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Phylogenetic relationships of the genera of Epipsocetae (Psocoptera: Psocomorpha)

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Abstract

The phylogenetic relationships of the genera of Epipsocetae were inferred on the basis of 122 morphological characters of adult specimens, corroborating the monophyly of the group with ten synapomorphies. The genera are grouped in well defined clades consistent at family level. Dolabellopsocidae, Ptiloneuridae and Epipsocidae are recognized as monophyletic families. In each family, the genera appear as monophyletic units, except in Epipsocidae, where the relationships are ambiguous and monophyly of most genera is not supported. Results indicate that Cladiopsocidae is paraphyletic; it was divided into two monophyletic families: Spurostigmatidae and Cladiopsocidae (*sensu stricto*), represented by the genera *Spurostigma* and *Cladiopsocus* respectively. *Neurostigma* is recognized as a monophyletic genus closely related to other epipsocid genera, nevertheless due to the low resolution obtained within Epipsocidae, it is not possible to decide if it is a genus of that family or if it forms a different clade at family level. The genera *Parepipsocus* Badonnel, previously considered as *incertae sedis*, and *Dimidistriata* Li & Mockford, previously placed tentatively in Dolabellopsocidae, are included in Epipsocidae. *Loneuroides*, *Terryerwinia* and *Timnewia* are recognized as valid genera. Two well defined clades are recognized within E pipsocidae, one with exclusively American genera, and the other that includes Asiatic and American genera.

Key words: Psocoptera, Epipsocetae, phylogeny, cladistic analysis

Introduction

Epipsocetae is one of the six infraorders of Psocoptera recognized within the suborder Psocomorpha (Yoshizawa 2002). The group comprises approximately 36 genera with 275 described species, besides the incertae sedis genus *Parepipsocus* Badonnel (Eertmoed 1973, Mockford 1998, Lienhard & Smithers 2002, Li Fasheng 2002, García Aldrete 2004a, 2004b, 2005a, 2005b and in press). These genera are predominantly pantropical,

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only *Bertkauia* also occuring in temperate zones of North America and in most of Europe. Epipsocetae is distributed in the five continents, being more diverse in tropical America.

This group of hemipteroid insects is characterized by a pair of longitudinal labral sclerites, tarsi of two or three segments, veins Rs and M of forewing connected by a crossvein and the occasional presence of multiple veins, both in fore- and hind-wings. The species are found on bark, branches and foliage of trees and shrubs, in leaf litter and on rock surfaces. They feed on unicellular green algae, lichens, spores, fungal hyphae, and organic detritus, grazing in cortical and leaf surfaces of the plants and trees, as well as in leaf litter and soil (New 1987, Mockford 1993, Lienhard 1998).

At present, Epipsocetae is divided into five families: Epipsocidae, Neurostigmatidae, Dolabellopsocidae, Cladiopsocidae, and Ptiloneuridae. This widely accepted classification is based on Smithers (1972) and Eertmoed (1973), who used principles of phylogenetic systematics and numerical taxonomy. Smithers (1972) was one of first to investigate the phylogenetic relationships of Psocoptera. Recent studies (e.g. Yoshizawa 2002) have questioned the validity of some of the families, the evolutionary relationships between the genera, and even the methods used. Recently, new genera have been defined, others have been redefined, and some others present circumscription problems. In addition, several new species have been described and others considered valid have assignment problems. Current taxonomic problems indicate that a more stable classification is required that reflects reliable sister-group relationships derived from phylogenetic systematics.

In this work, a cladistic analysis was conducted based on adult morphology, in order to infer the phylogenetic relationships among the genera of Epipsocetae, and to verify the monophyly of the families.

Historical background

Epipsocetae was established by Pearman (1936) in his classification of Psocoptera on the basis of external morphology not previously considered. He recognized the family E pipsocidae within Epipsocetae, including the genera *Epipsocus* and *Bertkauia* and considered mainly the number of tarsal segments, mouth and female genital characters.

Following the system of Pearman, Roesler (1940a, 1940c) extended the classification of the group when he included the genera *Cladiopsocus*, *Euplocania*, *Loneura*, *Ptiloneura*, *Triplocania* and *Ptiloneuropsis* in Ptiloneuridae. He defined this family as having three segmented tarsi and by the presence of a second anal vein in the forewing. Roesler (1940b) added *Goja* and *Neurostigma* to Epipsocidae. Later, Roesler (1944) incorporated *Callistoptera* and *Psilopsocus* (previously considered as Epipsocetae) in two new families, Callistopteridae and Psilopsocidae, synonymized *Bertkauia* under *Epipsocus*, and regarded *Loneura* as a subgenus of *Ptiloneura*.

The genera *Epipsocopsis* and *Mesepipsocus* were described by Badonnel (1955, 1969) in the Epipsocidae. Mockford (1961), in a comparative study and description of a new species of *Psilopsocus*, transferred Psilopsocidae to the group Psocetae. On the other hand, New (1977) when re-evaluating *Callistoptera*, transferred Callistopteridae as a subfamily of Calopsocidae in the group Homilopsocidea. As a result, only the families Epipsocidae and Ptiloneuridae stayed in the group Epipsocetae.

Later, the genera *Dicropsocus* (Smithers & Thornton 1977), *Hinduipsocus* (Badonnel 1981), *Odontopsocus* (Badonnel 1987), *Cubitiglabra* (Li Fasheng 1995), *Heteroepipsocus* (Li Fasheng 1995), *Dichoepipsocus* (Li Fasheng & Mockford 1997) and *Dimidistriata* (Li Fasheng & Mockford 1997), were described and incorporated into Epipsocidae. *Perucania* was described by New & Thornton (1988) and was included in Ptiloneuridae, and Mockford (1998) transferred *Dimidistriata* to Dolabellopsocidae. Badonnel (1986) placed *Parepipsocus* in the Epipsocetae, but did not place it in any of the families known until then, considering it as "incertae sedis". Li Fasheng (2002) included *Liratepipsocus*, *Metepipsocus*, *Spordoepipsocus* and *Valvepipsocus* in Epipsocidae, and recently, García Aldrete (2004a, 2004b, 2005a, 2005b and in press) described *Ianthorntonia*, *Rogojiella*, *Incapsocus* and *Terryerwinia* in this family, and *Willreevesia*, *Loneuroides* and *Timnewia* in Ptiloneuridae.

The first attempt to establish a phylogeny of the order Psocoptera was by Enderlein (1911), who presented an elaborate tree with many suprageneric taxa, some of which have been useful. Mockford (1967), in an attempt to show the phylogenetic relationships of the electrentomoid psocids, presented a tree in which some of its branches need yet to be examined. Smithers (1972) presented several phylogenetic trees for higher taxa and genera of each family, as result of an extensive study on the phylogenetic relationships of the Psocoptera. However, some lineages in his dendrograms were defined by symplesiomorphies, and his phylogenetic classification has not been totally accepted (Smithers 1991, Lienhard 1998, Yoshizawa 2002).

Smithers (1972) considered Epipsocetae as a monophyletic group supported by six apomorphic characters. He concluded that: 1, Epipsocoidea and Ptiloneuroidea include monophyletic lineages; 2, *Neurostigma* + *Epipsocus* + *Epipsocopsis*, and *Goja* are sister taxa within Epipsocoidea, and they constitute a monophyletic family, Epipsocidae; 3, *E pipsocus* and *Epipsocopsis* are nearly related on the basis of genitalic specialization; 4, in Ptiloneuroidea, *Ptiloneura* and *Ptiloneuropsis* form the monophyletic family Ptiloneuridae; whereas 5, C*ladiopsocus* + *Euplocania* + *Triplocania* integrate a different lineage in a new family, Cladiopsocidae. In his analysis he did not consider *Mesepipsocus* and *Callistoptera*. However, in his classification he recognized Callistopteridae within the superfamily Epipsocoidea.

A year later, Eertmoed (1973) determined the phenetic relationships of the genera of E pipsocetae. As a result, he proposed a classification that was widely accepted. In his phenogram he recognized Epipsocidae, Spurostigmidae (= Cladiopsocidae *sensu* Smithers, Eertmoed 1986), and Ptiloneuridae. In Epipsocidae, *Bertkauia* and *Epipsocus* appear as independent genera. He included the new genus *Spurostigma* along with

C*ladiopsocus* within Spurostigmidae, and transferred *Euplocania* and *Triplocania* to Ptiloneuridae. Furthermore, he separated *Neurostigma* in a new family, Neurostigmidae (= Neurostigmatidae of Mockford 1998). Also, he described *Auroropsocus, Dolabellopsocus,* and *Isthmopsocus* with which the family Dolabellopsocidae was established. In his study *Callistoptera*, *Mesepipsopcus,* and *Ptiloneuropsis* were not included.

Yoshizawa (2002), inferred the phylogenetic relationships of the families of Psocomorpha using cladistic analysis and proposed a higher classification for the suborder. As part of his results, he recognized Epipsocetae as a monophyletic infraorder, supported by six stable apomorphies, and concluded that Caeciliusetae constitutes the sister group of Epipsocetae. He found that Epipsocidae, Dolabellopsocidae, and Ptiloneuridae form monophyletic clades, but supported by few reliable characters. On the contrary, Cladiopsocidae appears as a polyphyletic family that, according to him, could be divided into two independent families. In his classification, all the families of Epipsocetae are treated as "sedis mutabilis", with the exception of Neurostigmatidae, that was not considered in his analysis because it was established with a phenetic criterion.

Casasola-González & García-Aldrete (2002) inferred the generic phylogenetic relationships of Epipsocidae. They found that Epipsocidae constitutes a monophyletic family supported by two stable synapomorphies, and found three monophyletic clades within the family, correlated with the geographic distribution of the genera. The American genera *Epipsocus* and *Mesepipsocus* are grouped in one clade. In another clade, *Dicropsocus* + *Epipsocopsis* appear as sister taxa to *Bertkauia* + *Odontopsocus*. In a third clade, *Cubitiglabra* + *Heteroepipsocus* are sister taxa to the clade *Goja* + *Dichoepipsocus* + *Hinduipsocus*. These latter genera are predominantly Asiatic, except *Goja* that is exclusively neotropical. Finally, García Aldrete (2005) presented a phylogeny of Ptiloneuridae at the generic level; in his cladogram two clades are recognized, one comprising *Perucania* as sister group of *Euplocania* + *Triplocania*, and the other with *Willreevesia* as sister group of *Ptiloneuropsis* + *Ptiloneura* + *Loneura*.

Material and methods

Taxa sampling

This study includes all genera now recognized in the group Epipsocetae (Lienhard & Smithers 2002, Li Fasheng 2002, García Aldrete 2004a, 2004b, 2005a, 2005b and in press). The species (terminal taxa) were examined directly or through the literature (Appendix I). Sampling decisions were based on the available material, the number of well known species, and the actual stability of each genus. Both sexes are represented, except in those species in which either the male or the female is unknown.

Since most genera are well defined, only two representative species that show all characters were selected from each, except *Epipsocus* and *Mesepipsocus* that are represented by a large number of species because both present circumscription problems.

Dimidistriata, *Liratepipsocus*, *Metepipsocus*, *Parepipsocus*, *Perucania*, *Ptiloneura*, *Ptiloneuropsis* and *Valvepipsocus* are monotypic. The new species *Epipsocopsis* sp.1 and sp. 2 were included because they were considered conflictive within the genus. Seven species mostly belonging to Epipsocetae were added as terminal taxa. Three of them, still undescribed, constitute new genera, whereas the remaining four have assignment problems (García Aldrete per. com.) (Appendix I).

Outgroup taxa were selected from groups closely related to Epipsocetae. According to Yoshizawa (2002), the infraorder Caeciliusetae represents the sister group of Epipsocetae, whereas Homilopsocidea is sister group to Caeciliusetae + Epipsocetae. Caeciliusetae was represented by two genera: *Asiopsocus* and *Stenopsocus* in the families Asiopsocidae and Stenopsocidae respectively, *Asiopsocus* is the most plesiomorphic of Asiopsocidae. A third outgroup was *Elipsocus* (Elipsocidae) as representative of Homilopsocidea (Appendix I).

Specimens prepared and mounted on slides were used to analyse morphological characters. Several additional specimens were dissected in 80% alcohol under a binocular microscope, and their parts were mounted either in Euparal or Canada balsam, following the process described by García Aldrete (1990). Observations were made using a stereoscopic microscope Zeiss-Stemi SV6 and a compound microscope Zeiss-Axiolab. A Zeiss drawing tube and a digital camera were used for the illustration of characters. In some cases, additional character information was taken directly from original published descriptions and illustrations (Appendix I). The terminology used follows Matsuda (1970, 1976), García Aldrete (1990), and Lienhard (1998).

Examined specimens come from the following collections: The Australian Museum, Sydney, Australia (AM); Illinois State University, Normal, Illinois, U.S.A. (ISU); Muséum d' Histoire Naturelle, Genève (MHNG); Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F. (CNIN); Department of Entomology, China Agricultural University (CAU).

Data analysis

The cladistic analysis was performed using external morphology of the head, thorax and abdomen of adult specimens of both sexes. The data matrix has 82 taxa and 122 characters (Table 1), and was constructed and edited using WinClada version 1.00.08 (Nixon 2002). Twenty two characters were multistate and the remainder binary. The characters for which one of the states was "absent" were recoded as two different characters, considering its absence in the comparison as "inapplicable" (Maddison 1993). A parsimony tree was produced with Nona version 2.1 (Goloboff 1999) using heuristic search with 2500 random additional sequences with TBR and retaining 20 trees. Also, each explored sequence was further analysed by a more exhaustive TBR, retaining 10 000 trees (10 times: h10 000 h/20 mu* 250 max* sv*). All characters were equally weighted and unordered. The most parsimonious trees (MPTs) found were recovered collapsing

TABLE 1. Characters matrix used for the phylogenetic analysis of Epipsocetae. The first three species are outgroups. Question marks (?) indicate missing data and dashes (-) inapplicable data.

	5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120
Asiopsocus tehuacanus	0-110-0-1100---00--00----00000000000--00000100001100-10-0000-00000111300011100000-00-000--000010-0-00---0000000---0010100-
Stenopsocus immaculatus	0-11110-1100---010-10----100010000011-10000300001201010-0000-00000111300011100000-00-000--00021120-010000011000---00111010
Elipsocus sp4	1111110-1100---00--00----100110100111-10000110001100-10-0000-00000111300011100100-00-000--00001120-010001011000---00111010
Auroropsocus orientis	0-1111111101110110-1100-11200??111011-11000200011300-1120000-100000111-001110000??0??????????11100-10---1011010---01111010
Auroropsocus strenus	??1111???101110?????1?????200??111011-11000200011300-1120000-1?0000111-0011?0000??0??????????11100-10---1?????????????????
Bertkauia crosbyana	0-110-110011001110-11111-00000010000--01000210002100-10-0000-10000011300011100100-00-100--010311111111401010010---0110000-
Bertkauia lucifuga	0-110-110011001110-11111-00000010000--01000210002100-10-0000-10000011300011100100-00-100--010311111111401010010---0110000-
Cladiopsocus garciai	11111110100100210--11111-100111100111-11000110002100-1100000-110000110-0011100100-00-100--011011210111101011010---01111010
Cladiopsocus ocotensis	11111110100100210--11111-100111100111-11000110002100-1100000-110000110-0011100100-00-1011101101121011110101101111101111010
Cubitiglabra polyphebia	??11???????100????????????000??1000????1221210002100-10-0000-1?000111300011100100-00-?00--??0?????????????????????????????
Cubitiglabra quadripunctata	1011??110011001110-11111-?000??1000????1221210002100-10-0000-10000111300011100100-00-100--010?????????????????????????????
Dichoepipsocus micropterus	0-??0-??0011001110-11010-01100000001000??411110011401010010---0110000-
Dichoepipsocus thimpuensis	????0-?????1?0??????1010-?000??10000--0??4111100114010100?0---0?10000-
Dicropsocus complexus	0-??11110011002110-0120-0100010100011-11110310003101110-0000-10??????????????????????????????010-1010---101101111001111011
Dicropsocus montanus	0-1111110011002110-0120-0100010100011-11110310003101110-0000-10000011300011100100-00-10110010010-1010---101101111001111011
Dimidistriata longicapita	????0-?????10101????1010-?000??00000--0??210-1?00---1?????????0?0-----
Dolabellopsocus sp2 PERU	0-0-0---1101110110-1100-1100011111011-11000400004000-1100000-11000011310011110100-010010--00010----------011000---00111010
Dolabellopsocus sp3 PERU	0-0-0---1101110110-1100-1?00011111011-11000400004000-1100000-11000011310011110100-010010--00010----------011000---00111010
Epipsocopsis greeni	0-1111110011002110-0110-2111011100011-11000210002100-10-0000-110001110-0011100101100-10110010010-1000---101101111011111011
Epipsocopsis prominens	101111110011002110-01111-111011100011-11000210002100-10-0000-11000111300011100100-00-10111010010-1010---101101111011111011
Epipsocopsis sp1 WMALAY	101111110011002110-01111-111011100011-11000210002100-10-0000-11000111300011100100-00-10111010010-1010---101101111011111011
Epipsocopsis sp2 LAOS	0-1111110011002110-0110-2111011100011-11000210002100-10-0000-110001110-0011100101100-10110010010-1000---101101111011111011
Epipsocus argutus	10111110?011002110-11111-?000?11000????1000110002100-10-0000-110000110-100------1000-1010-010?????????????????????????????
Epipsocus petenensis	101111100011002111011111-?00011100011-11000110002100-10-0000-1100001130000------0-00-1011001031121011130101001111001111011
Epipsocus sp2 MEX	101111100011002110-11111-100011100011-11000110002100-10-0000-1100001130000------0-00-1011001031121011130101001111001111011
Euplocania badonneli	111111101101110110-11111-100111100011-11010130011310-1100000-11101-0-----11100001100-1011111001121011111112101110101111010
Euplocania pictaoides	111111101101110110-11111-100111100011-11010130011310-1100000-11101-0-----11100001100-1011111001121011111112101110101111010
Goja montieli	10110-110011002110-11111-000000100010001221310002100-10-1011211000111300011100211100-101100100112101111010320111100110110-
Goja plaumanni	10110-110011002110-11111-00000010000--01000310002100-10-1000-110001110-0011100211100-1010-01001121011110103201101-0110110-
Heteroepipsocus brevicellus	0-11??110011001110-11010-?000??1000????1000210003100-10-0000-10000111300011?00100-00-?00--??0?????????????????????????????
Heteroepipsocus longicellus	??11???????100??????101?-?000??1000????1000210003100-10-0000-1?000111300011?00100-00-?00--??0?????????????????????????????
Heteroepipsocus maculatus	??1111?????100????????????000??100011-11000110003100-10-0000-1???????????????????????????????010-1?10?--1?100?0---0?111011
Hinduipsocus atratus	????0-??00?1002110-?1111-00000010001010??4111101114010100111100110100-
Hinduipsocus sp THAI	10110-110011002110-11111-000000100010101000310003100-10-0000-10000011300011100100-00-101100104111101114010100111100110100-
Ianthorntonia annae	1011??110011002110-11111-?000??1000????1220310003100-10-00111110001110-1011001111100-10110010?????????????????????????????
Ianthorntonia loisae	1011??110011002110-11111-?000??1000????1220310003100-10-00111110001110-1011001111100-10110010?????????????????????????????
Incapsocus penai	1011??100011002110-11111-?000??1000????1120020002100-10-0001011000011320010000100-00-10110010?????????????????????????????
Isthmopsocus sp2 PERU	111010111101110110-1100-1100011111011-11000400004100-1110000-10001-110-00111000011011000--000010-10111401021000---00111010
Isthmopsocus sp BELICE	111010111101110110-1100-1100011111011-11000400004100-1110000-10001-110-00111000011011000--000010-10111401021000---00111010
Liratepipsocus jinghongicus	????0-?????100??????1010-???0??000011-1??010?0-00---1?100?0---0?0-----

to be continued

TABLE 1 (continued).

	5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120
Loneura leonilae	111111101101110110-11111-100111100011-11011210001300-1100001111101-10----11101001100-1011101001121011110111101111101111010
Loneura splendida	111111101101110110-11111-100111100011-11011210001300-1100001111101-10----11100001100-1011101001121011110112101111101111010
Loneuroides venezolanus	11??11101101110110-11111-100111100011-11010230001100-1100001111??????????????????????????????01121011110112101110101111010
Mesepipsocus capitulatus	101111100011002110-11111-100011100011-11011110002100-10-0000-1100001132000------0-00-10110010010-1011130101101111001111011
Mesepipsocus fuscivenatus	1011??100011002112-11111-?000??1000????1000110002100-10-0000-1100001132000------0-00-10110010?????????????????????????????
Mesepipsocus proctus	101111100011002110-11111-?000??100011-11000110002100-10-0000-1100001130000------0-00-1010-010210-10111301042110---01111011
Mesepipsocus sp1 PERU	101111100011002112-11111-1000??100011-11001110002100-10-0000-1100001130000------0-00-1011001001121011130111001111001111011
Mesepipsocus sp6 PERU	10??11100011002112-11111-1000??100011-11001010002100-10-0000-11??????????????????????????????310-1011130101001111001111011
Mesepipsocus sp11 CR	10??11100011002110-11111-1000??100011-11001110003100-10-0000-11??????????????????????????????31121011130100001111001111011
Mesepipsocus sp15 DOMINICANA	101111110011002110-11111-100011100011-11001110002100-10-0000-110101110-1111001100-10-120--010010-1011130101101111101111011
Mesepipsocus sp17 ECUA	101111100011002111011111-100011100011-11000110002100-10-0000-11000011300010000100-00-10110010010-1011130101101111001111011
Mesepipsocus sp1022 ECUA	10??11100011002110-11111-?000??100011-11000110002100-10-0000-11??????????????????????????????310-1011130101001111101111011
Mesepipsocus sp1041 ECUA	101111100011002110-11111-?000??100011-11001110002100-10-0000-1100011130000------1100-10110010010-1011130111101111001111011
Mesepipsocus sp BELICE	1011??100011002110-11111-?000??1-00????1001110002100--0-0000-110000110-1010000100-00-1111010??????????????????????????????
Mesepipsocus sp DOMINICA	101111110011002110-11111-1000111-0011-11001110002100--0-0000-110101110-1111001100-10-120--010010-1011130101101111001111011
Mesepipsocus sp NICA	10??11100011002110-11111-1000111-0011-11000110002100--0-0000-11??????????????????????????????010-10111301042110---01111011
Metepipsocus beijingicus	????0-?????100?1????1111-???0??10000--0??????????1???310-1?111101?100?0---0?0-----
Neurostigma dispositum	0-1111100011002110-11111-100010100011-11000021001100-00-0100-1100001132000------0-00-000--000010-10111401111000---00111010
Neurostigma enderleini	0-1111100011002110-11111-100010100011-11000121000100-00-0100-1100001132000------1000-000--000010-10111401111000---00111010
Odontopsocus orghidani	????0-??0??100??????1010-00000000000--0??011110111401000?10---0110000-
Odontopsocus sp VENEZ	0-11??110011001110-11010-?000??0000????1000210003100-10-0000-10000011300011100101100-100--010??????????????0??????????????
Papillopsocus oriximinaensis	0-11??100011002110-11111-?000??100011-11000110002100-10-0000-100001110-000------1100-10111010010-1011110101001111001111011
Parepipsocus obscurus	????0-?????100?11???1110-00000011101000???10-1?111101?110?0---0?101010
Perucania longiareola	111111111101110110-11111-?001??100011-11000300005000-1100000-11101-10----11100001100-101110100112101111011210?11110?111010
Ptiloneura bidorsalis	??1111?????111??????1111-?001??100011-11030210000100-110000101?001-?????????????1100-?0?????0?????????????????????????????
Ptiloneuropsis immaculata	111111101101110110-11111-?001??1000????101031000120101100001111001-10----11100001100-10111010?????????????????????????????
Rogojiella mariateresae	1011??110011001110-11111-?000??1000????1000310004000-10-0000-110001110-1011101101100-10110010?????????????????????????????
Spordoepipsocus formosus	??11???????100?1????11??-???0??1000????1000210002100-10-0000-1?000011300011100100-00-?00--??0?????????????????????????????
Spordoepipsocus perforatus	??11???????100?1????11??-???0??1000????1000210002100-10-1000-1?000011300011100100-00-?00--????????????????????????????????
Spurostigma sp2 MEX	11111111100111210--01111-100011100011-11000020102100-1100000-110000112-0011100101000-100--01001110111101010010---01111010
Spurostigma sp DOMINICA	11111111100111210--01111-100011100011-11000020102300-1100000-110000112-0011100100-00-100--01001110111101010010---01111010
Terryerwinia acutiphallica	0-11111000110021111111111-100010100011-11000210002100-10-0000-110001110-110------1000-10110010010-1011130111101111001111011
Terryerwinia sp PERU	0-11111000110021111111111-100010100011-11000210002100-10-0000-110001110-110------0-00-10110010010-1011130111101111001111011
Timnewia greeni	11??11101101110110-11111-100111100011-11010130000100-1100000-11??????????????????????????????01121011111113101110101111010
Triplocania brailovskyana	111111111101110110-11111-100111100011-11000310001300-1100000-11101-10----11100001100-1011101001111011110112101111101111010
Triplocania cervantesi	111111111101110110-11111-100111100011-11000310002300-1100000-11101-10----11100001100-1011101001111011110112101111101111010
Valvepipsocus diodematus	????0-?????100??????????????0??10000--0??31121??11201?110?0---0?0-----
Willreevesia dominica	111111101101100110-11111-100111100011-11011210001300-1100000-11001-10----11110001100-1011101001121011110112101111101111010
Sp1 BRUN	0-110-110011002110-11111-00000010000--01000310003100-10-0000-100001?????????????1100-10110010010-1010---111101101-0110100-
Sp2 MALAY	0-11??110011001110-11010-?000??0000????1000310003100-10-0000-10000011300011100100-00-10110010?????????????????????????????
Sp3 BORNE	0-110-110011002110-11010-00000000000--01000310003100-10-0000-10000011300011100100-00-10111010010-10111401010011110010-----
Sp4 THAI	0-11??110011002110-?1111-?000??1000????1000310003100-10-0000-100000110-0011100101100-10110010?????????????????????????????

their not supported branches. Then identical trees were removed and a strict consensus tree was generated with WinClada (Nixon 2002). Only unambiguously optimized characters present in all most parsimonious trees were mapped onto the consensus tree using the command "apo[;" of Nona (Goloboff 1999). The displayed cladograms are metafile archives saved in WinClada and edited in PowerPoint.

A second test was performed removing taxa with many missing data (maximum 70%). The potential ambiguity was evaluated using the option “ambiguity filter” in Winclada (Nixon 2002). This option highlights taxa that have the selected level of ambiguity, thus taxa with more than 55% of ambiguous cells due to missing values (Nixon 1996) were sequentially removed and the resulting matrices were analyzed in the same way as the complete matrix, using the search described above. The topology of the resulting consensus trees was visually compared to evaluate the effect of removing “floating taxa” (ambiguous taxa) in the topology of the consensus of the MPTs.

Characters and character states

The 122 characters listed below were derived from a complete bibliographical investigation and from detailed microscopic examination of the selected specimens. Most characters have been used traditionally to define different genera and families. Others have been demonstrated to be informative in previous phenetic and phylogenetic studies of some genera of the group (Smithers 1972, Eertmoed 1973, Casasola & García Aldrete 2002, Yoshizawa 2002). In some cases, character states were modified so that they coincide with the set of terminal taxa. Quantitative type characters were not considered due to lack of confidence in the establishment of their states and its acceptance as homology hypothesis (Stevens 1991).

1. Interommatidial setae: (0) absent (Fig. 1); (1) present (Fig. 2).
2. Distribution of interommatidial setae in the compound eye: (0) few, mainly in the dorsal median surface (Fig. 3); (1) abundant over all the surface (Fig. 2).
3. Male ocelli: (0) absent (Fig. 4); (1) present (Fig. 5).
4. Male median ocellus: (0) absent (Fig. 18); (1) present (Fig. 5).
5. Female ocelli: (0) absent (same as Fig. 4); (1) present (same as Fig. 5).
6. Female median ocellus: (0) absent (same as Fig. 8); (1) present (same as Fig. 5).
7. Pair of setae at the base of ocellar group: (0) absent (Fig. 5); (1) present (Fig. 6).
8. Position of the pair of setae at the base of ocellar group: (0) at level of median ocellus (Fig. 6); (1) at level of dorsal ocelli (Fig. 7).
9. Consistency of the antero-ventral surface of scape: (0) membranous (Fig. 9); (1) sclerotized (Fig. 10).
10. Dorsal end of epistomal suture: (0) absent (Fig. 11); (1) present (Fig. 12).
11. Anterior ends of epistomal suture: (0) on ventral margin of cranium (Fig. 13); (1) separated from ventral margin of cranium (Fig. 14).

12. Labral sclerites: (0) absent (Fig. 15); (1) present (Fig. 16).
13. Position of labral sclerites: (0) oblique (Fig. 17); (1) vertical (Fig. 16).
14. Posterior end of labral sclerites: (0) extended to posterior margin of labrum, curving towards the sides (Fig. 17); (1) fading before reaching posterior margin (Fig. 16).
15. Anterior end of labral sclerites: (0) separated (Fig. 16); (1) prolonged medially but not joined (Fig. 17); (2) joined by a sclerotic strip (Fig. 18).
16. Disposition of the five distal inner labral sensilla: (0) equidistant (Fig. 19); (1) trichoids closer to the lateral placoids than to the median placoid (Fig. 20).
17. Labral tubercles: (0) absent (Fig. 21); (1) present (Fig. 22).
18. Distal border of labral tubercles: (0) smooth (Fig. 22); (1) with small pointed projections (Fig. 23); (2) with microspines (Fig. 24).
19. Number of pointed projections in distal border of labral tubercles: (0) one; (1) two.
20. Premolar cusp on right mandible: (0) absent (Fig. 25); (1) present (Fig. 26).
21. Degree of development of the cusps in the lacinial tip: (0) equally developed (Fig. 27); (1) outer cusp more developed than inner cusp (Fig. 28).
22. Outer cusp of lacinial tip: (0) narrow (Fig. 27); (1) wide (Fig. 32); (2) expanded preapically (Fig. 30).
23. Denticles in outer cusp: (0) absent (Fig. 28); (1) present (Fig. 32).
24. Number of denticles in outer cusp: (0) three-four (Fig. 31); (1) five-eight (Fig. 32).
25. Apex of outer cusp without denticles: (0) pointed (Fig. 30); (1) truncated (Fig. 28) (2) with notches (Fig. 29).
26. Pearman’s organ in female hind coxa: (0) absent (Fig. 33); (1) present (Fig. 34).
27. Ventral surface of fore femur: (0) with a row of setae (Fig. 35); (1) with a row of cones at bases of setae (Fig. 36); (2) with a row of spines (Fig. 37).
28. Ventral surface of hind femur: (0) with a row of setae (just as Fig. 35); (1) with a row of cones at bases of setae (same as Fig. 36).
29. Tarsomeres: (0) two (Fig. 38); (1) three (Fig. 40).
30. Ctenidiobothria on t1 of female hind leg: (0) absent (Fig. 38); (1) present (Fig, 39).
31. Ctenidiobothria on t2 of female hind leg: (0) absent (Fig. 38); (1) present (Fig. 39).
32. Preapical denticle on pretarsal claw: (0) absent (Fig. 41); (1) present (Fig. 42).
33. Pulvillus of pretarsal claw: (0) straight (Fig. 41); (1) curved (Fig. 44).
34. Pulvillus apex: (0) pointed (Fig. 41); (1) broad (Fig. 44).
35. Setae-shaped spine anterior to pulvillus: (0) absent (Fig. 41); (1) present (Fig. 43).
36. Female forewing: (0) absent; (1) present.
37. Degree of development of female forewing: (0) little developed (brachypterous) (Fig. 45); (1) well developed (macropterous) (Fig. 48).
38. Brachypterous wing: (0) ovoid (Fig. 45); (1) triangular (Fig. 46).
39. Female hindwing: (0) absent; (1) present.
40. Veins Rs and M of macropterous forewing (male or female): (0) fused for a length (Fig. 47); (1) connected by a crossvein (Fig. 48).

41. Number of primary branches in vein Rs of macropterous forewing: (0) two (Fig. 48); (1) three (Fig. 49); (2) four-five (Fig. 50).

42. Number of primary branches in vein M of macropterous forewing: (0) three (Fig. 48); (1) four-five (Fig. 49); (2) six- seven (Fig. 50); (3) eight (Fig. 51).

43. Primary branch of vein M next to areola postica: (0) not forked (Fig. 48); (1) forked (Fig. 50).

44. Length of pterostigma: (0) three times its width ; (1) four times its width; (2) five times its width; (3) six times its width; (4) seven times its width.

45. Shape of pterostigma: (0) flattened (Fig. 54); (1) rounded (Fig. 55); (2) triangular (Fig. 49); (3) sinuous (Fig. 63).

46. Crossveins within pterostigma: (0) absent (Fig. 55); (1) present (Fig. 56).

47. Spurvein at apex of pterostigma: (0) absent (Fig. 55); (1) present (Fig. 57).

48. Setae on the membrane at distal margin of macropterous forewing, between pterostigma and areola postica: (0) absent (Fig. 48); (1) present (Fig. 63).

49. Length of areola postica: (0) one time its width; (1) two times its width; (2) three times its width; (3) four times its width; (4) five times its width; (5) six times its width.

50. Shape of areola postica: (0) flattened (Fig. 58); (1) rounded (Fig. 59); (2) triangular (Fig. 60); (3) sinuous (Fig. 61).

51. Setae within areola postica: (0) absent (Fig. 59); (1) present (Fig. 63).

52. Areola postica and vein M: (0) separated (Fig. 48); (1) connected by crossveins (Fig. 60).

53. Number of crossveins between areola postica and vein M: (0) one; (1) two.

54. Areola postica and vein CuA: (0) separated (Fig. 62); (1) joined (Fig. 59).

55. Second anal vein in macropterous forewing: (0) absent (Fig. 48); (1) present (Fig. 64).

56. Distal end of second anal vein: (0) joined to wing margin (Fig. 64); (1) joined to first anal vein (Fig. 65); (2) fading before reaching wing margin (Fig. 66).

57. Veins Rs and M of macropterous hindwing (male or female): (0) fused basally for a length (fig. 52); (1) connected basally by a crossvein (Fig. 53).

58. Length of vein R_{2+3} of macropterous hindwing: (0) less than length of vein R_{4+5}; (1) same as length of vein R_{4+5}.

59. Number of primary branches in vein Rs of macropterous hindwing: (0) two (Fig. 52); (1) three-four (Fig. 53).

60. Vein M of macropterous hindwing: (0) not branched (Fig. 52); (1) branched (Fig. 53).

61. Number of primary branches in vein M of macropterous hindwing: (0) two; (1) three-four; (2) five-six.

62. Setae on veins Rs and M of macropterous hindwing: (0) absent; (1) present.

63. Row of fine setae on proximal end of costal margin of macropterous hindwing: (0) absent (Fig. 67); (1) present (Fig. 68).

64. Hypandrium: (0) simple (Fig. 69); (1) divided into a large central sclerite and two small side sclerites (Fig. 70).

65. Sharp lateral projections on hypandrium: (0) absent (Fig. 69); (1) present (Fig. 71).
66. Struts of phallobase: (0) vertical (Fig. 74); (1) oblique, V-shaped (Fig. 73).
67. Anterior ends of phallobase struts: (0) separated (open phallosome) (Fig. 74); (1) joined by sclerotic band (closed phallosome) (Fig. 75).
68. Inner parameres of phallosome: (0) absent (Fig. 72); (1) present (Fig. 73).
69. Posterior ends of inner parameres: (0) separated (Fig. 73); (1) fused to form an arch (aedeagal arch) (Fig. 74).
70. Shape of aedeagal arch: (0) rounded; (1) straight; (2) sharp; (3) projected posteriorly.
71. Apex of posterior projection of aedeagal arch: (0) rounded; (1) sharp; (2) straight.
72. Median process of aedeagal arch: (0) absent (Fig. 74); (1) present (Fig. 76).
73. Lateral processes of aedeagal arch: (0) absent (Fig. 74); (1) present (Fig. 76).
74. External parameres of phallosome: (0) absent (Fig. 74); (1) present (Fig. 79).
75. Degree of development of external parameres: (0) poorly developed (Fig. 78); (1) well developed (Fig. 79).
76. Pores on distal ends of external parameres: (0) absent (Fig. 78); (1) present (Fig. 80).
77. Apex of external parameres: (0) rounded (Fig. 79); (1) sharp (fig. 80).
78. Surface of external parameres: (0) smooth (Fig. 80); (1) ornamented (Fig. 81).
79. Position of external parameres: (0) outside of the endophallus (Fig. 75); (1) partially in the endophallus (Fig. 79); (2) totally immersed in the endophallus (Fig. 82).
80. External parameres associated to endophallic sclerites: (0) absent (Fig. 79); (1) present (Fig. 82).
81. Endophallic sclerites: (0) absent (Fig. 74); (1) present (Fig. 76).
82. Arrangement of endophallic sclerites: (0) grouped centrally forming a radula (Fig. 76); (1) arranged longitudinally in symmetrical pairs (Fig. 77).
83. Sharp lateral projections on male clunium: (0) absent (Fig. 83); (1) present (Fig. 84).
84. Ornamentations on posterior median border of male clunium: (0) absent (Fig. 83); (1) present (Fig. 85).
85. Shape of ornamentations of posterior median border of male clunium: (0) a comb (Fig. 85); (1) papillate protuberances (Fig. 86).
86. Microspines on posterior border of male epiproct: (0) absent (Fig. 87); (1) present (Fig. 88).
87. Posterior surface of male epiproct: (0) smooth (Fig. 87); (1) with little papillate protuberances (Fig. 89); (2) with a granulose tubercle (Fig. 84).
88. Macrosetae on basal third of male epiproct: (0) absent (Fig. 90); (1) present (Fig. 91).
89. Number of macrosetae on basal third of male epiproct: (0) one; (1) three.
90. Arrangement of three macrosetae on male epiproct: (0) in straight line (Fig. 91); (1) forming a triangle (Fig. 92).
91. Microspines on anterior border of male epiproct: (0) absent (Fig. 90); (1) present (Fig. 93).
92. Microspines on posterior border of male paraprocts: (0) absent; (1) present.

93. Sclerotized, hook-shaped prong on posterior border of male paraprocts: (0) absent (Fig. 83); (1) present (Fig. 94).

94. Posterior margin of subgenital plate: (0)) rounded (Fig. 95); (1) straight (Fig. 96); (2) bilobed (Fig. 97); (3) with an median prominence (Fig. 98); (4) projected posteriorly to form of bilobed tongue (Fig. 99).

95. Ovipositor valvulae (gonapophyses) of female: (0) absent (Fig. 100); (1) present (Fig. 101).

96. Ventral valvula (v1): (0) absent (Fig. 104); (1) present (Fig. 107).

97. Basal end of ventral valvula (v1): (0) joined to base of dorsal valvula (v2) (Fig. 105); (1) joined to clunium by a membranous segment (Fig. 106); (2) joined to clunium by a sclerotized segment (Fig. 107).

98. Distal end of dorsal valvula (v2): (0) uniform (Fig. 103); (1) forming a long, pointed, distal process (Fig. 104).

99. Microspines on distal process of dorsal valvula (v2): (0) disordered over surface (Fig. 111); (1) ordered in a longitudinal row (Fig. 112).

100. Anterior projection (heel), at base of dorsal valvula (v2): (0) absent (Fig. 109); (1) present (Fig. 108).

101. External valvula (v3): (0) absent (Fig. 104); (1) present (103).

102. Dorsal (v2) and external (v3) valvulae: (0) separated (Fig. 103); (1) v3 a lobe on side of v2, forming a composite valvula (v2+3) (Fig. 107).

103. Shape of external valvula (v3): (0) a flap (Fig. 103); (1) a lobe (Fig. 107); (2) a globule (Fig. 110); (3) an elongate blister (Fig. 108); (4) a protuberance (Fig. 106).

104. Apex of external valvula (v3): (0) rounded; (1) sharp.

105. Setae on external valvula (v3): (0) absent; (1) present.

106. Ninth sternum: (0) membranous (Fig. 101); (1) sclerotized (Fig. 102).

107. Shape of female epiproct: (0) semicircular (Fig. 113); (1) trapeziform (Fig. 114); (2) triangular (Fig. 115); (3) bell-shaped (fig. 116); (4) elliptic (Fig. 117).

108. Length of female epiproct: (0) ~ ½ the width of its base; (1) same as the width of its base; (2) ~ 1 ½ times the width of its base.

109. Setae on female epiproct: (0) on posterior half (Fig. 114); (1) distributed over the surface (Fig. 117).

110. Microspines on posterior border of female epiproct: (0) absent (same as Fig. 87); (1) present (same as Fig. 88).

111. Macrosetae on female epiproct: (0) absent (same as Fig. 90); (1) present (same as Fig. 91).

112. Number of macrosetae on female epiproct: (0) one; (1) three.

113. Position of macrosetae on female epiproct: (0) on the middle; (1) on basal third.

114. Arrangement of three macrosetae on female epiproct: (0) in straight line (same as Fig. 91); (1) forming a triangle (same as Fig. 92).

115. Posterior border of female paraprocts: (0) rounded (Fig. 118); (1) straight (Fig. 121).

116. Microspines on posterior border of female paraprocts: (0) absent; (1) present.
117. Trichobothria on female paraprocts: (0) absent (Fig. 118); (1) present (Fig. 120).
118. Number of trichobothria on female paraprocts: (0) one-nine (Fig. 119); (1) fifteen-twenty (Fig. 120).
119. Rosette at base of each trichobothria on female paraprocts: (0) absent (Fig. 119); (1) present (Fig. 120).
120. Length of trichobothria on female paraprocts: (0) all of same length; (1) one longer than the others.
121. Arrangement of trichobothria on female paraprocts: (0) grouped in a not well defined sensory field (Fig. 119); (1) grouped in a well defined sensory field (Fig. 120).
122. Shape of sensory field on female paraprocts: (0) circular (Fig. 120); (1) elliptic (Fig. 121).

Results

The resulting matrix (Table 1) contains 1831 cells (18%) with missing values and 977 cells (9%) with inapplicable values. The total ambiguity (missing and inapplicable data) is widely distributed, and the ambiguity caused by missing data concentrates in some particular taxa; those showing most ambiguity were *Valvepipsocus diodematus*, *Dimidistriata longicapita*, *Liratepipsocus jinghongicus*, *Metepipsocus beijingicus*, *Dichoepipsocus thimpuensis*, *Parepipsocus obscurus* and *Odontopsocus orghidani* (Table 2). All of them were represented by a single specimen, and character information was obtained exclusively from the corresponding original publication.

The cladistic analysis produced 57189 equally most parsimonious trees (MPTs) of 393 steps, with a consistency index (CI) of 0.40 and a retention index (RI) of 0.78. In the consensus cladogram, Epipsocetae appear as a monophyletic group (Fig. 122), but many of the relationships between terminal taxa were not resolved. However, the topology of the tree shows that basal nodes constitute well defined clades corresponding to the traditional classification at family level (Smithers 1972, Eertmoed 1973). The mapping of unambiguous characters supporting the branches in all the MPTs (Fig. 123) shows that almost all the clades are supported at the suprageneric level by a unique combination of characters that, with few exceptions, includes at least one synapomorphy.

The genera *Isthmopsocus*, *Auroropsocus* and *Dolabellopsocus* were grouped in a clade that corresponds to the family Dolabellopsocidae. The genera *Perucania*, *Triplocania*, *Ptiloneuropsis*, *Ptiloneura*, *Loneura*, *Willreevesia*, *Loneuroides*, *Timnewia* and *Euplocania* correspond to Ptiloneuridae. The most numerous sets of terminal taxa formed a large monophyletic clade that coincides with the family Epipsocidae. The species of the genera *Cladiopsocus* and *Spurostigma*, belonging in the family Cladiopsocidae, were grouped in independent clades, suggesting that Cladiopsocidae is a paraphyletic group. The species of *Neurostigma*, the only genus known in the family Neurostigmatidae, appear as part of the clade that corresponds to Epipsocidae, which puts in doubt the validity of the former family. On the other hand, *Parepipsocus* and *Terryerwinia* grouped in the Epipsocidae, and *Loneuroides* grouped in the Ptiloneuridae. Remaining species with assignment problems are grouped within the clade Epipsocidae, but with ununresolved relationships.

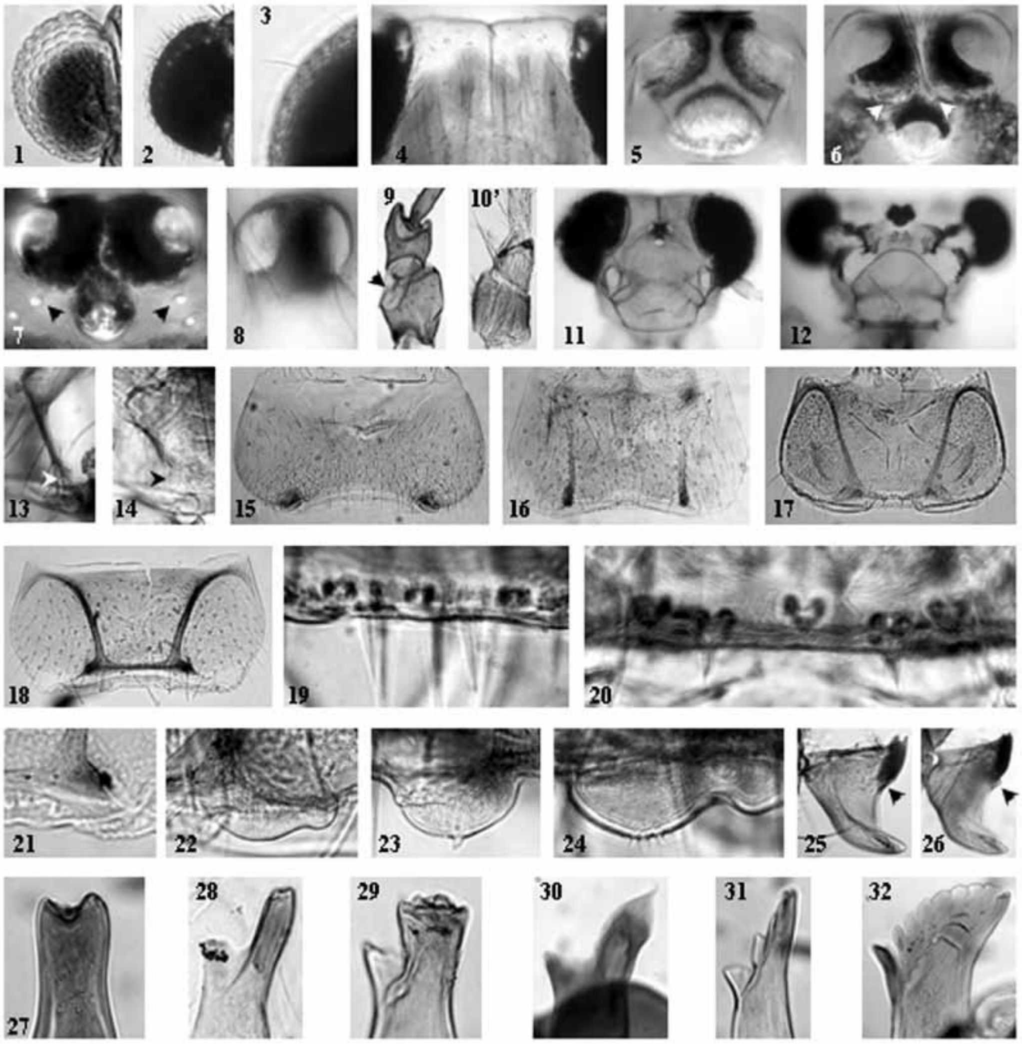
TABLE 2. Exclusion test results for taxa with missing data.

Taxa	Ambiguous cells (%)	MPTs	L	CI	RI
V. diodematus	68.8	78519	385	0.41	0.79
D. longicapita	66.4	87479	389	0.40	0.79
L. jinghongicus	63.9	37924	388	0.40	0.79
M. beijingicus	62.3	27393	391	0.40	0.78
D. thimpuensis	61.5	30880	387	0.41	0.78
P. obscurus	59.0	20960	387	0.41	0.79
O. orghidani	56.5	19710	390	0.40	0.79

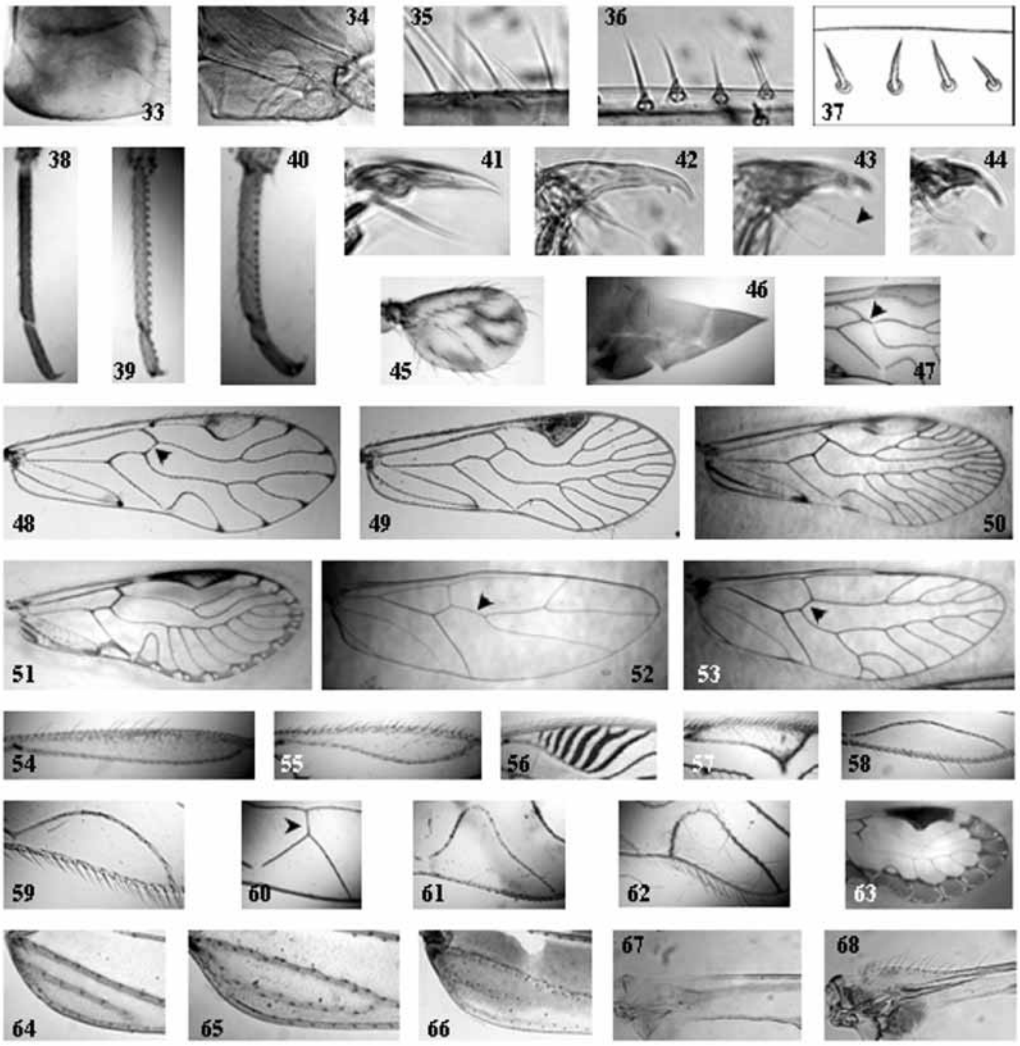
(MPTs) equally most parsimonious trees. (L) length. (CI) consistency index. (RI) retention index.

The exclusion test for taxa with missing data gave as a result that in all cases, when each taxon was removed sequentially, the topology of the consensus tree was almost identical as in the analysis where all taxa were included. Besides, the number of trees generated in each test was also similar (Table 2). Only when *P. obscurus* and *O. orghidani* were removed simultaneously, considerably less trees were obtained (104 MPTs; L = 384; CI = 0.41; RI = 0.78) and the resolution of the consensus tree improved remarkably (Fig. 124). In this case the monophyletic condition of Epipsocetae and the clades at family level remained identical as in the original analysis. The change appeared within the clade E pipsocidae, where two main monophyletic clades were formed (Fig. 124). Clade A shows close relationship among the species of the genera *Epipsocus*, *Incapsocus*, *Mesepipsocus*, *Neurostigma*, *Terryerwinia* and *Papillopsocus,* and clade B grouped the remaining genera and species known, and those with assignment problems. In both cases, the relationships within each node were solved in an important manner.

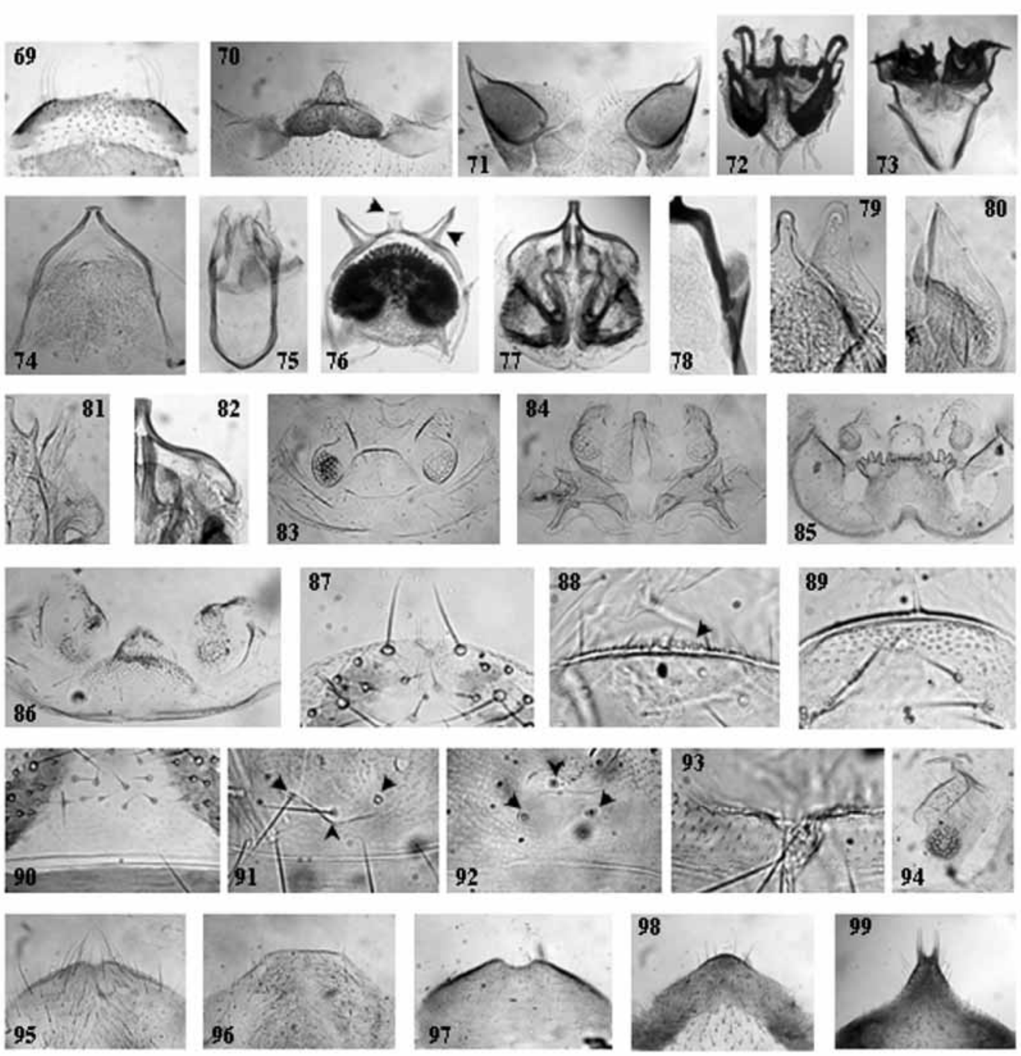
It is recommended that the results of this test be taken with caution until solving the missing data problem for floating taxa and confirming this hypothesis as independent. It is important to emphasize that in a cladistic analysis all available information must be included, although incomplete, and the resulting hypothesis must be considered as the most corroborated and therefore the best at the moment (Kluge & Wolf 1993), although sometimes the ambiguity codified for a taxon may weaken the parsimony test (Nixon 1996).



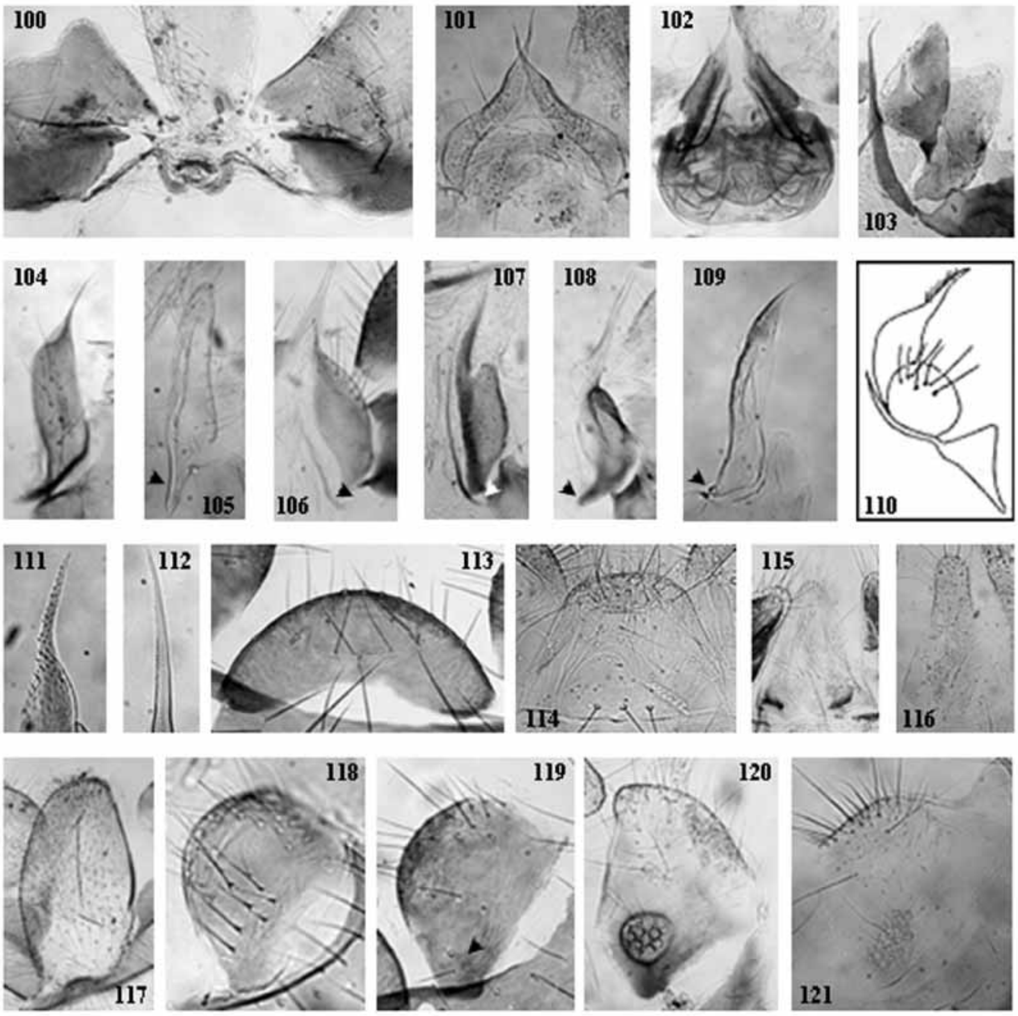
FIGURES 1–32. Compound eye of *Bertkauia crosbyana* (1), *Isthmopsocus* sp. 2 (2) and *Goja montieli* (3). Frons of *Dolabellopsocus* sp. 2 (4). Ocelli of *Elipsocus* sp. 4 (5), *Epipsocus* sp. 2 (6), *Goja montieli* (7) and *Isthmopsocus* sp. 2 (8). Scape and pedicel of *Dicropsocus montanus* (9) and *loneura leonilae* (10). Front view of head of *Cladiopsocus ocotensis* (11) and *Triplocania brailovskyana* (12). Anterior ends of epistomal suture of *Euplocania badonneli* (13) and *Goja plaumanni* (14). Labrum of *Stenopsocus immaculatus* (15), *Dolabellopsocus* sp. 2 (16), *Bertkauia crosbyana* (17) and *Cladiopsocus ocotensis* (18). Distal inner labral sensilla of *Elipsocus* sp. 4 (19) and *Ianthorntonia annae* (20). Anterior ends of labrum of *Cladiopsocus garciai* (21) and labral tubercles of *Ianthorntonia annae* (22), *Terryerwinia acutiphallica* (23) and *Mesepipsocus* sp. 1 (24). Right mandible of *Spurostigma* sp. 2 (25) and *Ianthorntonia annae* (26). Lacinial apex of *Stenopsocus immaculatus* (27), *Dolabellopsocus* sp. 2 (28), *Epipsocopsis greeni* (29), *Dicropsocus complexus* (30), *Dichoepipsocus micropterus* (31) and *Ianthorntonia annae* (32).



FIGURES 33–68. Female hind coxa of *Hinduipsocus atratus* (33) and *Cladiopsocus ocotensis* (34). Ventral surface of fore femur of *Goja montieli* (35), *Epipsocopsis prominens* (36) and *Auroropsocus orientis* (37). Tarsus of *Bertkauia crosbyana* (38), *Dolabellopsocus* sp. 2 (39) and *Elipsocus* sp. 4 (40). Pretarsal claw of *Dichoepipsocus micropterus* (41), *Ianthorntonia annae* (42), *Cladiopsocus ocotensis* (43) and *Isthmopsocus* sp. 2 (44). Female fore wing of *Goja montieli* (45) and *Hinduipsocus* sp. (46). Middle view of forewing of *Elipsocus* sp. 4 (47). Forewing of *Epipsocus* sp. 2 (48), *Incapsocus penai* (49), *Goja montieli* (50) and *Ptiloneura bidorsalis* (51). Hindwing of *Stenopsocus immaculatus* (52) and *Goja montieli* (53). Pterostigma of *Dolabellopsocus* sp. 2 (54), *Bertkauia crosbyana* (55), *Neurostigma enderleini* (56) and *Spurostigma* sp. 2 (57). Areola postica of *Dolabellopsocus* sp. 2 (58), *Bertkauia crosbyana* (59), *Stenopsocus immaculatus* (60), *Auroropsocus orientis* (61) and *Neurostigma enderleini* (62). Posterior view of forewing of *Euplocania badonneli* (63). Anal margin of forewing of *Spurostigma* sp. 2 (64), *Isthmopsocus* sp. (65) and *Auroropsocus orientis* (66). Costal margin of hindwing of *Stenopsocus immaculatus* (67) and *Euplocania badonneli* (68).



FIGURES 69–99. Hypandrium of *Goja montieli* (69), *Loneura leonilae* (70) and *Mesepipsocus* sp. 15 (71). Phallosome of *Euplocania badonneli* (72), *Triplocania brailovskyana* (73), *Epipsocus* sp. 2 (74), *Elipsocus* sp. 4 (75), *Terryerwinia acutiphallica* (76) and *Goja montieli* (77). External parameres of *Mesepipsocus* sp. BELICE (78), *Bertkauia crosbyana* (79), *Dolabellopsocus* sp. 2 (80), *Mesepipsocus* sp. 15 (81) and *Goja montieli* (82). Male clunium, epiproct and paraprocts of *Epipsocus* sp. 2 (83), *Mesepipsocus* sp. 15 (84), *Dolabellopsocus* sp. 2 (85) and *Isthmopsocus* sp. BELICE (86). Posterior view of male epiproct of *Elipsocus* sp. 4 (87), *Epipsocus* sp. 2 (88) and *Dolabellopsocus* sp. 3 (89). Anterior view of male epiproct of *Elipsocus* sp. 4 (90), *Hinduipsocus* sp. (91), *Willreevesia dominica* (92) and *Euplocania badonneli* (93). Male paraproct of *Cladiopsocus ocotensis* (94). Posterior view of subgenital plate of *Goja montieli* (95), *Dolabellopsocus* sp. 2 (96), *Mesepipsocus proctus* (97), *Bertkauia crosbyana* (98) and *Hinduipsocus atratus* (99).



FIGURES 100–121. Ovipositor valvulae and ninth sternum of *Dolabellopsocus* sp. 3 (100), *Epipsocopsis prominens* (101) and *Euplocania badonneli* (102). Gonapophyses of *Elipsocus* sp. 4 (103), *Dichoepipsocus complexus* (104), *Auroropsocus orientis* (105), *Hinduipsocus atratus* (106), *Loneura leonilae* (107), *Mesepipsocus proctus* (108), *Epipsocopsis greeni* (109) and *Valvepipsocus diodematus* (110) (from Li Fasheng 2002). Distal process of v2+3 of *Euplocania pictaoides* (111) and *Bertkauia crosbyana* (112). Female epiproct of *Odontopsocus orghidani* (113), *Terryerwinia* sp. PERU (114), *Euplocania pictaoides* (115), *Goja plaumanni* (116) and *Mesepipsocus proctus* (117). Female paraproct of sp. 3. SABAH (118), *Odontopsocus orghidani* (119), *Cladiopsocus garciai* (120) and *Epipsocopsis* sp. 1 (121).

Discussion

Smithers (1972) was the first to consider Epipsocetae as a monophyletic lineage, supported by long head, long genae, a pair of longitudinal labral sclerites, outer margin of mandibles angled, and external valvula (v3) fused to dorsal valvula (v2), to form a composite valvula. Later, Yoshizawa (2002) confirmed the monophyly of the group on the basis of six apomorphies: anterior tentorial pit separated from ventral margin of cranium, labrum with a pair of longitudinal sclerites, forewing veins with more than one row of setae (reversed in Epipsocidae), presence of second anal vein (A_2) (reversed in Epipsocidae), hindwing veins with two rows of setae, and dorsal (v2) and external (v3) valvulae of gonapophyses (partly) fused. In this analysis Epipsocetae is confirmed as a strongly supported monophyletic group (Fig. 123). Four characters are corroborated as

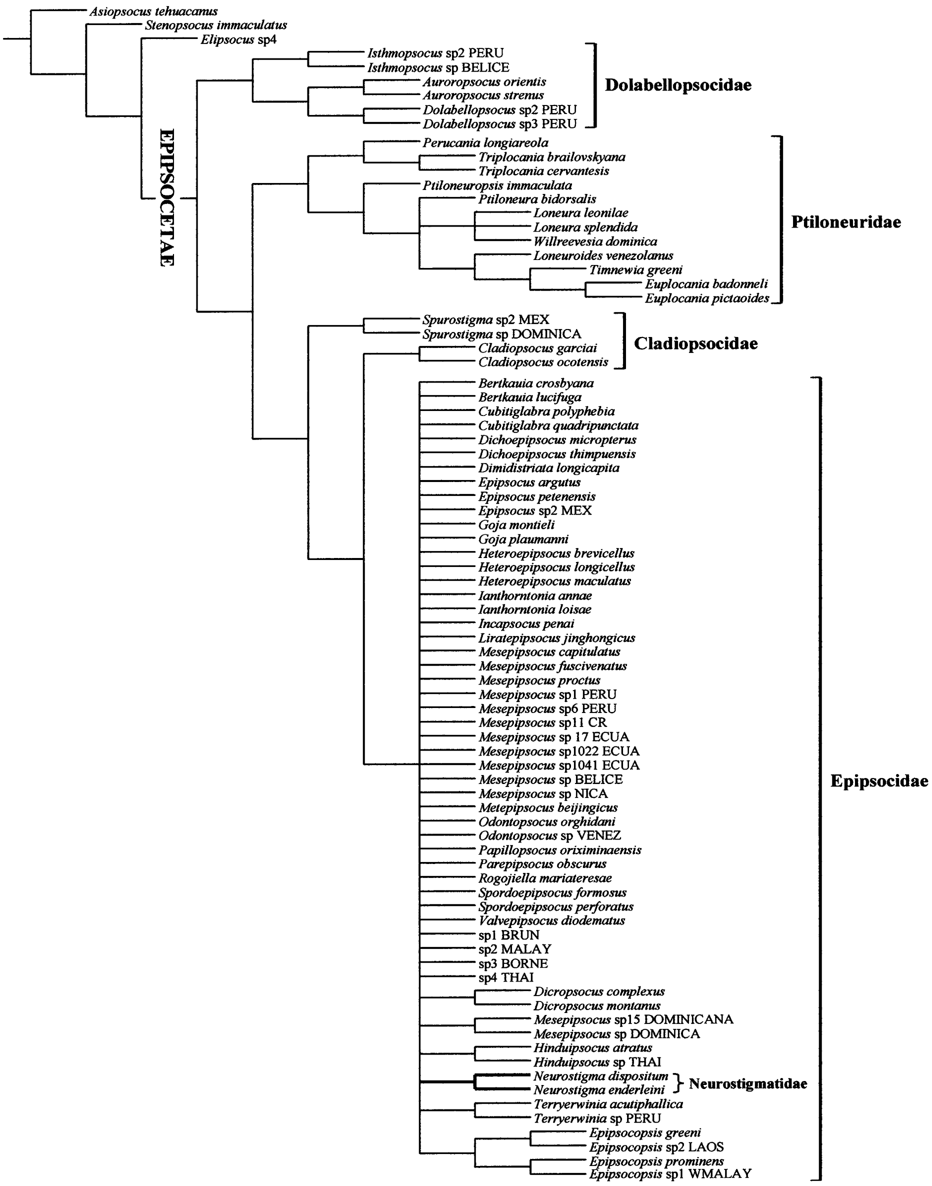


FIGURE 122. Strict consensus of 57189 equally most parsimonious trees (L = 393; IC = 0.40; IR = 0.78).

apomorphies at group level: a pair of longitudinal labral sclerites (12:1), presence of a second anal vein (A_2) in fore wing (55:1) (reversed in Epipsocidae), setae on veins Rs and M of the hindwing (62:1) (two rows for Yoshizawa (2002)) and external valvula (v3) joined on the side of dorsal vavula (v2), forming a composite valvula (102:1).

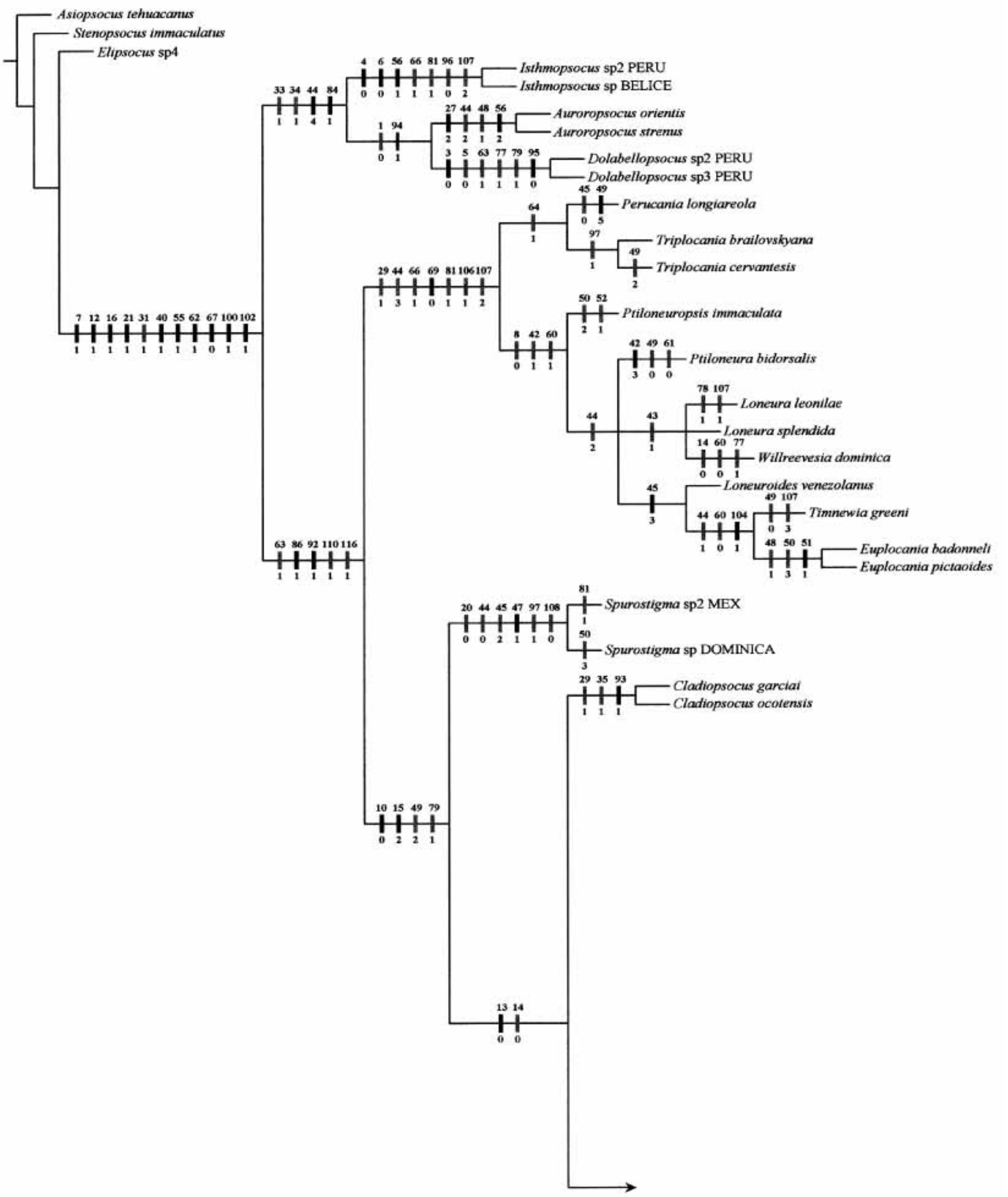


FIGURE 123. Consensus tree showing the character states that can be unambiguously optimized in all the MPTs. Black bars are apomorphic characters and grey bars are homoplastic characters. The arrow (?) indicates that the cladogram continues in the next page.

to be continued

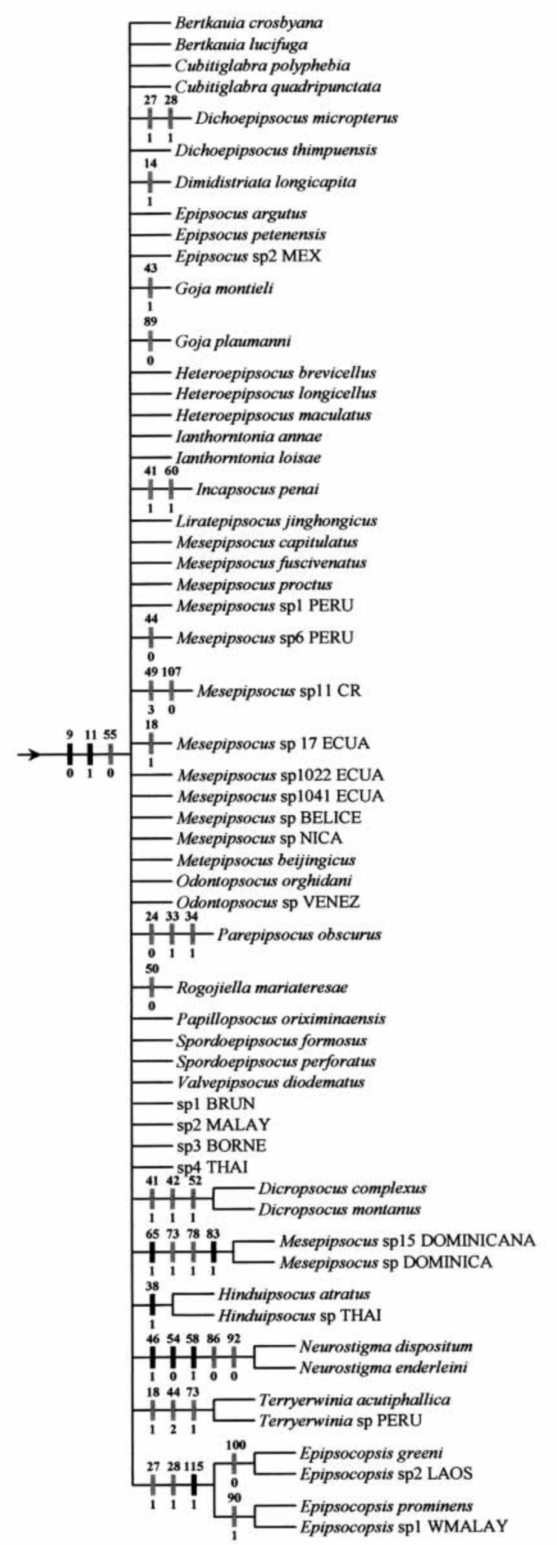


FIGURE 123 (continued).

FIGURE 124. Strict consensus tree of 104 MPTs, generated by removing *O. orghidani* and *P. obscurus* (L = 384, IC = 0.41, IR = 0.78). A and B indicate the two main clades topologies for Epipsocidae.

In this analysis the following additional characters were found to support monophyly: presence of a pair of setae at the base of the ocellar group (7:1), trichoid labral sensilla closer to the lateral placoids than to the median placoid (16:1), lacinial outer cusp more developed than the inner cusp (21:1), female with ctenidiobothria on t2 of hind leg (31:1), veins Rs and M of forewing joined by a crossvein (40:1), verticals struts of phallobase separated (open phallosome) (67:0), and presence of a basal heel on the dorsal valvula (v2) (100:1). The character anterior tentorial pit separated from ventral margin of cranium (codified here as anterior end of epistomal suture separated from ventral margin of cranium (11:1)) was apomorphic for Epipsocidae. The characters outer margin of mandible angled and fore wing veins with more than one row of setae were not considered in this analysis because are non-informative, as well as long head and long genae because both are quantitative characters.

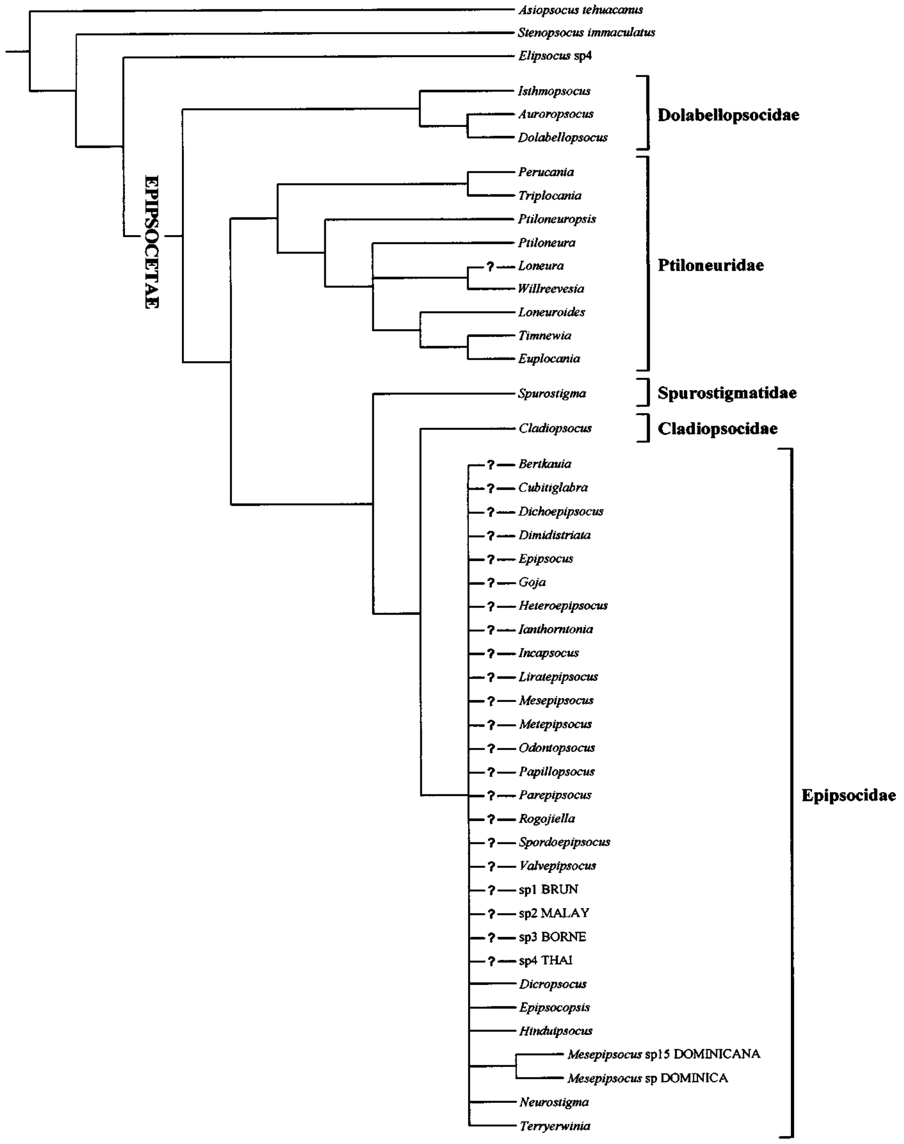


FIGURE 125. Phylogenetic relationships among genera of Epipsocetae and sister families. Question marks (?) indicate that monophyly is not supported.

In my results only Dolabellopsocidae, Ptiloneuridae, and Epipsocidae are recognized as monophyletic (Fig. 122). Dolabellopsocidae constitutes the basalmost clade, supported by four character states: pulvillus of pretarsal claw curved (33:1), pulvillus apex broad (34:1), length of pterostigma seven times its width (44:4), and presence of ornamentations on the posterior median border of the male clunium (84:1). Genera grouped in this family constitute well supported monophyletic clades, with *Isthmopsocus* as sister group of *Auroropsocus* + *Dolabellopsocus* (Fig. 125). *Dimidistriata*, previously placed here (Mockford 1998) on basis of labrum characters, was placed within Epipsocidae.

Ptiloneuridae, *Spurostigma* + *Cladiopsocus* (Cladiopsocidae) and Epipsocidae comprise a monophyletic group supported by the following apomorphies: presence of a row of fine setae at the proximal end of the costal margin of the hindwing (63:1), presence of microspines on the posterior border of the epiproct (86:1) and posterior border of the male paraprocts (92:1), and presence of microspines on the posterior border of the epiproct (110:1) and posterior border of female paraprocts (116:1). Within this clade Ptiloneuridae is located as the sister group of Cladiopsocidae (paraphyletic) + Epipsocidae.

Monophyly of Ptiloneuridae is supported by a single synapomorphy: posterior ends of the inner parameres separated (69:0); and the following homoplasies: three-segmented tarsi (29:1), length of pterostigma six times its width (44:3), struts of the phallobase oblique, V-shaped (66:1), presence of endophallic sclerites (81:1), ninth sternum sclerotized (106:1), and female epiproct triangular (107:2). All genera of Ptiloneuridae are clearly monophyletic, except *Loneura*. Within the family (Fig. 125), *Perucania* and *Triplocania* are closely related on the basis of a single homoplasic character: hypandrium formed by a large, central sclerite and two smaller side sclerites (64:1). The remaining genera are separated in another clade supported by three also homoplasic characters: pair of basal setae of the ocelli at the level of the median ocellus (8:0), vein M of forewing with four to five primary branches (42:1), and vein M of hindwing branched (60:1) (reversed in *Willreevesia* and *Euplocania*). *Ptiloneuropsis* is sister group to the clade that groups *Ptiloneura*, the polytomy of *L. leonilae*, *L. splendida*, and *Willreevesia*, and *Loneuroides* + *Euplocania*. Within this clade, the relationships are not resolved.

Spurostigma, *Cladiopsocus* and Epipsocidae are separated from the other families by the absence of the dorsal border of the epistomal suture (10:0), anterior ends of labral sclerites joined by a sclerotic strip (15:2), length of areola postica three times its width (49:2), and external parameres partially on the endophallus (79:1). The clade with the species of *Spurostigma* is supported by the synapomorphic character state, presence of a spurvein arising at the apex of pterostigma (47:1), and by the following homoplasies: absence of the premolar cusp on the right mandible (20:0), length of pterostigma three times its width (44:0), pterostigma triangular (45:2), base of the ventral valvula (v1) joined to clunium by a membranous segment (97:1), and length of female epiproct approximately half the width of its base (108:0). The monophyly of *Cladiopsocus* is supported by the synapomorphic character, presence of a sclerotized prong on the posterior border of the male paraprocts (93:1), and the following homoplasies: three-segmented tarsi (29:1), and presence of a setae-shaped spine anterior to the pulvillus (35:1).

Spurostigma and *Cladiopsocus* were initially placed in the family Cladiopsocidae (E ertmoed 1973), but, as a result of this analysis, both genera constitute monophyletic clades, clearly separated and placed paraphyletically without sharing the same ancestor. Here I propose to divide Cladiopsocidae in two monophyletic families, Spurostigmatidae (Eertmoed 1973) and Cladiopsocidae (*sensu stricto*) each represented by a single genus, *Spurostigma* and *Cladiopsocus* respectively (Fig. 125). As for its relationships, *Spurostigma* (Spurostigmatidae) appears as sister group of *Cladiopsocus* (Cladiopsocidae) + Epipsocidae. This latter clade is supported by two apomorphies, labral sclerites oblique (13:0), and labral sclerites prolonged up to the posterior margin of the labrum, curving towards the sides (14:0) (reversed in *Dimidistriata*).

Monophyly of Epipsocidae was proposed earlier (Casasola González & García Aldrete 2002, Yoshizawa 2002), supported by four synapomorphies: epistomal suture dorsally absent, membranous antero-ventral surface of scape, absence of second anal vein (A_2) in forewing, and presence of ventral setae in forewing. In this analysis the monophyly is corroborated, although the first character is not considered a synapomorphy for the family, whereas the latter is not considered in the analysis. Additionally, the anterior ends of the epistomal suture, separated from the ventral margin of cranium (11:1) also supports the monophyly of the clade.

Within Epipsocidae the relationships among the genera are not resolved (Fig. 122) and the monophyly in most of them is not supported (Fig. 125). Only some genera as *Dicropsocus*, *Dimidistriata*, *Goja*, *Incapsocus*, *Parepipsocus*, *Rogojiella* and *Terryerwinia* are supported by few characters and several homoplasies (Fig. 123). *Epipsocopsis*, *Hinduipsocus* and *Neurostigma* seem to be monophyletic genera, since are supported by at least one synapomorphic character. Also interesting is the relationship between the *M*. sp15 DOMINICANA and *M*. sp DOMINICA, which were grouped in a monophyletic clade supported by four characters, two of them synapomorphic. The previous relationship indicates that both species could constitute a distinct, different genus.

When *P. obscurus* and *O*. *orghidani* are eliminated from the analysis, the remaining genera are grouped in two main clades (Fig. 124). In clade A the relationships between the species of *Mesepipsocus* are distinct, but in several of these subclades other genera also appear, such as *Epipsocus*, *Incapsocus*, *Neurostigma,* and *Terryerwinia*. This indicates that these genera are polyphyletic and some of their species may be closely related to some of the species of *Mesepipsocus*. It also indicates that the genus presents circumscription problems, the species represented possibly belonging in other genera and not forming a monophyletic group. On the other hand, Casasola González & García Aldrete (2002) proposed close relationships between *Epipsocus* and *Mesepipsocus*, on the basis of the absence of external parameres on the phallosome. In this analysis the relationship is observed solely with some species of *Epipsocus* and *Mesepipsocus*.

Neurostigma was initially considered as a genus of Epipsocidae. Later, Smithers (1972) endorsed the hypothesis on the basis of the following main apomorphies: two-segmented tarsi, few setae on the wing veins, and the presence of a single anal vein. E ertmoed (1973), based on phenetic evidence suggested the inclusion of the genus in the family Neurostigmatidae. In my results, the position of *Neurostigma* is not resolved (Fig. 122) but shows a much closer relationship to the genera of Epipsocidae than to any other family. This partly supports the hypothesis of Smithers (1972) and questions the consistency of the diagnostic characters proposed by Eertmoed (1973) for Neurostigmatidae. When the floating taxa are eliminated, the genus is placed again within the clade Epipsocidae, in a position close to *Incapsocus* and to some species of *Mesepipsocus* (Fig. 124). This suggests that in fact it is very likely that *Neurostigma* is a genus of Epipsocidae.

In clade B, *Epipsocopsis* is located at the base as sister group to the remaining genera. Next appear *H. maculatus*, *Dicropsocus,* and species 1 of Brunei as independent clades. At the cusp of the tree most relationships are resolved, although some ambiguities persist. *Metepipsocus* + *Valvepipsocus* are closely related to the clade integrated by *Dimidistriata*, *Liratepipsocus*, species 2 of Malaysia and species 3 of Borneo. Species of *Goja* and *Rogojiella* are grouped together with *Ianthorntonia* in the same clade. Near this group is located the species 4 of Thailand. Finally, at the top clade appear the remaining Asian genera *Cubitiglabra*, *Dichoepipsocus*, *Heteroepipsocus*, *Hinduipsocus* and *Spordoepipsocus*. Within this clade also appear *Odontopsocus*, of American distribution, and *Bertkauia* from America, Europe, and Asia.

The results of the test of exclusion of floating taxa show that the ambiguity due to the lack of information of unexamined species can produce similar results at family level, but also, these taxa cause the lack of resolution in an important sector of the topology of the cladogram. For future studies it is necessary to get as much information as possible from those taxa with a high percentage of ambiguity, especially *P. obscurus* and *O. orghidani*. It is also important to include more characters to test the monophyly of several of the analyzed genera. Finally, it is important to revise the taxonomy of *Mesepipsocus* in a phylogenetic context because of the circumscription problems presented here.

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Appendix I

List of terminal taxa examined. The acronyms at the end of each name indicate the origin collection (see text). (^{1}) species selected from literature, the data of the original publication appear between [ ]. (^{2}) species with assignment problems. The arrangement of families and genera corresponds with the results presented in Fig.4.

ASIOPSOCIDAE

Asiopsocus

A. tehuacanus García Aldrete & Casasola González 1995. MEXICO. 1♂ (holotype), 1♀ (allotype). CNIN.

STENOPSOCIDAE

Stenopsocus

S. immaculatus (Stephens) 1866. FRANCE. 1♂, 1♀. CNIN.

ELIPSOCIDAE

Elipsocus

E. sp. 4. MEXICO. 1♂, 1♀. CNIN.

DOLABELLOPSOCIDAE

Isthmopsocus

I. sp. 2. PERU. 1♂, 1♀. CNIN.

I. sp. BELIZE. 1♂, 1♀. CNIN.

Auroropsocus

A. orientis Eertmoed 1973. INDIA 1♂ [Eertmoed 1973:388]. MALAYSIA 1♀ (CNIN).

A. strenus ^{1} Li Fasheng 2002 [Li Fasheng 2002: 189]. CHINA. 1♂, 1♀.

Dolabellopsocus

D. sp. 2. PERU. 1♂, 1♀. CNIN.

D. sp. 3. PERU. 1♂, 1♀. CNIN.

PTILONEURIDAE

Perucania

P. longiareola New & Thornton 1988. PERU. 1♂ (CNIN), 1♀ [New & Thornton 1988:233].

Triplocania

T. brailovskyana García Aldrete 1999. MEXICO. 1♂ (holotype), 1♀ (allotype). CNIN.

T. cervantesi García Aldrete 1999. BELIZE. 1♂ (holotype), 1♀ (allotype). CNIN.

Ptiloneuropsis

P. immaculata Roesler 1940. BRAZIL. 1♂. CNIN.

Ptiloneura

P. bidorsalis ^{1} Enderlein 1900 [Enderlein 1900: 149]. PERU. 1♂.

Loneura

L. leonilae García Aldrete 1995. MEXICO. 1♂, 1♀. CNIN.

L. splendida Mockford 1957. MEXICO 1♂. BELIZE 1♀. CNIN.

Willreevesia

W. dominica García Aldrete 2005. DOMINICA. 1♂ (holotype), 1♀ (allotype). MHNG.

Loneuroides

L. venezolanus García Aldrete VENEZUELA. 1♀. MHNG.

Timnewia

T. greeni García Aldrete 2005. BRAZIL. 1♂, 1♀. CNIN.

Euplocania

E. badonneli New & Thornton 1988. BRAZIL. 1♂, 1♀. CNIN.

E. pictaoides García Aldrete 1998. PERU. 1♂ (holotype), 1♀ (allotype). CNIN.

SPUROSTIGMATIDAE

Spurostigma

S. sp. 2. MEXICO. 1♂, 1♀. CNIN.

S. sp. DOMINICA. 1♂, 1♀. MHNG.

CLADIOPSOCIDAE

Cladiopsocus

C. garciai Eertmoed 1986. MEXICO. 1♂, 1♀. CNIN.

C. ocotensis García Aldrete 1996. MEXICO. 1♂, 1♀. CNIN.

EPIPSOCIDAE

Bertkauia

B. crosbyana Chapman 1930. USA. 1♂, 1♀. ISU.

B. lucifuga (Rambur) 1919. GERMANY, SWITZERLAND. 1♂, 1♀. MHNG.

Cubitiglabra

C. polyphebia [1] Li Fasheng 1995 [Li Fasheng 1995: 144]. CHINA. 1♂.

C. quadripunctata Li Fasheng 1995. CHINA. 1♂. CAU.

Dichoepipsocus

D. micropterus Li Fasheng & Mockford 1997. CHINA. 1♀. CAU.

D. thimpuensis [1] (New) 1978 [New 1978: 68]. BHUTAN. 1♀.

Dimidistriata

D. longicapita [1] Li Fasheng & Mockford 1997 [Li Fasheng & Mockford 1997: 141]. CHINA. 1♀.

Epipsocus

E. argutus New 1980. PERU. 1♂. CNIN.

E. petenensis Mockford 1957. BELIZE. 1♂, 1♀. CNIN.

E. sp. 2. MEXICO. 1♂, 1♀. CNIN.

Goja

G. montieli Casasola & García Aldrete 2002. MEXICO. 1♂ (holotype), 1♀ (allotype). CNIN.

G. plaumanni (Roesler) 1940. BRAZIL. 1♂, 1♀. CNIN.

Heteroepipsocus

H. brevicellus Li Fasheng 1995. CHINA. 1♂. CAU.

H. longicellus [1] Li Fasheng 1995 [Li Fasheng 1995: 65]. CHINA. 1♂.

H. maculatus [1] Li Fasheng 2002 [Li Fasheng 2002: 200]. CHINA. 1♀.

Ianthorntonia

I. annae. García Aldrete 2005. BOLIVIA. 1♂ (holotype). CNIN.

I. loisae García Aldrete 2005. BOLIVIA. 1♂ (holotype). CNIN.

Incapsocus

I. penai García Aldrete. PERU. 1♂ (holotype). CNIN.

Liratepipsocus

L. jinghongicus [1] Li Fasheng 2002 [Li Fasheng 2002: 213]. CHINA. 1♀.

Mesepipsocus

M. capitulatus (New) 1980. PERU. 1♂, 1♀. CNIN.

M. fuscivenatus (New & Thornton) 1988. PERU. 1♂. CNIN.

M. proctus (New & Thornton) 1988. PERU. 1♂, 1♀. CNIN.

M. sp. 1. PERU. 1♂, 1♀. CNIN.

M. sp. 6. PERU. 1♀. CNIN.

M. sp. 11. COSTA RICA. 1♀. CNIN.

M. sp. 17. ECUADOR. 1♂, 1♀. CNIN.

M. sp. 1022. ECUADOR. 1♀. CNIN.

M. sp. 1041. ECUADOR. 1♂, 1♀. CNIN.

M. sp. BELIZE. 1♂. CNIN.

M. sp. NICARAGUA. 1♀. CNIN.

Metepipsocus

M. beijingicus [1] Li Fasheng 2002 [Li Fasheng 2002: 215]. CHINA. 1♀.

Odontopsocus

O. orghidani Badonnel 1987. VENEZUELA. 1♀ (holotype). MHNG.

O. sp. VENEZUELA. 1♂. MHNG.

Papillopsocus

P. oriximinaensis García Aldrete. BRAZIL. 1♂ (holotype), 1♀ (allotype). CNIN.

Parepipsocus

P. obscurus [1] Badonnel 1986 [Badonnel 1986: 194]. COLOMBIA. 1♀.

Rogojiella

R. mariateresae García Aldrete 2005. BOLIVIA. 1♂ (holotype). CNIN.

Spordoepipsocus

S. formosus [1] Li Fasheng 2002 [Li Fasheng 2002: 204]. CHINA. 1♂.

S. perforatus [1] Li Fasheng 2002 [Li Fasheng 2002: 202]. CHINA. 1♂.

Valvepipsocus

V. diodematus [1] Li Fasheng 2002 [Li Fasheng 2002: 223]. CHINA. 1♀.

([2]) sp. 1. BRUNEI, SABAH, 1♂, 1♀. MHNG.

([2]) sp. 2. MALAYSIA. 1♂. MHNG.

([2]) sp. 3. BORNEO, SABAH. 1♂, 1♀. MHNG.

([2]) sp. 4. THAILAND. 1♂. MHNG.

Dicropsocus

D. complexus Smithers & Thornton 1977. NEW GUINEA. 1♀ (holotype). AM.

D. montanus Smithers & Thornton 1977. NEW GUINEA. 1♂ (holotype), 1♀ (allotype). AM.

Epipsocopsis

E. greeni New 1977. SRI LANKA. 1♂, 1♀. ISU.

E. prominens (Banks) 1937. PHILIPPINES. 1♂, 1♀. ISU.

E. sp. 1. WEST MALAYSIA. 1♂, 1♀. MHNG.

E. sp. 2. LAOS. 1♂, 1♀. MHNG.

Hinduipsocus

H. atratus Badonnel 1981. INDIA. 1♀ (holotype). MHNG.

H. sp. THAILAND. 1♂, 1♀. MHNG.

([2]) *M.* sp. 15. DOMINICAN REPUBLIC. 1♂, 1♀. CNIN.

M. sp. DOMINICA. 1♂, 1♀. MHNG.

Neurostigma

N. dispositum Roesler 1940. MEXICO. 1♂, 1♀. CNIN.

N. enderleini New 1980. BRAZIL. 1♂, 1♀. CNIN.

Terryerwinia

T. acutiphallica García Aldrete. PERU. 1♂ (holotype), 1♀ (allotype). CNIN.

T. sp. PERU. 1♂ , 1♀ . CNIN.