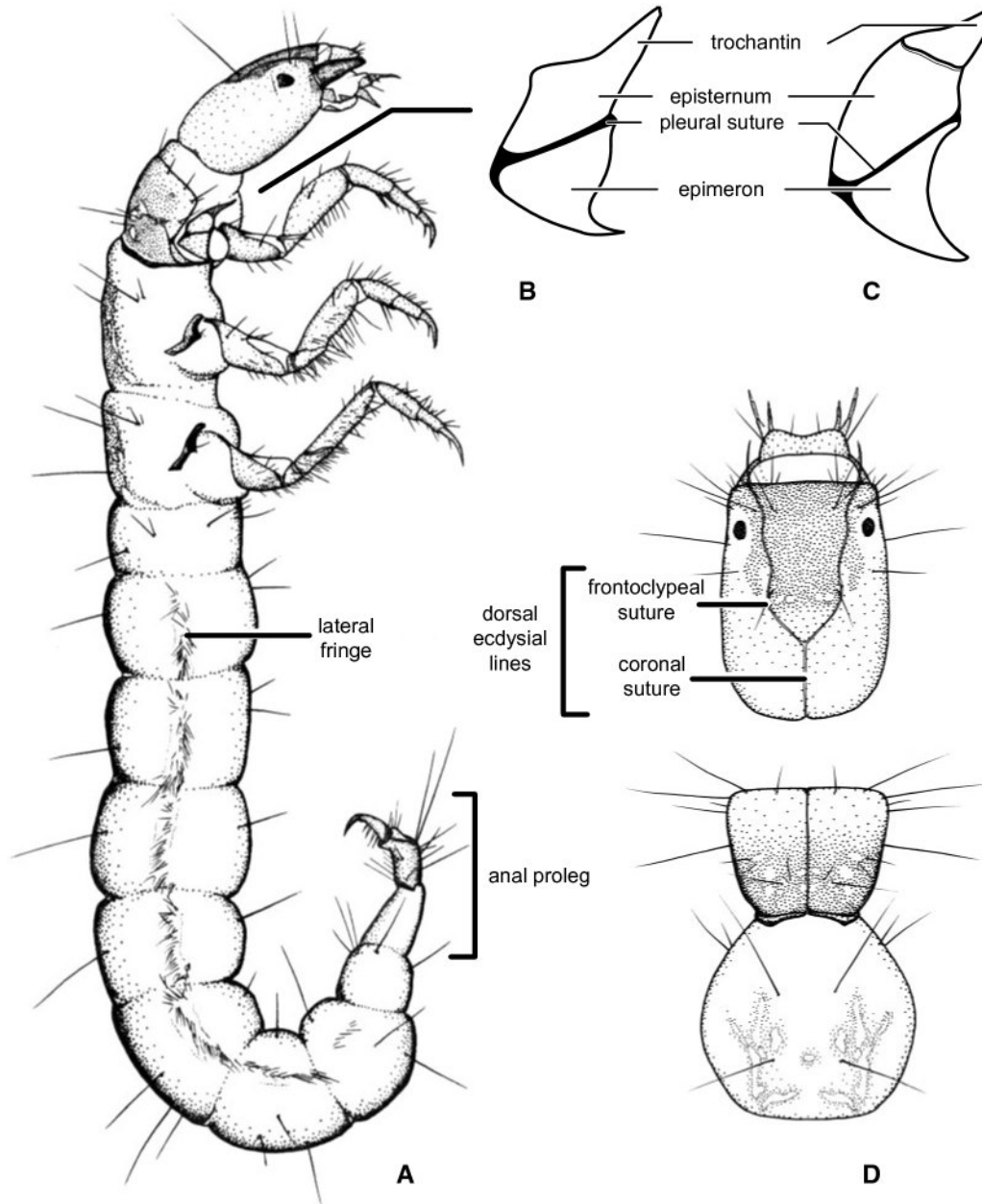


Fig. 3. Polycentropodidae, larval characters. (A) *Polyplectropus* sp., larval habitus, lateral; (B) *Neureclipsis bimaculata*, foretrochantin and associated structures, lateral (after Wiggins 1996); (C) *Pseudoneureclipsis lusitanicus*, foretrochantin and associated structures, lateral (after Tachet *et al.* 2001); (D) *Polyplectropus* sp., head and thorax, dorsal.

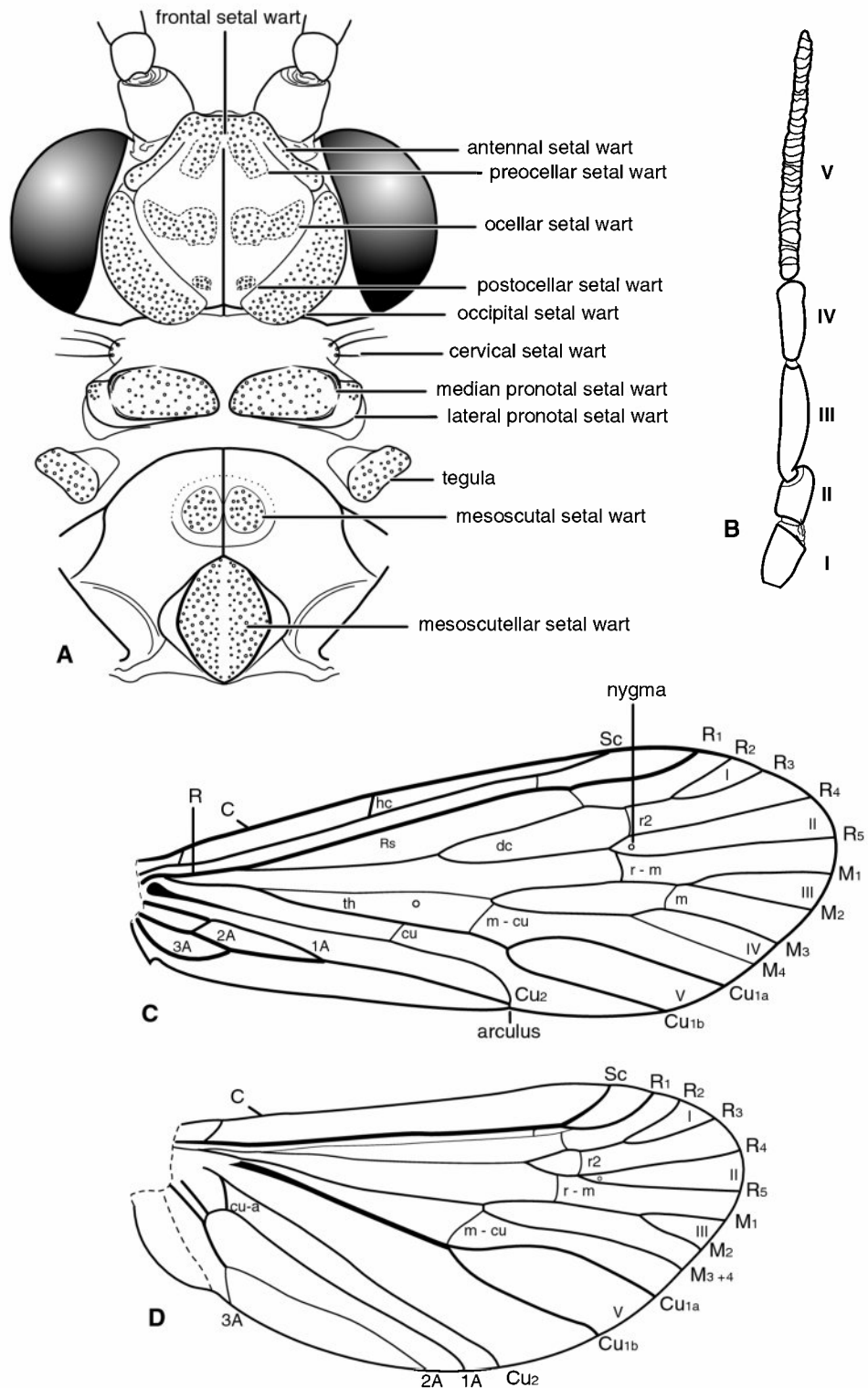


Fig. 4. Polycentropodidae, adult characters. *Polyplectropus deltoides* (A–B). (A) Head, pro- and mesothorax, dorsal; (B) maxillary palp, dorsal; *Polycentropus weedi* (C–D). (C) Forewing; (D) hind wing. Abbreviations: C = costa; Sc = subcosta; R = Radius, radial vein; Rs = radial sector; M = Media, median veins; Cu = cubitus; A = anal veins; dc = discoidal cell; hc = humeral crossvein; m-cu = median-cubital crossvein; r-m = radial-medial crossvein; th = thyridial cell; I–V = wing forks 1–5.

two palpomeres short, and fifth long (usually) and annulated; adults with oblong median pronotal setal wart and circular mesoscutal setal warts (Figs 4A, 5); a more or less circular to quadrate segment IX of the male genitalia; female sternum VIII divided into a pair of lobes (Fig. 6F); and female lateral papillae present (Fig. 6E, F).

Genus *Nyctiophylax* *sensu lato* (100 extant species, 6 sampled)

Six species of *Nyctiophylax sensu lato* (to include *Paranyctiophylax*) were sampled for this study. Placement of the type species of the genus, *Nyctiophylax sinensis*, was

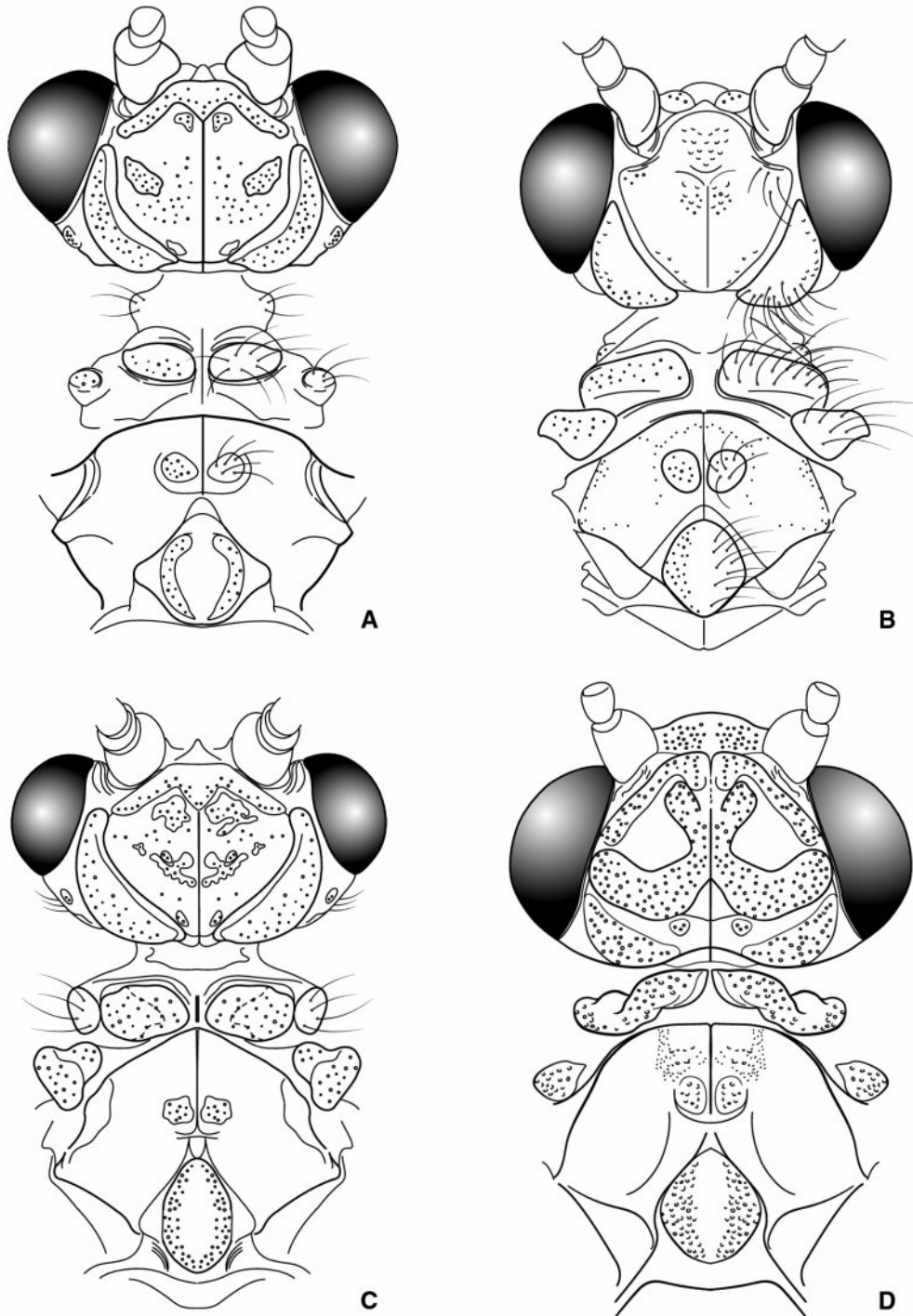


Fig. 5. Polycentropodidae, adult characters, head, pro- and mesothorax, dorsal. (A) *Adeptophylax volutus*, (B) *Cernotina taeniata*, (C) *Plectrocnemia spilota*, (D) *Antillopsyche tubicola*.

equivocal. The few characters coded for this species were unable to provide signal to accurately place it in the phylogeny (Wiens 1998; Wiens and Moen 2008). The immature stages are unknown for this species.

Placement of the Australian species of *Nyctiophylax* (*Nyctiophylax* sp. AU) also remained equivocal. Fourteen species of *Nyctiophylax* s. l. are currently found in Australia. All of them have looped anal veins in the forewing (see below) and were included in *Paranyctiophylax* by Neboiss (1993, 1994). The new species of *Nyctiophylax* from Australia included in this analysis (*Nyctiophylax* sp. AU) does not have looped anal veins.

A species currently in *Nyctiophylax* from the Neotropical region, *Nyctiophylax neotropicalis* Flint, 1971, as well as an undescribed *Nyctiophylax* from the Neotropics were included in the analysis. In his description of *N. neotropicalis*, Flint (1971) discussed the distinctiveness of this species and expressed uncertainty as to its proper placement within *Nyctiophylax*. All relevant analyses and the possession of several unambiguous character states support the establishment of a separate genus comprising at least two species from the Neotropical region, with the possible inclusion of Genus B sp. 1 (Figs 11, 15). Character states minimally supporting the Neotropical *Nyctiophylax* (minus

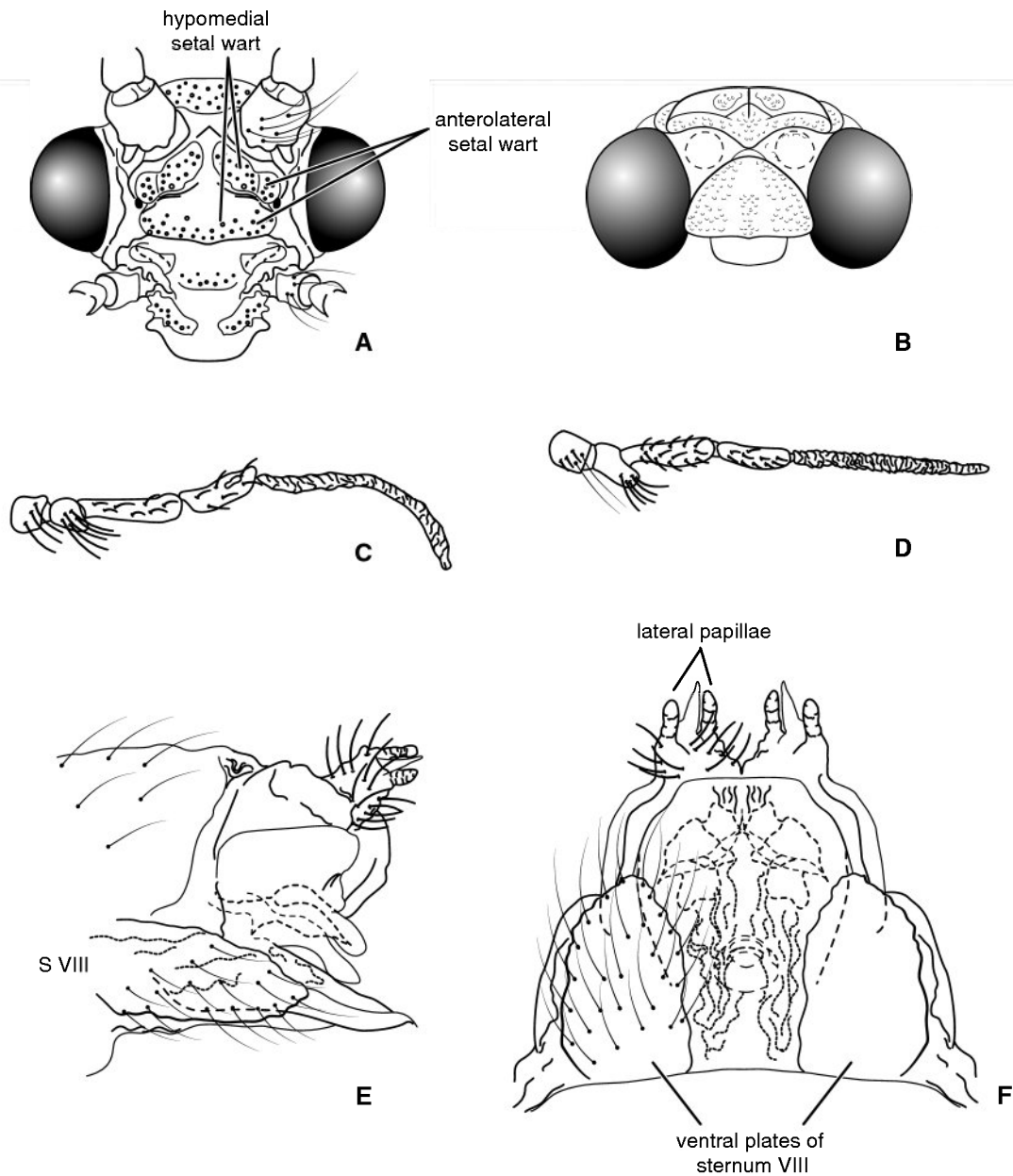


Fig. 6. Polycentropodidae, adult characters. (A) *Plectrocnemia spilota*, head, frontal; (B) *Antillopsyche tubicola*, head, frontal. Left maxillary palp (C–D). (C) *Plectrocnemia spilota*, (D) *Cernotina taeniata*. Female genitalia, *Polyplectropus bredini* (E–F). (E) Lateral, (F) ventral view.

Genus B) clade include: ratio of discoidal cell to radial sector (R_s) more than 3 : 1 (Fig. 7D) (character 64); fork V of the forewing sessile (character 70); tergum IX present as irregularly shaped laterodorsal sclerite (vestige) (character 93); mesolateral process of preanal appendage 1.5 to $2\times$ longer than tall (character 100);

and paired sclerotised structures of the phallus arising externally from the phallobase (character 118).

Species included in *Nyctiophylax* (*Paranyctiophylax*) form a monophyletic group based on the possession of several unambiguous character states, including: forewing A1 and A2

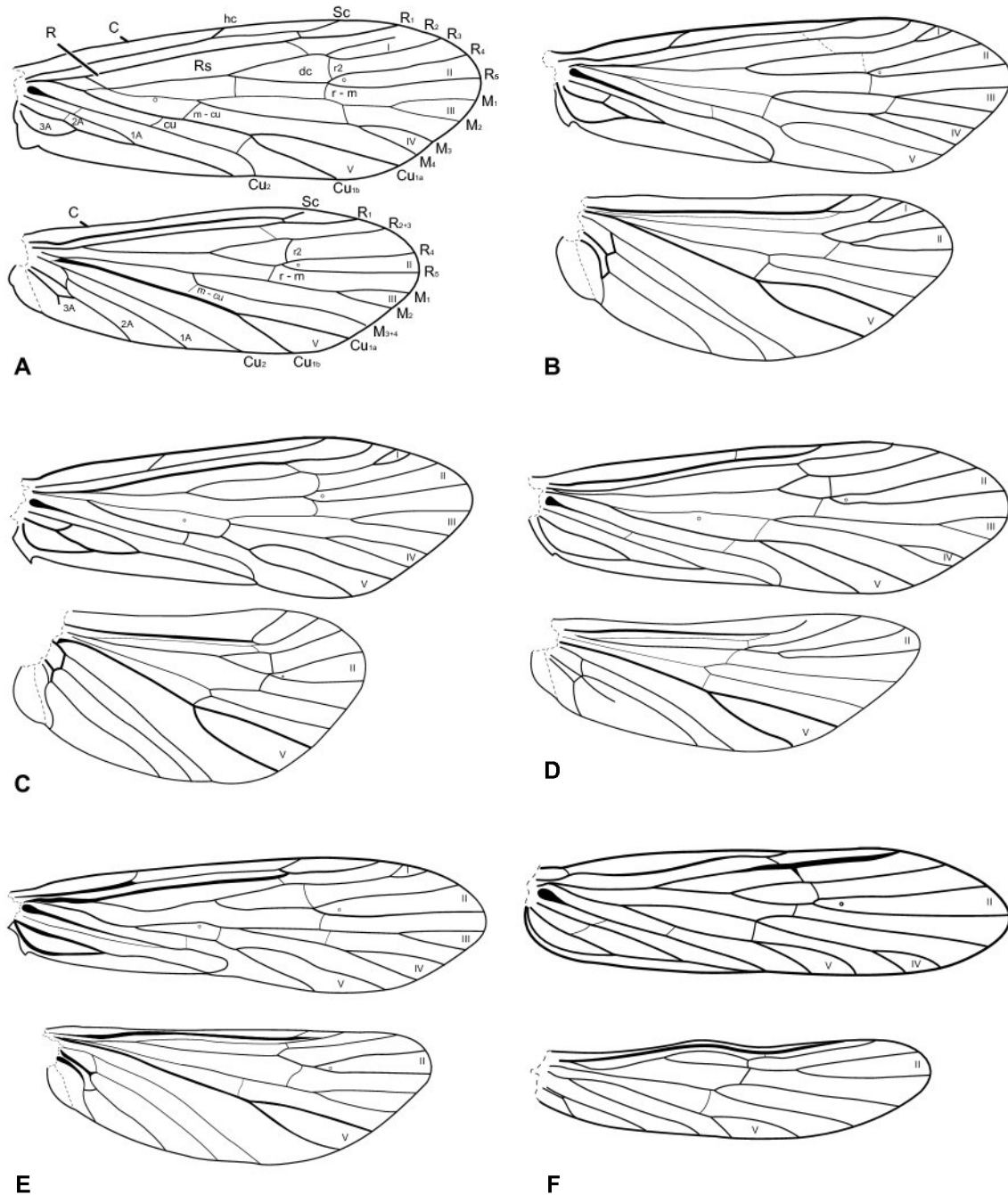


Fig. 7. Polycentropodidae, adult characters, fore- and hind wing venation. (A) *Phylocentropus placidus*, (B) *Polycentropus chilensis*, (C) *Holocentropus interruptus*, (D) *Nyctiophylax neotropicalis*, (E) *Polyplectropus deltoides*, (F) *Cernotina calcea*. Wings among species not to scale. Abbreviations: C = costa; Sc = subcosta; R = Radius, radial vein; R_s = radial sector; M = Media, median veins; Cu = cubitus; A = anal veins; dc = discoidal cell; hc = humeral crossvein; m-cu = median-cubital crossvein; r-m = radial-medial crossvein; th = thyridial cell; I–V = wing forks 1–5.

meeting at the same point on A3 (looped anal veins) (character 74, synapomorphy); inferior appendage of male genitalia with ventral branch present as small stub and dorsal branch well developed (character 111); and paired sclerotised structure of the phallus arising apically and internally (character 118). The presence of looped anal veins in the forewing was a character identified by Neboiss (1993) to recognise *Paranyctiophylax* as a valid genus, which this study confirms to be a synapomorphy. This character is

shared by 36 species from the Nearctic, Afrotropical, Oriental and Australasian regions.

Genus *Polycentropus* (165 species, 5 sampled)

Nine species from four biogeographic regions (Afrotropical, Nearctic, Neotropical and West Palearctic), considered by some authors (Nimmo 1986; Ross 1944) to belong in

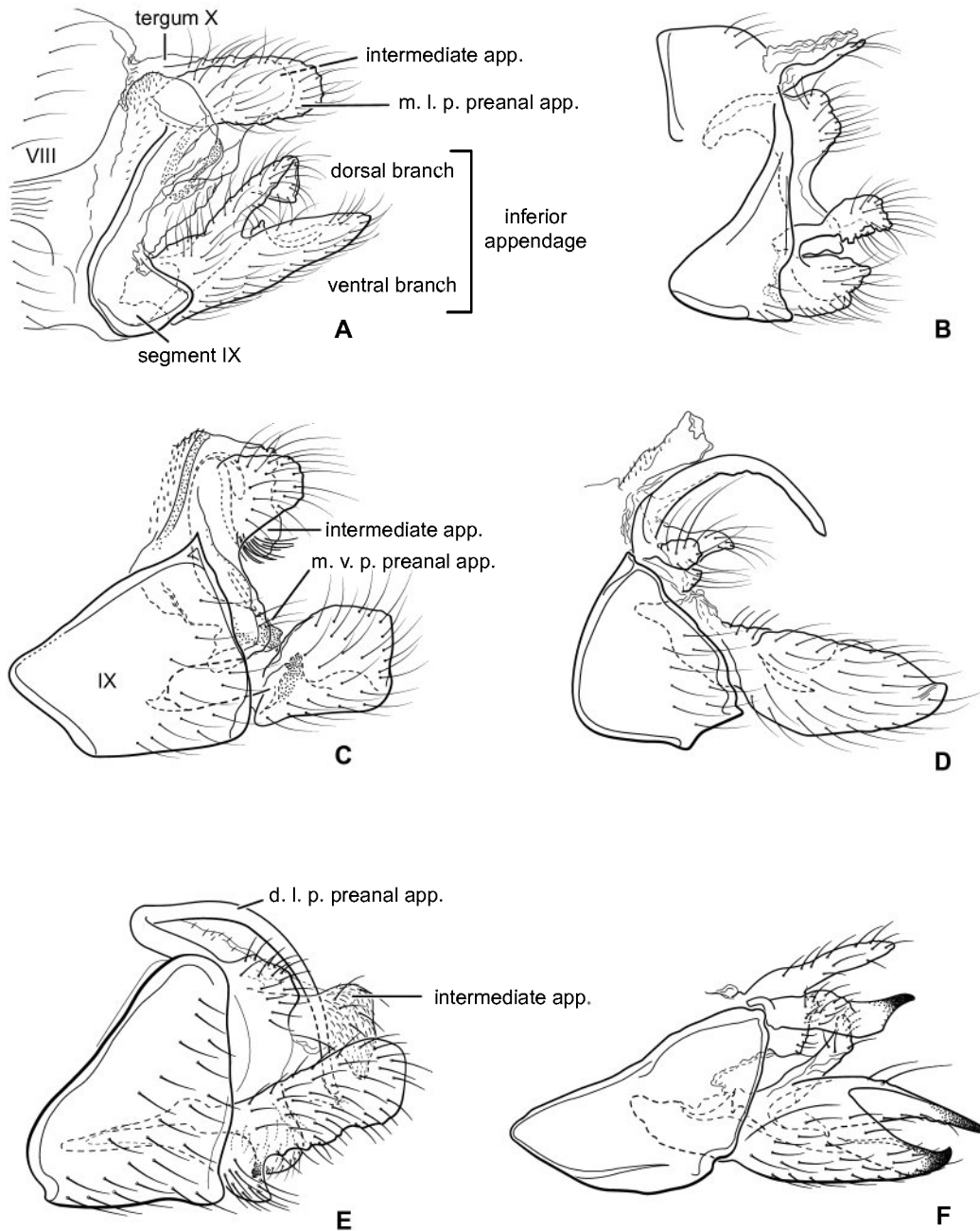


Fig. 8. Polycentropodidae, adult characters, male genitalia, lateral. (A) *Antillopsyche tubicola*, (B) *Adeptophylax volutus*, (C) *Polycentropus chilensis*, (D) *Plectrocnemia spilota*, (E) *Polyplectropus recurvatus*, (F) *Cernotina* sp. Abbreviations: d. l. p = dorsolateral process of preanal appendage; m. l. p = mesolateral process of preanal appendage; m. v. p. = mesoventral process of preanal appendage; VIII, IX, X = abdominal segments 8, 9, 10, respectively.

Polycentropus, were included in this study. Ross (1944) included *Holocentropus* and *Plectrocnemia* species from North America under *Polycentropus*, first without formally designating these two genera as junior synonyms of *Polycentropus* and second, with very little evidence to support his decision other than stating that there were few differences between the larvae, pupae and adults

among the genera. Ross (1944: 58) stated 'I am making no attempt at this time to judge the validity of either *Plectrocnemia* or *Holocentropus*; the study of larvae of the species from various continents, as well as a critical study of the genotypes, will be necessary before the names can be applied even to subgeneric categories of North American species'. Since then, workers

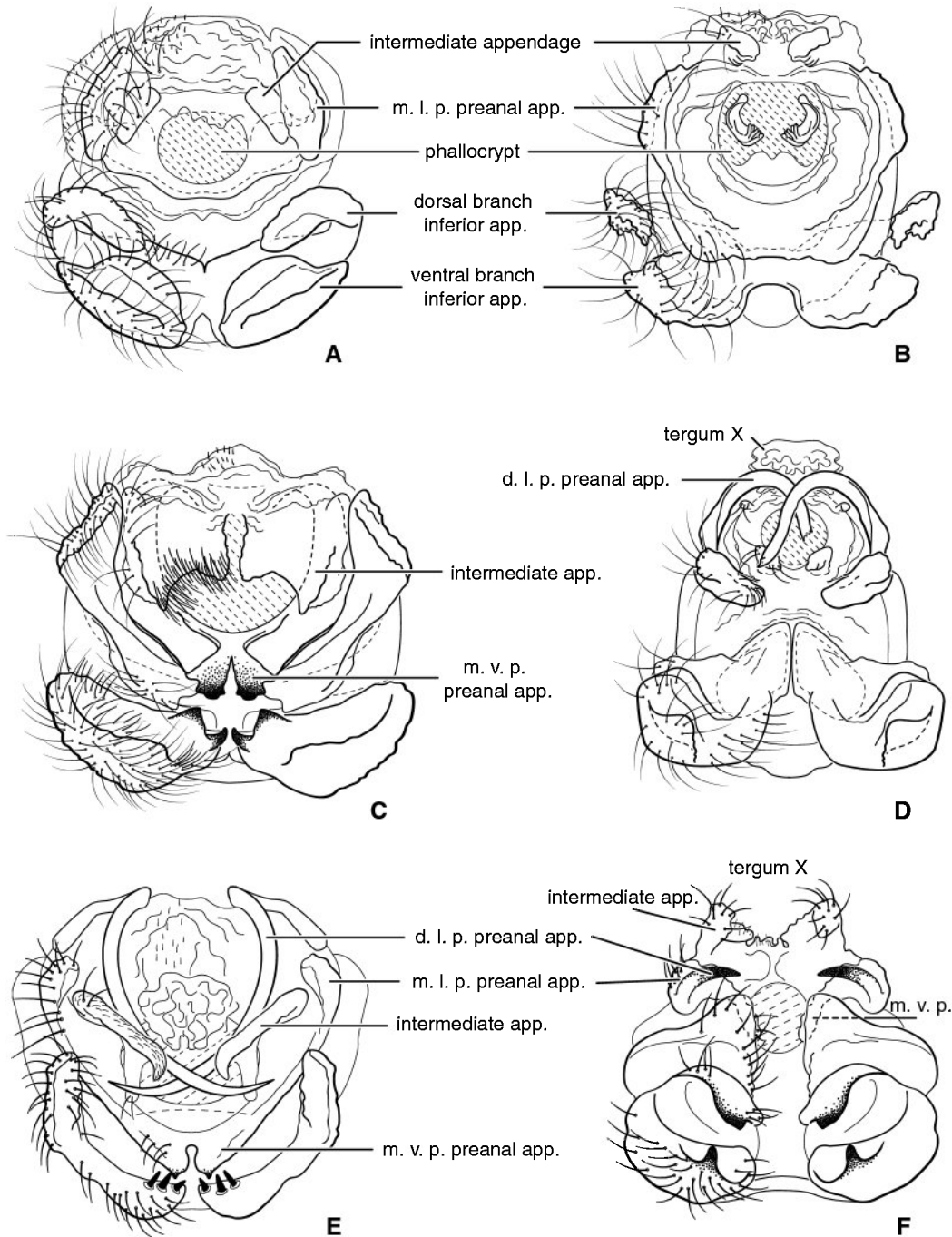


Fig. 9. Polycentropodidae, adult characters, male genitalia, caudal. (A) *Antillopsyche tubicola*, (B) *Adectophylax volutus*, (C) *Polycentropus chilensis*, (D) *Plectrocnemia spilota*, (E) *Polyplectropus recurvatus*, (F) *Cernotina* sp. Abbreviations: d. l. p. = dorsolateral process of preanal appendage; m. l. p. = mesolateral process of preanal appendage; m. v. p. = mesoventral process of preanal appendage; X = abdominal segment 10.

studying the American fauna have recognised the classification proposed by Ross (Armitage and Hamilton 1990; Nimmo 1986); however, those studying the Old World fauna continue to follow a pre-Ross (1944) classification of recognising three separate genera. Furthermore, workers studying the European fauna (Edington and Hildrew 1995; Vieira-Lanero 2000) have identified larval, pupal and adult characters to distinguish among these genera. Some of these characters include the extent of the curvature of the larval anal claw and presence or absence of forks in the hind wing. A lack of agreement becomes particularly confusing for taxa with range extensions over much of the Northern Hemisphere. For example, *Holocentropus picicornis* (Stephens, 1836) is assigned in Europe to *Holocentropus*, ignoring Ross' (1944) classification; however, the same species is otherwise assigned in North America to *Polycentropus*.

Twelve *Polycentropus* species are currently known from Africa (Tobias and Tobias 2009), two of which were included in this study (*Polycentropus brongus* Gibbs, 1973 from Ghana and *P. flavomaculatus* from Algeria). The placement of *P. brongus* is equivocal. *Polycentropus brongus* possesses the unique feature of having a small pouch or pocket at the base of A2 in the hind wing (character 91). This is the first known reference to this character for any polycentropodid and may represent a synapomorphy for *Polycentropus* species from the Afrotropical region. The other species also found in Africa, *P. flavomaculatus*, occurs from northern Africa (West Palearctic) to Siberia in Russia (East Palearctic region) (Morse 2011).

The present study found support (LPA parsimony analysis, LPA and TOTAL Bayesian analyses) for the monophyly of *P. flavomaculatus* and *P. vanderpooli*, the latter species restricted to the Greater Antilles. *Polycentropus* species having

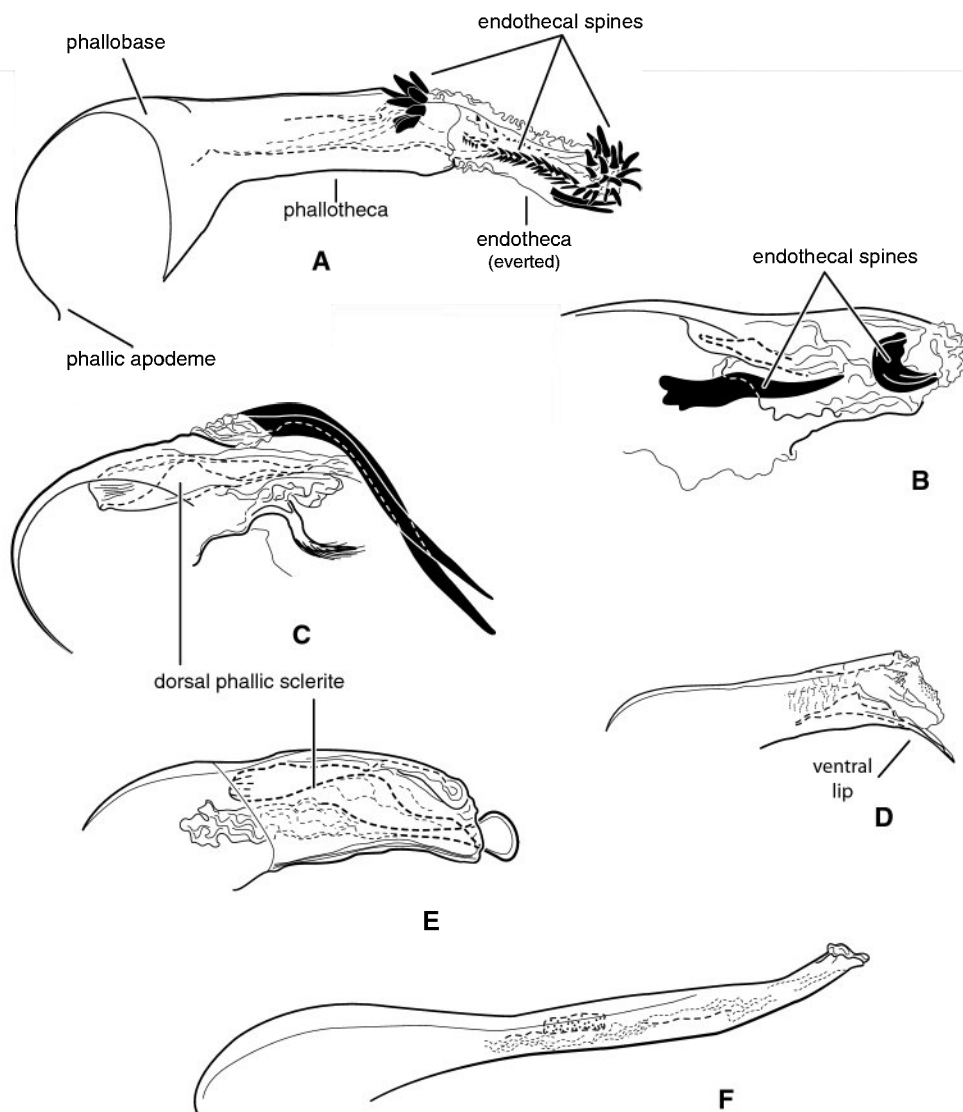


Fig. 10. Polycentropodidae, adult characters, male phallus, lateral. (A) *Antillopsyche tubicola*, (B) *Adeptophylax volutus*, (C) *Polycentropus chilensis*, (D) *Plectrocnemia spilota*, (E) *Polyplectropus recurvatus*, (F) *Cernotina* sp.

a *cu-a* crossvein in the hind wing, a characteristic shared by both of these species, constitute *Polycentropus sensu stricto* (character 87, synapomorphy). This clade was also supported by the following characters: larval protarsus half as long as protibia (character 22, synapomorphy); fork I (R2 and R3) of the hind wing present (Figs 4D, 7B) (character 84); sternum IX terminating at or beyond preanal appendage, height 3/4 of entire male genitalia (Fig. 9A, B, E) (character 95); and the possession of differentiated dorsal and ventral branches of the inferior appendage of the male genitalia (character 110).

Schmid (1955) established the genus *Placocentropus* to include a single species from Chile (*Polycentropus obtusus* (Schmid, 1955)). The discovery of three additional species from Chile (*P. aspinosus* Schmid, 1964, *P. quadriappendiculatus* Schmid, 1964 and *P. quadriaspinosus* Schmid, 1964) and an

increased familiarity with the New World fauna, led Schmid (1964) to designate *Placocentropus* as a junior synonym of *Polycentropus*. This decision was based on affinities in wing venation between the two taxa (open discoidal cell and presence of fork I in the hind wing). The two species included in this analysis (*P. aspinosus* and *P. chilensis*) constituted a monophyletic group based minimally on a distal position of *cu-a* on the forewing (Fig. 7B) (character 77); intermediate appendages fused along mesal margin to tergum X (Fig. 9C) (character 96); intermediate appendage broad (Fig. 9C) (character 97); dorsolateral process of preanal appendage absent (Fig. 8A–C) (character 101); anterior surface of inferior appendage of male genitalia with paired processes forming a fossa (Fig. 9C) (character 114); phallus with a ventral sclerotised projection (Fig. 10C) (character 116) located medially (Fig. 10C)

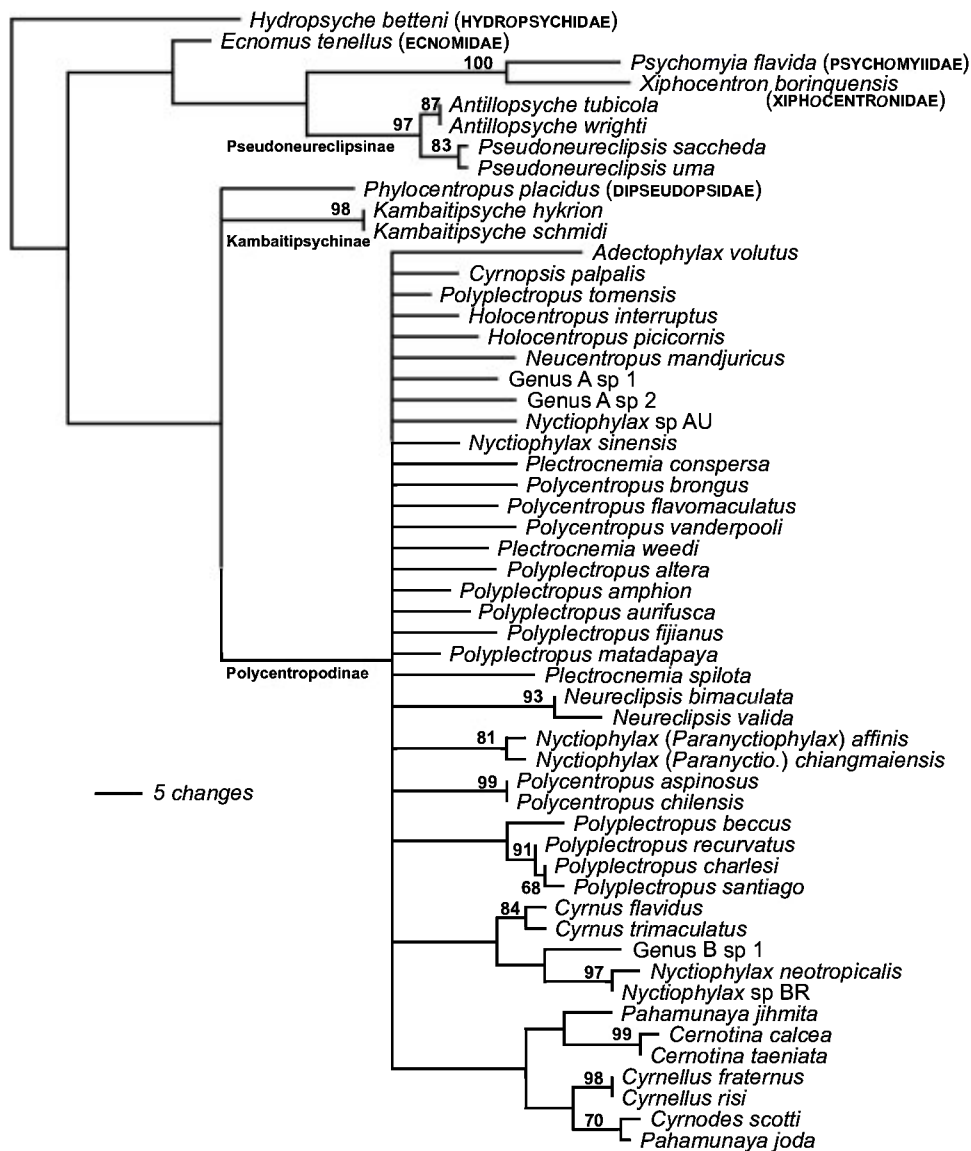


Fig. 11. Phylogeny of polycentropodid caddisflies based on parsimony analysis of the TOTAL morphological dataset (54 taxa, 122 characters). Strict consensus of 7799 equally parsimonious trees (length: 436; CI: 0.349; RI: 0.632; RC: 0.231). Numbers along internodes indicate bootstrap values.

(character 117, synapomorphy); and paired phallic structures arising apicodorsally and not from phallobase (Fig. 10C) (character 118). The current results and a careful study of the group in question substantiate the resurrection of *Placocentropus* to incorporate species currently in the *Polycentropus obtusus* group. A revision of the species in this group is currently underway by the authors.

Genus *Plectrocnemia* (91 species, 3 sampled)

The genus is well represented in most regions of the world, except the Neotropical. *Plectrocnemia* species occurring in the Northern Hemisphere are included in a broadly defined *Polycentropus* by New World workers (Armitage and Hamilton 1990; Nimmo

1986) (see above discussion of *Polycentropus sensu lato*). To avoid further confusion, the recommendation is made for the arbitrary decision by Ross (1944) to be ignored. Therefore, North American *Polycentropus* species belonging in *Plectrocnemia* before 1944 are herein reinstated to *Plectrocnemia* based primarily on original designation and second on the classification of Fischer (1962, 1972). Furthermore, for consistency, species described in *Polycentropus* post-1944 in North America, and listed by Fischer (1962, 1972) under *Plectrocnemia* or included in Nimmo's (1986) species groups 'A', 'B', 'D' and 'G', are transferred to *Plectrocnemia*.

New or revised combinations in this genus include: *Plectrocnemia albipuncta* Banks, 1930 **comb. rev.**; *Plectrocnemia aureola* Banks, 1930 **comb. rev.**; *Plectrocnemia*

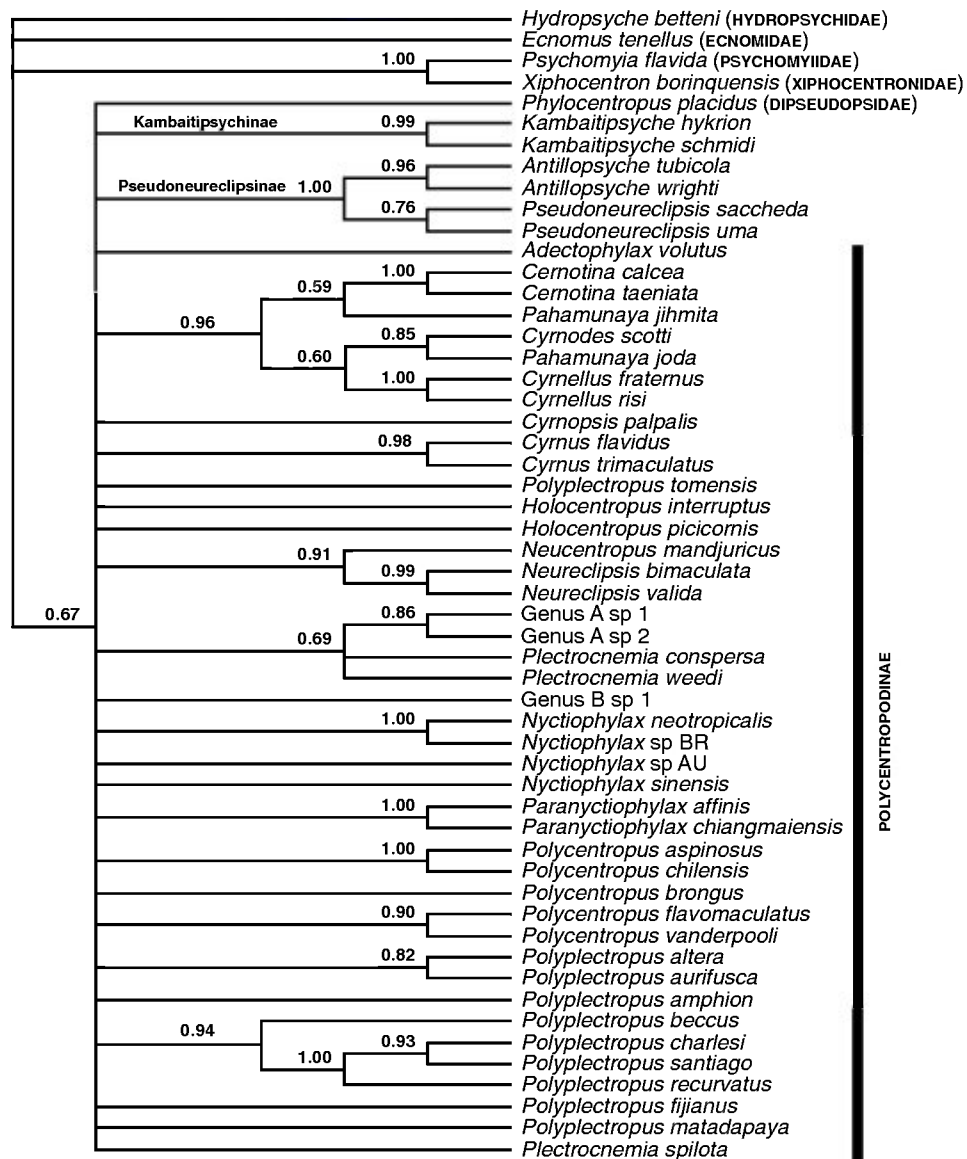
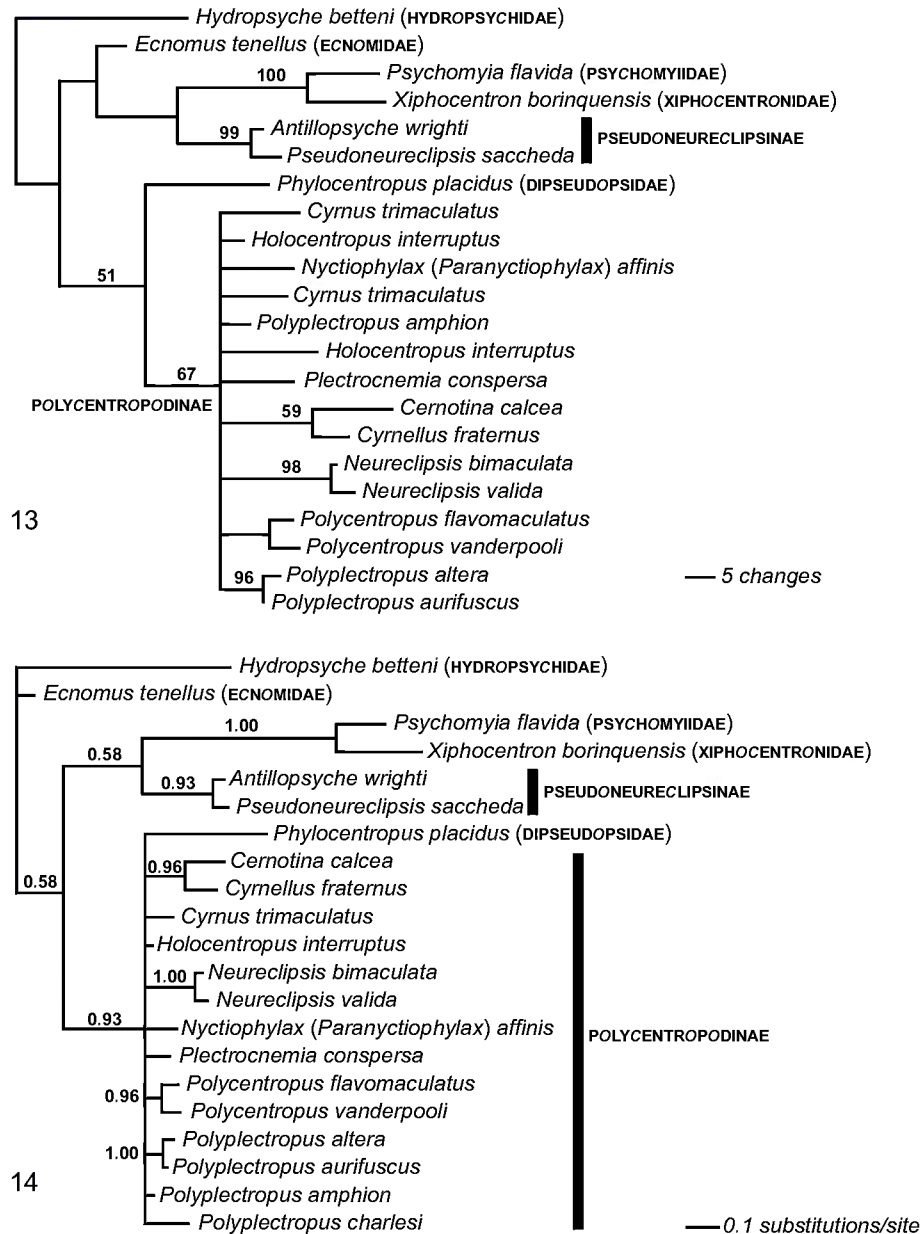


Fig. 12. Phylogeny of polycentropodid caddisflies based on Bayesian analysis of TOTAL morphological dataset (54 taxa, 122 characters) under an Mk + Gamma model (harmonic mean $\ln L = -1823.32$). Numbers above internodes indicate posterior probabilities.

cinerea (Hagen, 1861) **comb. nov.**; *Plectrocnemia clinei* Milne, 1936 **comb. rev.**; *Plectrocnemia crassicornis* (Walker, 1852) **comb. rev.**; *Plectrocnemia jenula* (Denning, in Denning and Sykora, 1966) **comb. nov.**; *Plectrocnemia icula* (Ross, 1941) **comb. nov.**; *Plectrocnemia nascotia* (Ross, 1941) **comb. nov.**; *Plectrocnemia remota* (Banks, 1911) **comb. rev.**; *Plectrocnemia sabulosa* (Leonard & Leonard, 1949) **comb. nov.**; *Plectrocnemia smithae* (Denning, 1949) **comb. nov.**; *Plectrocnemia vigilatrix*

Navás, 1933 **comb. rev.**; *Plectrocnemia weedi* (Blickle & Morse, 1955) **comb. nov.**

Tasmanoplegas, with a single included species known only from western Tasmania, was recently synonymised with *Plectrocnemia* (Oláh and Johanson 2010); however, it differs from *Plectrocnemia* in having stalked fork II in the hind wing, as well as differences in the male and female genitalia (Neboiss 1977). The placement of *P. spilota* (Neboiss, 1977) was unresolved in our analysis.



Figs 13, 14. Phylogeny of polycentropodid caddisflies. *13*, Parsimony analysis of LPA (larval, pupal, adult) morphological dataset (25 taxa, 122 characters). Strict consensus of seven equally parsimonious trees (length: 257; CI: 0.482; RI: 0.576; RC: 0.278). Numbers on internodes indicate bootstrap values. *14*, Bayesian analysis of LPA morphological dataset (25 taxa, 122 characters) under an Mk+Gamma model (harmonic mean lnL = -1078.23). Numbers above internodes indicate posterior probabilities. Scale bar indicates model based genetic distance.

Genus *Holocentropus* (12 species, 2 sampled)

Species traditionally placed in *Holocentropus* are restricted to the Nearctic and Palearctic regions. Like *Plectrocnemia*, *Holocentropus* species are placed in a broadly defined *Polycentropus* by North American workers following Ross' (1944) classification (Nimmo 1986; Armitage and Hamilton 1990;) (see above discussion of *Polycentropus sensu lato*). The two *Holocentropus* species included in this study, *H. picicornis* and *H. interruptus* (Banks, 1914), did not constitute a monophyletic group, except with weak support in the ADULT parsimony analysis. Nonetheless, a similar recommendation is made, as for *Plectrocnemia*, to ignore the decision by Ross (1944). Therefore, *Holocentropus* is treated as a valid genus to include *Polycentropus* species previously

belonging in *Holocentropus* based primarily on original designation, but also following the classification of Fischer (1962, 1972). Furthermore, for consistency, species described in *Polycentropus* post-1944 in North America, and listed by Fischer (1962, 1972) under *Holocentropus* or included in Nimmo's (1986) species groups 'E' and 'I', are transferred to *Holocentropus*.

New or revised combinations include: *Holocentropus chellus* (Denning, 1964) **comb. nov.**; *Holocentropus flavus* Banks, 1908 **comb. rev.**; *Holocentropus glacialis* Ross, 1938 **comb. rev.**; *Holocentropus grellus* Milne, 1936 **comb. rev.**; *Holocentropus interruptus* Banks, 1914 **comb. rev.**; *Holocentropus melanae* Ross, 1938 **comb. rev.**; *Holocentropus milaca* (Etnier, 1968) **comb. nov.**; and *Holocentropus picicornis* (Stephens, 1836) **comb. nov.**

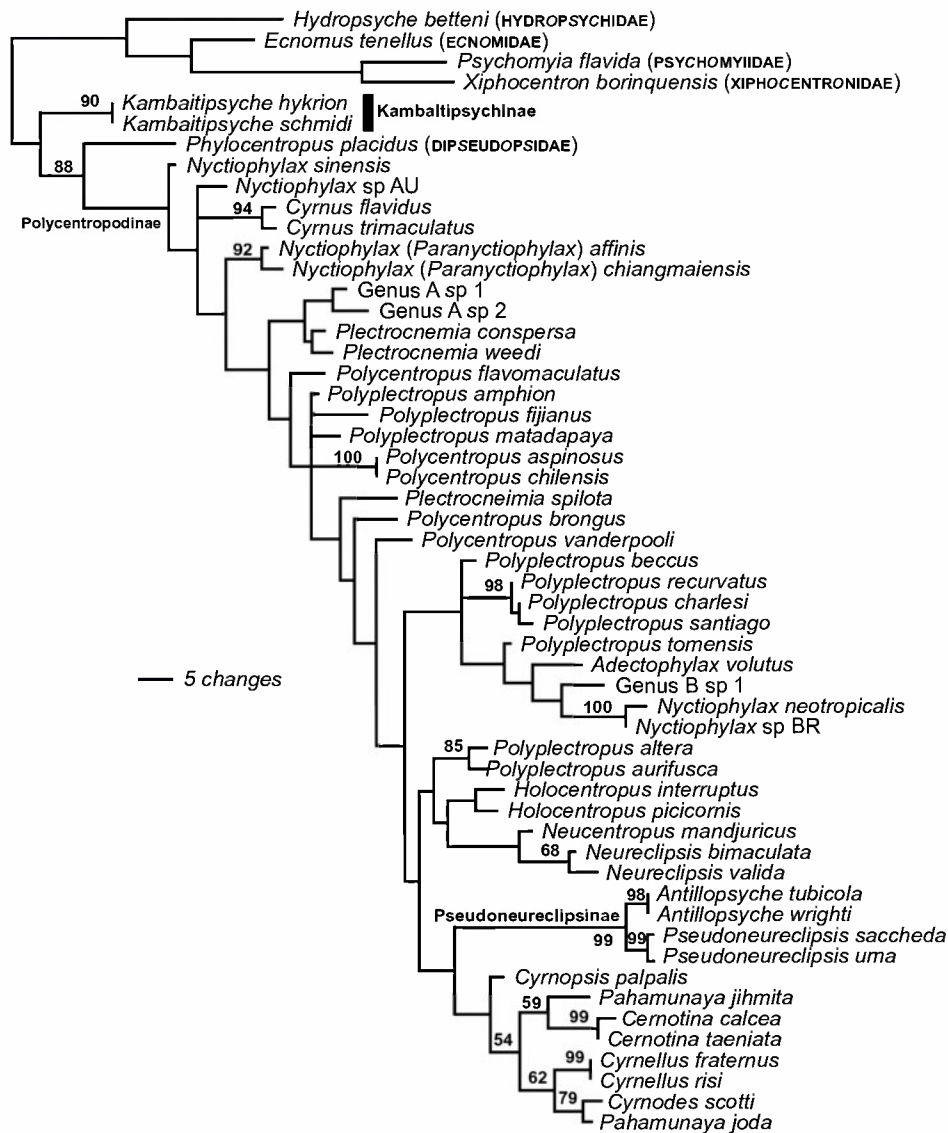


Fig. 15. Phylogeny of polycentropodid caddisflies based on parsimony analysis of ADULT morphological dataset (54 taxa, 86 characters). Strict consensus of 48 equally parsimonious trees (length: 385; CI: 0.330; RI: 0.636; RC: 0.210). Numbers along internodes indicate bootstrap values.

Genus *Polyplectropus* *sensu lato* (219 species, 10 sampled)

Polyplectropus is widespread and has been recorded from the tropical and subtropical regions of the world with most species occurring in the Oriental and Neotropical regions. In total, 10 species of *Polyplectropus* from throughout its biogeographic range were incorporated in this study to test the monophyly of the genus. Species were included from Sri Lanka (*Polyplectropus matadapaya* Schmid, 1958), Fiji Islands (*Polyplectropus fijianus* Banks, 1936), Nepal (*Polyplectropus amphion* Malicky, 1997), New Zealand (*Polyplectropus aurifuscus* McFarlane, 1956 and *Polyplectropus altera* McFarlane, 1981, in McFarlane and Cowie 1981), North and Central America (*P. charlesi* (Ross, 1941) and *P. santiago* (Ross, 1947)), northern South America

(*Polyplectropus beccus* Hamilton & Holzenthal, 2005 and *P. recurvatus* (Yamamoto, 1966)) and Gabon, Africa (*P. tomensis*, until recently the single species in the genus *Eodipseudopsis*).

Polyplectropus tomensis was originally described from the island of São Tome off the coast of Gabon, Africa, and is known only from female specimens. It has also been recorded from the Democratic Republic of Congo (Marlier 1962). Marlier (1959) initially described *Eodipseudopsis* in Dipseudopsidae and the genus was later transferred to Polycentropodidae by Weaver and Malicky (1994). *Eodipseudopsis* was recently synonymised with *Polyplectropus* (Oláh and Johanson 2010). Our results do not corroborate this decision. The immature stages are unknown.

This study neither supports nor rejects a monophyletic *Polyplectropus* as currently recognised. A monophyletic New

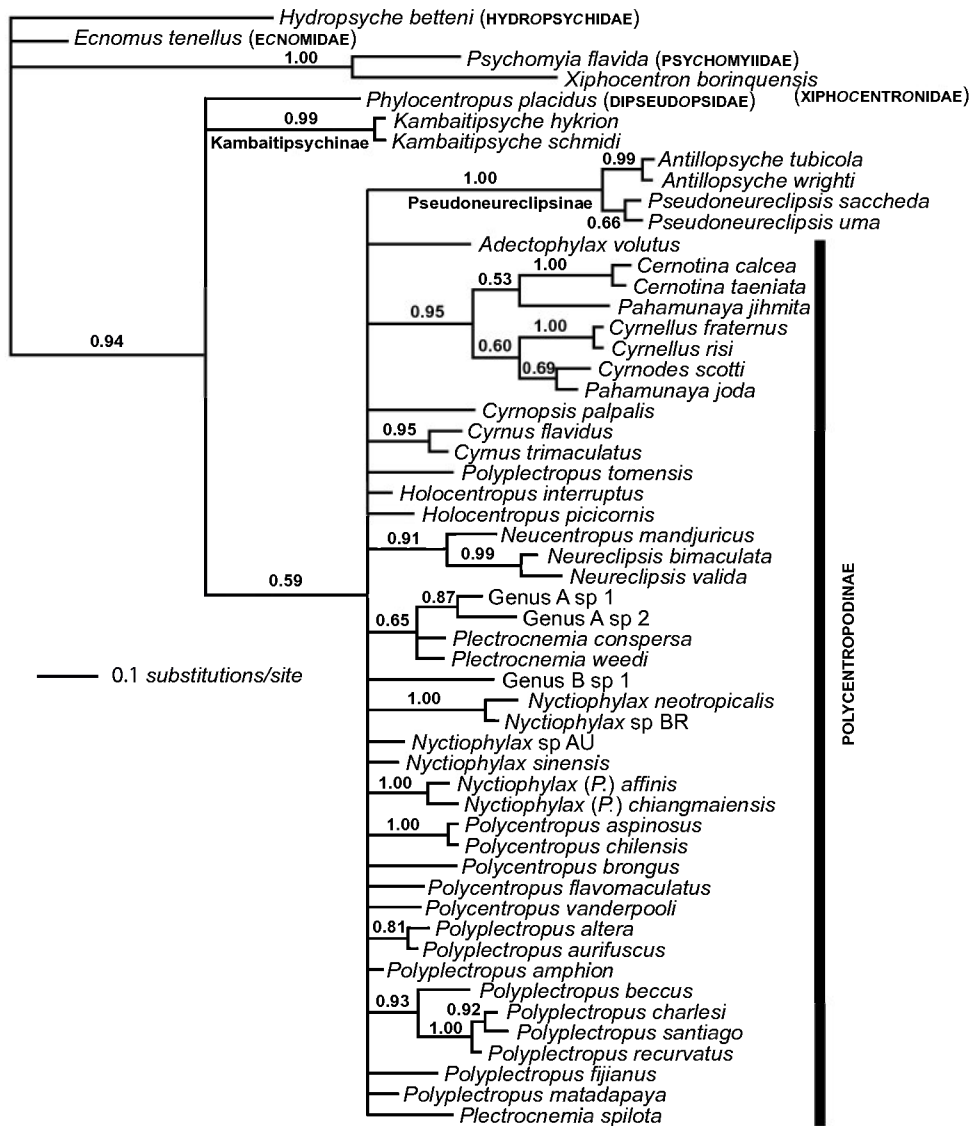


Fig. 16. Phylogeny of polycentropodid caddisflies based on Bayesian analysis of ADULT morphological dataset (54 taxa, 86 characters) under an Mk + Gamma model (harmonic mean lnL = -1580.10). Numbers above internodes indicate posterior probabilities. Scale bar indicates model based genetic distance.

World *Polyplectropus* (i.e. with the exception of *Polyplectropus beccus*, here referred to as New World *Polyplectropus sensu stricto*) was consistently recovered in all analyses (see also Chamorro and Holzenthal 2010). Synapomorphies of New World *Polyplectropus s. s.* are a lightly pigmented A1 vein of the forewing (Fig. 7E) (character 78), which is positioned anterad towards vein Cu₂ (character 76). The presence of an apically bent Cu₂ vein in the forewing (character 72) (Fig. 7E) was found to be a synapomorphy for all New World *Polyplectropus*, including *P. beccus*, in all relevant analyses except in the ADULT parsimony analysis (Fig. 15).

The monophyly of New Zealand *Polyplectropus* (*P. aurifuscus* and *P. altera*) was supported in analyses of the LPA dataset and in the Bayesian analysis of the ADULT dataset. This clade is supported by the presence of the following traits: apex of pupal mandible with long apical ‘whip’ (character 32); intermediate appendage present as a free structure from tergum X (Figs 8B, E, 9B, E) (character 96); and paired processes forming a fossa on the anterior surface of the inferior appendage (character 114). In addition to the three *Polyplectropus* species included in this study from the Australasian region, seven more species are also known to occur in the region. Formal designation of a new genus to contain New Zealand *Polyplectropus* may take place once additional adult and larval material has been examined. Placement of *Polyplectropus* species from the Oriental region and the Polynesian subregion of the Australasian region, represented

by *P. matadapaya*, *P. amphion* and *P. fijianus* in this analysis (Figs 11, 12), remains unresolved.

Two new genera

Three species from Brazil and one from Venezuela identified as belonging to Genus A and two more species in Genus B will be described and assigned to new genera in subsequent publications. New Genus A species lack a visible sclerotised ring surrounding the phallocrypt as a result of the fusion of the plates of the preanal appendage of the male genitalia (character 107) and have a hyper-sessile fork V relative to *m-cu* in the hind wing (character 90).

Genus B sp. 1 has a synscleritous sternum IX (character 95), sclerotised intermediate appendage (character 98), elongate inferior appendage of the male genitalia (character 112) and a ventral sclerotised projection on the phallus (character 116). These features are also present in *Nyctiophylax tacuarembu* Angrisano, 1994 from Uruguay, a species not included in this study, but clearly belonging in Genus B.

General conclusions

The present morphology-based study is the first to hypothesise phylogenetic relationships among Polycentropodidae *sensu lato*. This study incorporates characters of the larvae, pupae and adults and a large taxon sample, incorporating representatives from all currently recognised genera and from all biogeographic regions, to infer the phylogeny of polycentropodids. Phylogenetic estimates change when different data partitions are used. The addition of highly incomplete characters when the overall number of characters is low and non-missing characters evolve either very quickly or very slowly (high variation in rates of change), contributes greatly to ambiguity and results in consensus trees with poor resolution. Our understanding of phylogenetic relationships within Polycentropodidae has improved as a result of this study; however, gaps in our knowledge clearly exist. Information on biology, ecology and morphology of immature stages for many important polycentropodid lineages remain unknown; future studies aimed at obtaining this knowledge will only enhance our phylogenetic estimates. Nevertheless, this study is a positive contribution towards a stable phylogenetic system of polycentropodid caddisflies and their relatives rooted in cladistic principles.

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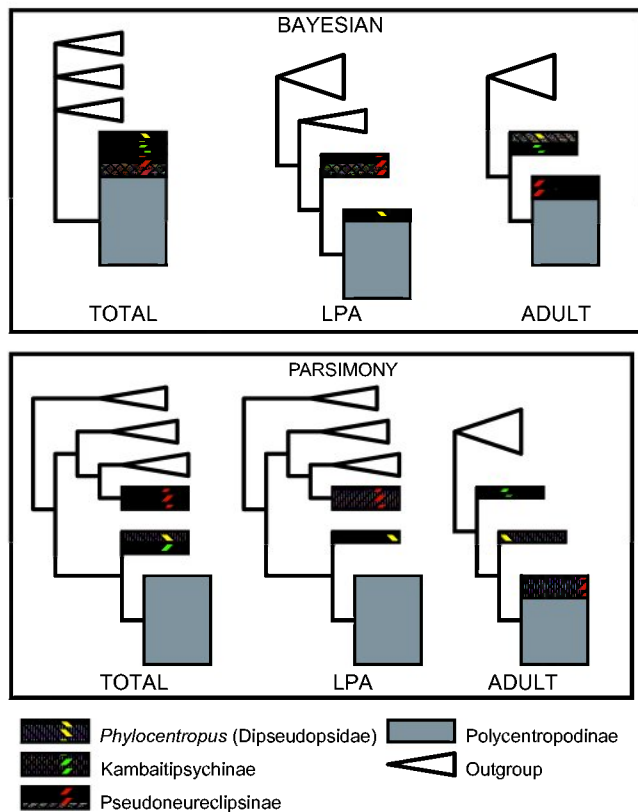


Fig. 17. Diagrammatic summary of results of Bayesian and parsimony analyses of TOTAL, LPA (larval, pupal, adult) and ADULT datasets.

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Appendix 1. Characters and states for cladistic analysis

Larval characters

1. *Shape of prelabio-hypopharyngeal lobe* (F&W6) (P9): **0**, relatively short, apex broadly rounded; **1**, elongate, tapered to apex. The prelabio-hypopharyngeal lobe is located basad of the prementum and encompasses the hypopharynx. State 1 is observed in all taxa except the outgroup species, *Hydropsyche betteni*.
2. *Sclerotisation of prelabio-hypopharyngeal lobe* (F&W7) (P10): **0**, prelabio-hypopharyngeal lobe largely membranous, except for palpiger and associated sclerites and prementum; **1**, at least basal portion of dorsal surface of lobe and most or all of ventral surface heavily sclerotised, prementum not distinguishable. State 1 is observed in all taxa except the outgroup species *Hydropsyche betteni* Ross.
3. *Labium (spinneret)* (W&M5): **0**, short; **1**, (Fig. 2F), longer than other mouthparts (Fig. 2G). An elongate labium is observed in psychomyiids, xiphocentronids, pseudoneureclipsines and dipseudopsids. All these taxa construct dwelling tubes with associated matter, such as large sand grains.
4. *Labial palpi* (F&W8) (P 11) (LMT16, in part): **0**, present; **1**, absent (Fig. 2G). State 1 is characteristic of taxa having an elongate labium.
5. *Condition of labial palpi* (F&W8) (P 11) (LMT16, in part): **0**, prominent; **1**, appressed to sides of prelabio-hypopharyngeal lobe (Fig. 2F). State 1 is characteristic of polycentropodines.
6. *Mandibles* (Wiggins 1996): **0**, both mandibles with mesal brushes; **1**, right mandible never with a brush (Fig. 2H). Dipseudopsids have mesal brushes in both mandibles; an autapomorphy of *Phylocentropus placidus* (Banks).
7. *Anterior tentorial pits* (F&W11) (P7) (Fig. 3D): **0**, in contact with anterior arms of dorsal ecdysial line; **1**, arising on dorsal (frontoclypeal) apotome some distance mesad of cleavage line. State 1 is an autapomorphy of the outgroup taxon *Hydropsyche betteni*.
8. *Muscle scars of head and pronotum*: **0**, darker than surrounding area; **1**, as light as or lighter than surrounding area (Fig. 3D). Muscle scars are round spots evident on the dorsum of the head and indicate points of muscle attachment (Wiggins 1996). State 1 is evident in ecnomids, psychomyiids, xiphocentronids, pseudoneureclipsines, *Paranyctiophylax*, *Cyrnellus* and *Polyplectropus*.
9. *Ventral apotomes* (F&W12) (P14) (Fig. 2E): **0**, anterior apotome only; **1**, anterior and posterior apotomes present. State 1 is an autapomorphy of the outgroup taxon, *Hydropsyche betteni*.
10. *Submental sclerites* (Fig. 2F): **0**, present; **1**, absent. Xiphocentronids lack submental sclerites.
11. *Condition of submental sclerites* (Fig. 2F): **0**, fused; **1**, separate. Psychomyiids have separated submental sclerites.
12. *Pronotal tergal ridge* (F&W16, in part) (P22): **0**, absent; **1**, entire. *Hydropsyche betteni* has an entire pronotal tergal ridge.
13. *Pronotum hind angles* (F&W18) (P24): **0**, not prominent, separated by entire width of sternum; **1**, extending ventrally and coming into contact on sternum behind procoxae. Portions of the pronotum extend ventrally and are visible behind the procoxae in all taxa studied except for *Hydropsyche betteni*.
14. *Larval fore-trochantin* (LMT13) (Fig. 3B, C): **0**, free from episternum; **1**, fused with episternum, with or without suture. The structure of the trochantin is useful for distinguishing among genera in Psychomyioidea. The trochantin derives from the prothoracic pleuron (Snodgrass 1935; Wiggins 1996).
15. *Suture of larval fore-trochantin* (LMT13) (Fig. 3B, C): **0**, fused, but with suture distinguishing trochantin from episternum; **1**, trochantin fused with episternum and without suture. State 0 is characteristic of psychomyiids, xiphocentronids and pseudoneureclipsines. State 1 is observed in dipseudopsids and polycentropodines.
16. *Shape of trochantin* (LMT14) (W&M1) in part (Fig. 3B): **0**, acute and short; **1**, acute and elongate; **2**, truncate and broad. An acute and elongate trochantin is present in ecnomids, dipseudopsids and polycentropodines. Psychomyiids have a truncate and broad trochantin.
17. *Mesonotum sclerites* (F&W27) (P28) in part (2A, D): **0**, membranous. **1**, sclerotised, dorsal ecdysial line present or absent. A membranous mesonotum is characteristic of psychomyiids, xiphocentronids, dipseudopsids and polycentropodines.
18. *Larval mesopleuron*: **0**, unmodified; **1**, with flat process extending anteriorly. This is an autapomorphy of *Xiphocentron* Brauer.
19. *Metanotal sclerites* (F&W23) (P31) in part (Fig. 3A): **0**, membranous; **1**, sclerotised, dorsal ecdysial line present or absent. A membranous metanotum is characteristic of psychomyiids, xiphocentronids, dipseudopsids and polycentropodines.
20. *Metanotal parallel black lines* (Tachet *et al.* 2001; Flint 1964b): **0**, absent; **1**, present. These dark longitudinal lines are present in pseudoneureclipsines.
21. *Secondary setation of larval legs* (LMT12) (Fig. 3A): **0**, absent; **1**, present. Secondary setae are those appearing in later instars. This condition is present in all taxa examined except psychomyiids, xiphocentronids and pseudoneureclipsines.
22. *Larval protarsi length* (Hudson *et al.* 1981): **0**, nearly as long as protibia (at least 2/3 as long as protibia) (Fig. 3A); **1**, half as long as protibia; **2**, fused protarsi and protibia; **3**, longer than protibia. The relative length of the protarsi is informative at the generic level. State 1 is a synapomorphy for *Polycentropus sensu stricto* (*Polycentropus vanderpooli* + *Polycentropus flavomaculatus*). State 2 is observed in *Xiphocentron* and state 3 in *Phylocentropus placidus*.
23. *Pleural region of abdominal segments II-VIII* (F&W36) (P37) in part (Fig. 3A): **0**, with primary setae only; **1**, each segment with fringe of secondary setae (lateral fringe) that covers most of the pleural region. State 1 is characteristic of all taxa examined except psychomyiids, xiphocentronids and hydropsychids.
24. *Abdominal tergum IX* (F&W34) (P 45) in part: **0**, with two small sclerites, at least one long seta arising at posterior margin of each sclerite; **1**, membranous, at least one pair of long setae arising at posterior margin of tergum. This segment is near the anal proleg. State 1 is observed in ecnomids, psychomyiids, xiphocentronids and pseudoneureclipsines.
25. *Anal proleg orientation* (F&W38) (P47) in part (Figs 2B, 3A): **0**, all instars with anal proleg very prominent, but segment IX entire, claw pointing downwards; **1**, all instars with anal proleg very prominent, incorporating part of segment IX. State 1 is characteristic of all taxa examined except *Hydropsychidae betteni*, *Psychomyia flavida* Hagen and *Xiphocentron*.
26. *Larval abdominal gills* (Wiggins 1996). **0**, absent (Fig. 3A); **1**, present (branched). Of the taxa included in this analysis, only *Hydropsyche betteni* possesses gills.
27. *Basal segment of anal proleg* (Lepneva 1970; Hudson *et al.* 1981): **0**, longer than distal segment (Fig. 2B); **1**, shorter than distal segment (Fig. 3A). *Polyplectropus* and *Neureclipsis* possess a short distal segment.
28. *Basal segment of anal proleg* (Lepneva 1970; Hudson *et al.* 1981): **0**, bearing secondary setae (Fig. 3A); **1**, lacking secondary setae. All taxa, except *Neureclipsis*, *Psychomyia*, *Xiphocentron* and pseudoneureclipsines, lack secondary setae.
29. *Anal claw* (Wiggins 1996): **0**, lacking conspicuous pointed teeth on ventral concave margin (Fig. 2B, C); **1**, with row of small spines; **2**, teeth much shorter than claw; **3**, teeth almost as long as claw (Figs 2D, 3A). The concave margin of the anal claw of the proleg may have small teeth of several sizes and variedly arranged.
30. *Dorsal accessory spine on anal claws* (Wiggins 1996): **0**, absent (Fig. 2C, D); **1**, present (Fig. 2B).

(continued next page)

Appendix 1. (continued)

31. *Number of dorsal accessory spines on anal claws*. **0**, each with only 1 (Fig. 2B); **1**, each with 2.
 32. *Curvature of anal claw* (Hudson *et al.* 1981): **0**, curved to sharply curved, ~90 degrees (Fig. 2B, D); **1**, obtusely curved (Fig. 2C). New Zealand *Polyplectropus* (*Polyplectropus altera* and *Polyplectropus aurifuscus*), *Cyrnus trimaculatus*, *Cyrnus flavidus* and *Plectrocnemia conspersa* have an obtusely curved anal claw.

Pupal characters

33. *Apex of pupal mandible* (Flint 1964a, 1964b; Muñoz-Quesada and Holzenthal 1997): **0**, not tapering into a narrow whip-like process; **1**, with long apical 'whip'. State 1 is a synapomorphy of psychomyiids and xiphocentronids. Mandibles are used to clean pupal cases and for emergence during eclosion.
 34. *Pupal mandible* (Flint 1964a, 1964b): **0**, inner tooth absent; **1**, inner tooth present. The presence of an inner tooth is a synapomorphy of *Pseudoneureclipsis*.
 35. *Pupal pre-segmental hook-plates present on abdominal segments* (Flint 1964a, 1964b; Lepneva 1970; Gibbs 1973; Tachet *et al.* 2001) (Fig. 2A). **0**, 2–7; **1**, 2–8; **2**, 3–7; **3**, 3–8. These are small sclerites present on the anterior margin of a given abdominal segment bearing posteriorly directed crochets used to move forward and backwards in the pupal enclosure (Lepneva 1970). State 0 is present in xiphocentronids, state 1 in psychomyiids, state 2 in hydropsychids and state 3 in all other taxa examined.
 36. *Pupal post-segmental hook-plates present on abdominal segments* (Flint 1964a, 1964b; Lepneva 1970; Gibbs 1973; Tachet *et al.* 2001): **0**, 3–4; **1**, 5 (Fig. 2A). These are small sclerites present on the posterior margin of a given abdominal segment bearing anteriorly directed crochets, used for movement within the pupal enclosure (Lepneva 1970). State 1 is present in all except *Hydropsyche betteni*.

Adult characters

37. *Setae between ommatidia*: **0**, absent; **1**, present. Small setae are present between the facets of the compound eye in *Cyrnodes*, *Kambaitipsyche* and *Psychomyia*.
 38. *Frontal setal wart*: **0**, enlarged; **1**, small (Figs 4A, 5A–D).
 39. *Antennal setal wart* (Figs 4A, 5A–D): **0**, prominent (reaching or almost reaching occipital wart) (Figs 4A, 5A–D); **1**, half as long as inter frontal-occipital space (not reaching occipital wart); **2**, scattered (amorphous, unstructured).
 40. *Preocellar setal wart*: **0**, absent; **1**, present (Figs 4A, 5D).
 41. *Shape of preocellar setal wart*: **0**, fused posteriorly with ocellar wart (LMT5) (Fig. 5D); **1**, small, barely visible (Fig. 5A); **2**, deltoid to rectangular, edges obscured (Fig. 4A); **3**, rounded, prominent.
 42. *Ocellar setal wart*: **0**, oblong (length 2 × width) - 1 and one half times longer than tall (Fig. 5A); **1**, oblong, tapering laterally (angled), irregularly-shaped (triangular to oblong) (Fig. 4A); **2**, ovoid, short (length = width); **3**, quadrate to oblong not angled, largely perpendicular to midline; **4**, broadly deltoid; **5**, sparse, barely visible (Fig. 5B); **6**, narrowly oblong (3 × longer than tall); **7**, scattered, amorphous (Fig. 5C).
 43. *Location of ocellar setal wart*: **0**, midline (Fig. 5B, C); **1**, below midline (near occiput) (Fig. 5D); **2**, centre lateral (Fig. 5A).
 44. *Postoccipital setal wart* (Figs 4A, 5A–D): **0**, present; **1**, apparently absent.
 45. *Occipital setal wart*: **0**, long, at or extending beyond eye midline (Figs 4A, 5A–C); **1**, short, less than eye midline, without anterior taper (oblong to quadrate) (Fig. 5D).
 46. *Anterolateral and hypomedial setal warts*: **0**, fused (Fig. 6A, B); **1**, not fused.
 47. *Fusion and shape of anterolateral and hypomedial setal warts*: **0**, fused dorsally, face not bulging (Fig. 6A); **1**, fused, bulging, sclerotised (Fig. 6B).
 48. *Mesoscutal setal wart*: **0**, absent; **1**, present (Figs 4A, 5A–D).
 49. *Shape of mesoscutal setal wart*: **0**, quadrate fused along midline; **1**, angled with respect to midline; **2**, parallel to midline or circular (Figs 3A, 5A–D).
 50. *Shape of median pronotal setal wart*: **0**, oblong (Fig. 5A, D); **1**, quadrate to broadly rectangular (Figs 4A, 5B–C); **2**, ovoid.
 51. *Tegulae*: **0**, inversely deltoid (Fig. 5D); **1**, heart-shaped, lateral lobe more pronounced (Figs 4A, 5A–C); **2**, oblong, vertical.
 52. *Shape of maxillary palpomere 2* (F&W45) (P56) (Li and Morse 1997): **0**, cylindrical (length greater than twice diameter); **1**, ovoid (length approximately equal diameter) (Fig. 6C, D). Maxillary palpomere 2 in some taxa has an enlarged setose cushion. Once the palpomere is measured, including the setose cushion, the length is 2 × the diameter. However, for consistency the palpomere was coded as being ovoid and the presence of the setose cushion is addressed in the next 2 characters. The setose cushion begins where palpomere 3 inserts into palpomere 2.
 53. *Apex of maxillary palpomere 2*: **0**, unmodified; **1**, modified mesoapically (Figs 5D, 6C). See remarks for previous character.
 54. *Modification of apex of maxillary palpomere 2*: **0**, with stout mesoapical setae, but no pronounced cushion (Fig. 6C); **1**, with mesoapical lateral point; **2**, with slight cushion (half size of palpomere); **3**, with mesoapical setose cushion (setose cushion almost as long as 'base' of palpomere) (Fig. 6D). See remarks for character 52.
 55. *Maxillary palps*: **0**, apical insertion of palpomere 3 into palpomere 2; **1**, preapical insertion of palpomere 3 into palpomere 2 (Figs 4B, 6C, D).
 56. *Maxillary palpomere 3*: **0**, equal to or slightly longer in length than palpomere 2; **1**, shorter than palpomere 2; **2**, more than twice palpomere 2 (Figs 4B, 6C, D).
 57. *Maxillary palpomere 4*: **0**, equal to palpomere 3; **1**, shorter than palpomere 3 (Figs 4B, 6C, D).
 58. *Maxillary palpomere 5*: **0**, same as or slightly larger size than preceding segment; **1**, more than 3 × size of preceding segment (Figs 4B, 6C, D).
 59. *Labial palpomere 3*: **0**, more than twice preceding; **1**, equal to or slightly larger than preceding.
 60. *Adult fore tibia* (LMT7): **0**, with 3 spurs; **1**, with 2 spurs; **2**, with 1 spur.

Wing characters

Several features of the wing venation were included in this analysis. These include several conventional characters traditionally used in designation and recognition of taxa, such as the presence or absence of wing forks and of certain crossveins. Additional characters were identified, such as the relative placement of wing forks relative to a given crossvein (e.g. rooted, sessile, or petiolate), the relative position of crossveins, the position and pigmentation of certain wing veins in relation to adjacent veins and union of wing veins to the wing margin. Rooted is when a given wing fork originates towards the base of the wing relative to the nearest crossvein. 'Sessile' describes a fork originating at the point of contact with a given crossvein, and 'petiolate' refers to a given wing fork originating towards the apex of the wing relative to a given crossvein and having a kind of basal 'stem' (Figs 4C, D, 7A–F).

61. *Forewing (FW) crossvein c-sc between costa and subcosta (near mid-wing)*: **0**, present; **1**, absent.
 62. *Fork I FW (R2 and R3)*: **0**, present (veins not fused); **1**, absent (veins fused) (Fig. 7D, F).
 63. *Fork I FW in relation to crossvein radial 2 (r₂)*: **0**, rooted (in relation to r₂ crossvein) (Fig. 7A); **1**, petiolate (Fig. 7E).

(continued next page)

Appendix 1. (continued)

64. Ratio of discoidal cell to *Rs* (radial sector) FW: **0**, between 1 : 1 and 2 : 1 (Figs 4C, 7B, C); **1**, between 2 : 1 and 3 : 1 (Fig. 7A); **2**, more than 3 : 1 (Fig. 7D).
65. Median cell FW: **0**, closed (Fig. 4C); **1**, open (Fig. 7F).
66. Fork III FW (M_1 and M_2): **0**, present (not fused) (Fig. 4C); **1**, absent (fused) (Fig. 7F).
67. Fork III FW in relation to medial (*m*) crossvein: **0**, sessile; **1**, petiolate (Fig. 4C).
68. Fork IV FW (M_3 and M_4) in relation to *m* crossvein: **0**, sessile; **1**, petiolate; **2**, rooted (Fig. 7A).
69. Fork V FW (Cu_{1a} and Cu_{1b}) (LMT6) in part: **0**, present (not fused) (Figs 4C, 7); **1**, absent (fused).
70. Fork V FW (Cu_{1a} and Cu_{1b}) in relation to *m-cu* crossvein: **0**, sessile (Fig. 7D, F); **1**, petiolate (Figs 4C, 7B, C, E).
71. Thyridial cell forewing (F&W58) (P123) in part: **0**, contiguous with medial cell or fork (when medial cell not present) (medial cell sessile) (Figs 4C, 7A–D, F); **1**, both cells separated by at least one-quarter length of thyridial cell; **2**, *m-cu* beyond base of medial cell or fork by almost a quarter of medial cell.
72. Cu_2 fusion to margin: **0**, not bowed; **1**, bowed (Fig. 7E).
73. Crossvein anal 3-anal 2 (a_3 – a_2) FW: **0**, absent; **1**, present. Crossvein present in pseudoneureclipsines.
74. Anal veins FW: **0**, 2A and 1A meeting on 3A and space between veins less than or equal to 2A (Figs 4C, 7A–F); **1**, 2A and 1A meeting at same point on 3A (looped-anal veins); **2**, 3A + 2A meeting 1A distally; **3**, 2A meeting 1A not 3A.
75. $A1+2+3$ and Cu_2 : **0**, not meeting at arculus (Fig. 7A); **1**, meeting at arculus (Figs 4C, 7D).
76. Forewing $A1$ vein position **0**, towards A_{2+3} (Fig. 4C); **1**, towards Cu_2 (Fig. 7E).
77. Position of crossveins *cu-a* in the FW: **0**, proximal; **1**, mesal (Figs 4A, 7C, D, F); **2**, distal (Fig. 7B, E).
78. Forewing $A1$ pigmentation: **0**, lightly pigmented (hyaline) (Fig. 6E); **1**, pigmented (Fig. 4C).
79. Costa of hind wing (HW): **0**, sinuate (Fig. 7F); **1**, linear (Figs 4D, 7A–E).
80. Fusion of subcosta and radial 1 HW: **0**, not fused into highly sclerotised vein (R1 may be very light, apically only one vein) (Figs 4D, 7A–E); **1**, fused into single vein (Fig. 7F).
81. Sclerotisation of fused subcosta and radial 1 of HW: **0**, fused into single highly sclerotised vein (Fig. 7F); **1**, fused, but not into highly sclerotised vein.
82. Radial 1 vein of HW: **0**, reaching wing margin (Figs 4D, 7A–E); **1**, not reaching wing margin.
83. HW discoidal cell (P127): **0**, closed (Figs 4D, 7A, C); **1**, open (Fig. 7B, D–F).
84. Fork I (R_2 and R_3) HW: **0**, absent (fused) (Fig. 7A, C–F); **1**, present (not fused) (Figs 4D, 7B).
85. Fork I (R_2 and R_3) relative to crossvein r_2 : **0**, petiolate (Fig. 4D); **1**, sessile; **2**, rooted.
86. Fork II (R_4 and R_5) HW relative to crossvein *r-m*: **0**, rooted (Fig. 7A); **1**, sessile; **2**, petiolate (Figs 4D, 7B–F).
87. Cubito-anal (*cu-a*) crossvein HW: **0**, absent; **1**, present. This is a synapomorphy for *Polycentropus sensu stricto*.
88. Fork III (M_1 and M_2) HW: **0**, present (not fused) (Fig. 7A); **1**, absent (fused) (Figs 4D, 7B–F).
89. Fork of medial vein relative to crossvein *m-cu* HW: **0**, rooted (Fig. 7D); **1**, petiolate (Fig. 7E); **2**, sessile (Fig. 4D).
90. Fork V relative to crossvein *m-cu* HW: **0**, rooted; **1**, sessile (Fig. 7B, C); **2**, petiolate (Fig. 7A, D–F).
91. Sclerotised enlargement at base of A_2 HW: **0**, present; **1**, absent. Autapomorphy of *Polycentropus brongus* Gibbs.

Male genitalia characters

92. Sternum IX shape: **0**, uniformly broad (Fig. 8C–F); **1**, uniformly narrow; **2**, abruptly narrowing dorsally (Fig. 8A, B); **3**, posteromesally produced into enlarged sometimes ‘clasper-like’ lobes. Sternum IX is a large, sclerotised, entire stemite open dorsally and bearing setae on its posterior half.
93. Tergum IX: **0**, sclerotised and fused to sternum IX; **1**, membranous and intimately fused with TX, absent; **2**, ‘hinged’ (meeting) with sternum IX at pleural region (dorsally sclerotised); **3**, present as irregularly shaped laterodorsal sclerite (vestige). Segment IX may form a synscleritous structure and may be considered the primitive condition present in some polycentropodid groups, such as Genus B. However, the trend in the group is towards loss of dorsal sclerotisation of segment IX. Sternum IX is ‘open’ dorsally, whereas tergum IX is reduced to a latero-dorsal sclerite with poorly defined margins (*sensu* Roy *et al.* 1980) (Fig. 8C) or completely membranous and intimately fused with segment X (Nielsen 1957) (Fig. 8D, E). The degree of sclerotisation of tergum IX may be difficult to interpret in some groups (Fig. 8A).
94. Tergum X shape: **0**, broad membranous lobe (Figs 8, 9); **1**, elongate and narrow (longer than rest of genitalia); **2**, apically incised, long and setose. Tergum X may be intimately fused with the intermediate appendage or may have a discrete shape. In some cases the intermediate appendage is intimately associated with tergum X, but can be distinguished by the presence of lateral setae. Subsequent characters address the intermediate appendage and location, shape, etc.
95. Sternum IX height: **0**, synscleritous; **1**, terminating at or beyond preanal appendage, height three fourths of entire male genitalia (Fig. 8A, B, E); **2**, height equal to half of male genitalia (Fig. 8C, D, F); **3**, height less than half of entire male genitalia.
96. Intermediate appendage: **0**, not visible as a distinct structure from TX (absent) (Figs 8D, 9D); **1**, fused along mesal margin to TX (Figs 8C, 9C, F); **2**, present as free structure from TX (Figs 8B, E, 9B, E).
97. Intermediate appendage shape: **0**, broad (Fig. 9C); **1**, digitate (Figs 8B, E–F, 9B, E–F); **2**, plate-like; **3**, greatly enlarged.
98. Intermediate appendage sclerotisation: **0**, membranous; **1**, sclerotised.
99. Mesolateral process of preanal appendage: **0**, present (Fig. 8A–B, D–F); **1**, absent.
100. Shape of mesolateral process of preanal appendage: **0**, as long as tall (never more than twice the height), quadrate to deltoid (Fig. 8B, E); **1**, 1 and half to twice as long as tall (Fig. 8A, D); **2**, longer than twice the height (Fig. 8F).
101. Dorsolateral process preanal appendage: **0**, absent (Fig. 8A–C); **1**, present (Fig. 8D, E).
102. Relative origin of dorsolateral process preanal appendage: **0**, dorsal margin of mesolateral process (Fig. 8D, E); **1**, medial margin of mesolateral process; **2**, anterobasal margin of mesolateral process; **3**, posterior margin of mesolateral process (Figs 8F, 9F). The dorsolateral process is interpreted in this study as arising from the posterior margin of the mesolateral process of the preanal appendage for *Cernotina*, *Neucentropus* and *Neureclipsis*.
103. Orientation of dorsolateral process of the preanal appendage: **0**, above and outside of segment IX (Fig. 8D, E); **1**, medially and inside of abdomen; **2**, below and inside of segment IX (TIX); **3**, posteriorly and outside of TIX (Figs 8F, 9F).
104. Mesal lobe of preanal appendage: **0**, absent (Fig. 9C); **1**, present. This is a setose lobe sometimes found between the mesolateral and mesoventral processes of the preanal appendage.
105. Shape of mesal lobe of preanal appendage: **0**, present as small bulbous lobe; **2**, present as elongate digitate lobe.

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Appendix 1. (continued)

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106. *Preanal appendage plate fusion*: **0**, no sclerotised fusion (meeting) under phallocrypt (Fig. 9D); **1**, fusion of both plates (Fig. 9C, E). The bodies of the preanal appendage (meet below the phallocrypt with differing degrees of sclerotisation. Chilean *Polycentropus* possess a visible sclerotised 'ring', but not clearly visible in the illustration.
107. *Preanal appendage plate fusion*: **0**, fusion of both plates and forming a visible sclerotised 'ring' (Fig. 9C); **1**, fusion without visible sclerotised 'ring'. Chilean *Polycentropus* possess a visible sclerotised 'ring', but not rendered in the illustration.
108. *Preanal appendage plate projection (mesoventral process)*: **0**, mesoventral process absent (Fig. 9A, B); **1**, mesoventral processes present (Fig. 9C–F). The mesoventral process usually project from the junction of the bodies of the preanal appendages.
109. *Preanal appendage plate projection (mesoventral process)*: **0**, mesoventral process present as lateral bulbous or digitate, setose structure (Fig. 9D, F); **1**, mesoventral processes elongate, as long as inf. app.; **2**, mesoventral processes present as short structures (paired or fused to each other) (Fig. 9C, E).
110. *Inferior appendage*: **0**, dorsal and ventral branches not differentiated (Fig. 8C, D); **1**, dorsal and ventral branches differentiated (Fig. 8A, B, E, F).
111. *Differentiation of branches of the inferior appendage*: **0**, dorsal 'lateral' and ventral branches equally differentiated or ventral branch larger (Fig. 8A, B, E, F); **1**, ventral branch present as small stub, dorsal branch well developed.
112. *Inferior appendage length (ventral view)*: **0**, elongate (Fig. 8A, D, F); **1**, not elongate (Fig. 8B, C, E).
113. *Inferior appendage shape (ventral view)*: **0**, narrow (Fig. 8A, F); **1**, broad (Fig. 8D).
114. *Associated structures of inferior appendage*: **0**, dorsal surface (interior) with paired processes forming a fossa (Figs 8C, 9C); **1**, dorsal surface without paired processes forming a fossa.
115. *Segmentation of inferior appendages* (F&W70) (P108) (LMT10): **0**, one-segmented (Fig. 7); **1**, two-segmented.
116. *Phallus ventral sclerotised projection*: **0**, absent (Fig. 10A, B, E, F); **1**, present (Fig. 10C, D).
117. *Location of phallic ventral sclerotised projection*: **0**, basally; **1**, medially (Fig. 10C); **2**, apically as ventral lip (Fig. 10D).
118. *Sclerotised phallic extensions (spines)*: **0**, absent (Fig. 10A, B, D–F); **1**, paired, arising from phallobase (externally), from phallic apodeme; **2**, paired, arising apicodorsally and not from phallobase (Fig. 10C).

Female genitalia characters

119. *Female sternum VIII* (LMT3): **0**, undivided or incised; **1**, divided into a pair of lobes (Fig. 6F). This and the following female characters are informative at higher levels (family). Possibly internal membranous structures may reveal generic level characters. However, these were difficult to study due to their plastic nature. An undivided or incised female sternum VIII is present in dipseudopsids, xiphocentronids, psychomyiids and pseudoneureclipsines.
120. *Female segment IX* (LMT2): **0**, pleural region membranous (Fig. 6E); **1**, completely sclerotised cylinder. State 1 is a synapomorphy for the clade Xiphocentronidae + Psychomyiidae.
121. *Oviscapt apodemes*: **0**, present; **1**, absent. State 0 is a synapomorphy for the clade Xiphocentronidae + Psychomyiidae.
122. *Female lateral papillae* (F&W68) (P104) (W&M3): **0**, absent; **1**, present (Fig. 6E, F). State 0 is a synapomorphy for the clade Xiphocentronidae + Psychomyiidae.
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Appendix 2. (continued)

Taxa	Characters														
<i>Plectrocnemia conspersa</i>	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	1111111111	1111111111	11
<i>Polycentropus aspinosus</i>	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8888888889	9999999990	0000000001	1111111112	22	1111111112	22
<i>Polycentropus bronngus</i>	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12	1234567890	12
<i>Polycentropus chilensis</i>	1100110000	0011110000	1010100000	1003010101	1200000012	1110121100	0010001201	0000101010	-00102011	1030221000	0--1110121	01-100-010	11	01-100-010	11
<i>Polycentropus flavomaculatus</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Polycentropus vanderpooli</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Plectrocnemia weedi</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Polylectropus altera</i>	1100170000	0011110000	1010100000	1?122?0101	2100000121	1110121100	001000201	0000101010	-011-20101	1030221000	0--0-10120	-1-100-010	11	-1-100-010	11
<i>Polylectropus amphion</i>	1100110000	0011110000	1?10100000	-0?2?2?0101	2100000121	1110121100	0010001101	0000101010	-011-20101	1030221000	1000-0-100	-00000-010	11	-1-100-010	11
<i>Polylectropus aurifuscus</i>	1100110000	0011110000	101?100001	01?2?2?0101	2100000121	1110121100	0010001201	0000101010	-010-20100	1030221000	1000-0-100	-00000-010	11	-1-100-010	11
<i>Polylectropus beccus</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Polylectropus chartesi</i>	1100110100	0011110000	1010101030	-0?2?2?0101	2100000121	1110121100	0010001001	0100102010	-010-20120	1010121100	0--0-0-101	11-100-0??	??	11-100-0??	??
<i>Polylectropus fjianus</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Polylectropus matazapaya</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Polylectropus recurvatus</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Polylectropus santiago</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Pseudoneureclipsis saccheda</i>	1111-10100	0011001011	0011100100	-001310101	0310100120	1110120100	101000121-	0012101001	0010-20012	1200121000	0--110-101	000100-000	11	01-100-010	11
<i>Pseudoneureclipsis uma</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11
<i>Plectrocnemia spilotata</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	??????????	11	??????????	11

Appendix 3. Taxa for which larval data are included. Sources and composite taxa listed

Species	Source of larval data	Composite taxon
<i>Hydropsyche betteni</i>	Frانيا & Wiggins 1997	
<i>Ecnomus tenellus</i>	Lepneva 1970, Frانيا & Wiggins 1997	
<i>Psychomyia flavida</i>	Frانيا & Wiggins 1997	
<i>Phylocentropus placidus</i>	Frانيا & Wiggins 1997	
<i>Xiphocentron borinquensis</i>	Frانيا & Wiggins 1997	
<i>Antillopsyche wrightii</i>	Direct observation	
<i>Cernotina calcea</i>	Hudson <i>et al.</i> 1981	
<i>Cyrnellus fraternus</i>	Wiggins 1996	
<i>Cyrnus trimaculatus</i>	Lepneva 1970, Vieira-Lanero 2000	
<i>Holocentropus interruptus</i>	Lepneva 1970, Vieira-Lanero 2000	
<i>Neureclipsis bimaculata</i>	Lepneva 1970	
<i>Neureclipsis valida</i>	Lepneva 1970	
<i>Nyctiophylax (Paranyctiophylax) affinis</i>	Wiggins 1996	
<i>Plectrocnemia conspersa</i>	Lepneva 1970	
<i>Polycentropus flavomaculatus</i>	Lepneva 1970, Frانيا & Wiggins 1997	<i>Polycentropus zaneta</i>
<i>Polycentropus vanderpooli</i>	direct observation	
<i>Polyplectropus altera</i>	direct observation	
<i>Polyplectropus amphion</i>	Li & Morse 1997	
<i>Polycentropus aurifuscus</i>	direct observation	
<i>Polyplectropus charlesi</i>	direct observation	
<i>Pseudoneureclipsis saccheda</i>	Vieira-Lanero 2000, Tachet <i>et al.</i> 2001	<i>Pseudoneureclipsis lusitanicus</i>

Appendix 4. List of specimens examined

Species	Locality	Accession number
<i>Adectophylax volutus</i> Neboiss	Australia	T6256
<i>Antillopsyche tubicola</i> Flint	Puerto Rico	UMSP000108110
<i>Antillopsyche wrighti</i> Banks	Dominican Republic	UMSP000108113
<i>Cernotina calcea</i> Ross	Nicaragua	UMSP000063759
<i>Cernotina taeniata</i> Ross	Costa Rica	UMSP000102741
<i>Cyrnellus fraternus</i> (Banks)	Minnesota	UMSP000051220
<i>Cyrnellus risi</i> Ulmer	Brazil	UMSP000040722
<i>Cyrnus flavidus</i> McLachlan	Norway	UMSP000100706
<i>Cyrnus trimaculatus</i> (Curtis)	Norway	UMSP000100686
<i>Ecnomus tenellus</i> (Rambur)	Netherlands	UMSP000067845
<i>Ecnomus tenellus</i> (Rambur)	Netherlands	UMSP000029358
<i>Holocentropus interruptus</i> Banks	Minnesota	UMSP000051592
<i>Holocentropus picicornis</i> (Stephens)	Norway	UMSP000108117
<i>Hydropsyche betteni</i> Ross	Minnesota	UMSP000051346
<i>Kambaitipsyche hykriion</i> Malicky & Chantaramonkol	Thailand	UMSP000101040
<i>Kambaitipsyche schmidi</i> Malicky	Burma	UMSP000108122
<i>Neucentropus mandjuricus</i> Martynov	Russia	UMSP000208607
<i>Neucentropus mandjuricus</i> Martynov	China	UMSP000210933
<i>Neureclipsis bimaculata</i> (Linnaeus)	Russia	UMSP000118704
<i>Neureclipsis valida</i> (Walker)	Minnesota	UMSP000100951
<i>Nyctiophylax (Paranyctiophylax) affinis</i> (Banks)	Minnesota	UMSP000024545
<i>Nyctiophylax (P.) chiangmaiensis</i> Malicky & Chantaramonkol	Thailand	UMSP000101049
<i>Nyctiophylax neotropicalis</i> Flint	Brazil	UMSP000200474
<i>Nyctiophylax</i> sp. AU	Australia	UMSP000208626
<i>Nyctiophylax</i> sp. BR	Brazil	UMSP000200423
<i>Pahamunaya jhmita</i> Schmid & Denning	Thailand	UMSP000101053
<i>Pahamunaya joda</i> Malicky & Chantaramonkol	Thailand	UMSP000101039
<i>Phylocentropus placidus</i> (Banks)	Minnesota	UMSP00025032
<i>Plectrocnemia conspersa</i> (Curtis)	Norway	UMSP000100699
<i>Plectrocnemia conspersa</i> (Curtis)	Norway	UMSP000100696
<i>Plectrocnemia spilota</i> (Neboiss)	Tasmania	UMSP000108127
<i>Plectrocnemia weedi</i> (Blickle & Morse)	Minnesota	UMSP000051775
Polycentropodidae Genus A, sp. 1	Brazil	UMSP000100608
Polycentropodidae Genus A, sp. 2	Venezuela	UMSP000100999
Polycentropodidae Genus B, sp. 1	Brazil	UMSP000200456
<i>Polyplectropus aspinosus</i> Schmid	Chile	UMSP000108131
<i>Polycentropus aspinosus</i> Schmid	Chile	UMSP000085251
<i>Polycentropus broncus</i> Gibbs	Ghana	UMSP000100731
<i>Polycentropus chilensis</i> Yamamoto	Chile	UMSP000108135
<i>Polycentropus flavomaculatus</i> Pictet	Norway	UMSP000102840
<i>Polycentropus vanderpooli</i> Flint	Dominican Republic	UMSP000118446
<i>Polycentropus zaneta</i> Flint	Puerto Rico	UMSP000108141
<i>Polyplectropus altera</i> McFarlane	New Zealand	UMSP000102929
<i>Polyplectropus amphion</i> Malicky	Nepal	UMSP000101047
<i>Polyplectropus aurifuscus</i> McFarlane	New Zealand	UMSP000100738
<i>Polyplectropus beccus</i> Hamilton & Holzenthal	Venezuela	UMSP000108145
<i>Polyplectropus charlesi</i> (Ross)	Mexico, Texas	UMSP000108152
<i>Polyplectropus fijianus</i> Banks	Fiji	UMSP000101129
<i>Polyplectropus fijianus</i> Banks	Fiji	UMSP000101110
<i>Polyplectropus matadapaya</i> Schmid	Sri Lanka	UMSP000210928
<i>Polyplectropus matadapaya</i> Schmid	Sri Lanka	UMSP000101045
<i>Polyplectropus santiago</i> Ross	Texas	UMSP000100603
<i>Polyplectropus recurvatus</i> (Yamamoto)	Colombia, Venezuela	UMSP000108158
<i>Pseudoneureclipsis saccheda</i> Schmid & Denning	Thailand	UMSP000101059
<i>Pseudoneureclipsis uma</i> Malicky & Chantaramonkol	Malaysia	UMSP000101056
<i>Psychomyia flavida</i> Hagen	Minnesota	UMSP000051440
<i>Psychomyia flavida</i> Hagen	Arkansas	UMSP000102958
<i>Xiphocentron borinquensis</i> Flint	Puerto Rico	UMSP000103782
<i>Xiphocentron moncho</i> Muñoz-Quesada & Holzenthal	Costa Rica	UMSP000108162