

# Phylogeny and higher classification of suborder Psocomorpha (Insecta: Psocodea: 'Psocoptera')

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Phylogenetic relationships among all 24 families of suborder Psocomorpha (Insecta: Psocodea: 'Psocoptera') are inferred based on adult morphology. Monophyly of Psocomorpha is strongly supported by six autapomorphies. The presently accepted four infraorders – Psocetae, Homilopsocidea, Epipsocetae and Caeciliusetae – are regarded as monophyletic, but Archipsocidae and Hemipsocidae, previously assigned to Homilopsocidea and Psocetae, respectively, are regarded as the basalmost clades of the suborder. Based on the results of the cladistic analysis, a higher classification for Psocomorpha is proposed. Six infraorders (two new – **Archipsocetae**, **Hemipsocetae** – and the four aforementioned) are recognized. Four new superfamilies are recognized within Homilopsocidea: **Elipsocoidea**, **Lachesilloidea**, **Pseudocaecilioidea** and **Peripsocoidea**. Two superfamilies are recognized within Caeciliusetae: Asiopsocoidea and Caeciliusoidea. Descriptions of taxa above family level are provided. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, 136, 371–400

**ADDITIONAL KEYWORDS:** – new infraorder – superfamily – phylogeny – Psocomorpha – Psocoptera – systematics.

## INTRODUCTION

The order Psocoptera (psocids, booklice or barklice) is a small order of insects, comprising c. 4110 described species (García Aldrete, 1996). They range from 1 to 10 mm in length and are characterized by a well-developed postclypeus, long antennae, pick-like lacinia, reduced prothorax and well-developed pterothorax.

Psocomorpha is the largest suborder in Psocoptera, containing 24 of the 37 psocopteran families. Psocomorphan families are classified into four groups: Epipsocetae, Caeciliusetae, Homilopsocidea and Psocetae. This taxonomic system was first proposed by Pearman (1936) and remains widely adopted with some minor alterations.

Phylogenetic relationships within Psocoptera were first extensively studied by Smithers (1972). However, in his proposed dendrogram, some lineages were based on plesiomorphic or homoplastic character states; nearly 20 years later he admitted (Smithers,

1991) that his phylogenetic system needed revision. Psocomorphans exhibit a range of fascinating behaviours, including stridulation, aggregation, subsociality and nesting. Investigation into the evolutionary aspects of these behaviours requires a reliable phylogenetic system.

In the present paper, I infer the phylogenetic relationships among families of Psocomorpha based on adult morphology. Six infraorders (two of them new) are recognized. In addition, six superfamilies are recognized: two within Caeciliusetae and four (new) within infraorder Homilopsocidea.

## HISTORY OF THE HIGHER CLASSIFICATION OF PSOCOMORPHA

The presently accepted taxonomic categories above family level within Psocoptera were first proposed by Pearman (1936). Unlike earlier efforts based on a few prominent characters such as wing venation and number of tarsomeres, his classification was based on an analysis of a wide range of external morphological characters. He proposed eight family groups (infraorders of the present paper) in Psocoptera, of which four – Epipsocetae, Caecilietae (= Caeciliuse-

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**Table 1.** History of the higher classification of Psocomorpha

Pearman (1936)	Roesler (1944)	Badonnel (1951)	Smithers (1972)	Smithers (1996)	Yoshizawa (present)
<b>CAECILIETAE</b> Calopsocidae Caeciliusidae Amphipsocidae Stenopsocidae Polypsocidae	<b>CAECILIETAE</b> Calopsocidae  Polypsocidae	<b>CAECILIETAE</b> Calopsocidae Caeciliusidae Amphipsocidae Stenopsocidae Polypsocidae	<b>EIPSOCETAE</b> Callistopteridae Epipsocidae Cladiopsocidae Ptiloneuridae	<b>EIPSOCETAE</b> Epipsocidae Cladiopsocidae Dolabellopsocidae Ptiloneuridae	<b>ARCHIPSOCETAE, new</b> Archipsocidae <b>HEMIPSOCETAE, new</b> Hemipsocidae <b>PSOCETAE</b> Myopsocidae Psilopsocidae Psocidae
<b>EIPSOCETAE</b> Epipsocidae	<b>EIPSOCETAE</b> Epipsocidae Ptiloneuridae Callistopteridae Psilopsocidae	<b>EIPSOCETAE</b> Epipsocidae Ptiloneuridae Callistopteridae Psilopsocidae	<b>PSOCETAE</b> CALOPSOCOIDEA Polypsocidae Calopsocidae PSOCOIDEA Caeciliidae Pseudocaeciliinae Trichopsocini Pseudocaeciliini Caeciliinae Ectopsocini Caeciliini Psocidae Archipsocinae Archipsocini Lesneiini Psocinae Elipsocini Psocini	<b>CAECILIETAE</b> Asiopsocidae Caeciliusidae Amphipsocidae Stenopsocidae  <b>HOMILOPSOCIDEA</b> Lachesillidae Ectopsocidae Peripsocidae Trichopsocidae Archipsocidae Calopsocidae Pseudocaeciliidae Bryopsocidae Philotarsidae Elipsocidae Mesopsocidae	<b>ELIPSOCOIDEA</b> Elipsocidae LACHESILLOIDEA Ectopsocidae "Lachesillidae" PSEUDOCAECILIOIDEA Trichopsocidae "Pseudocaeciliidae" Calopsocidae PERIPSOCOIDEA Bryopsocidae Peripsocidae Philotarsidae Mesopsocidae <b>EIPSOCETAE</b> "Cladiopsocidae" Ptiloneuridae Dolabellopsocidae Epipsocidae <b>CAECILIUSETAE</b> ASIOPSOCOIDEA Asiopsocidae CAECILIUOIDEA Stenopsocidae Amphipsocidae "Caeciliusidae"
<b>PSOCETAE</b> Myopsocidae Thyrsophoridae Psocidae	<b>PSOCETAE</b> Myopsocidae  Psocidae	<b>PSOCETAE</b> Myopsocidae Thyrsophoridae Psocidae			
<b>HOMILOPSOCIDEA</b> Hemipsocidae Elipsocidae Philotarsidae Mesopsocidae Lachesillidae* Peripsocidae Pseudocaeciliidae Trichopsocidae Archipsocidae	Mesopsocidae      Pseudocaeciliidae	<b>HOMILOPSOCIDEA</b> Hemipsocidae Elipsocidae Philotarsidae Mesopsocidae Lachesillidae Peripsocidae Pseudocaeciliidae Trichopsocidae Archipsocidae			
				<b>PSOCETAE</b> Hemipsocidae Psocidae Psilopsocidae Myopsocidae	

tae), Homilopsocidea, and Psocetae – are presently assigned within Psocomorpha (Table 1).

Roesler (1944) proposed three suborders in Psocoptera, corresponding to the presently accepted Trogiomorpha, Troctomorpha, and Psocomorpha (= Eupsocida *sensu* Roesler). In Psocomorpha, he recognized three family groups: Epipsocetae, Psocetae and Caeciliusidae (= Caeciliusidae). Psocetae and Homilopsocidea of Pearman's system were included in Psocetae (*sensu* Roesler). He also grouped or split some of Pearman's families, as shown in Table 1.

The taxonomic system proposed by Badonnel (1951) is a combination of those of Pearman and Roesler. He retained all Pearman's families and family groups, and arranged them into Roesler's suborders. Badonnel's system has been widely accepted with only two modifications: Smithers (1967) transferred Calopsocidae from Caeciliusidae to Homilopsocidea and Mockford (1976) transferred Hemipsocidae from Homilopsocidea to Psocetae.

The monograph by Smithers (1972) is the most extensive study of the higher classification of Psocoptera. He also investigated the phylogenetic relationships among all families and genera of Psocoptera. However, as mentioned above, some lineages in his

dendrogram were defined by symplesiomorphic or homoplastic characters and his phylogenetic classification has not been accepted.

The classifications adopted by Smithers (1996) and Lienhard (1998) are based on Badonnel (1951) and include the previous updates. A few years prior to this Mockford (1993) raised the status of Dasydemellidae, formerly a subfamily of Amphipsocidae, but this was not followed by Smithers and Lienhard.

Within the family groups of Psocomorpha, the following phylogenetic hypotheses have been proposed:

- (1) Pseudocaeciliidae and Calopsocidae comprise a monophyletic group (Smithers, 1967; Thornton & Smithers, 1984)
- (2) Elipsocidae and Mesopsocidae comprise a monophyletic group, with Philotarsidae the sister group (Badonnel & Lienhard, 1988).
- (3) Caeciliusidae, Stenopsocidae, and Amphipsocidae comprise a monophyletic superfamily, Caeciliusoidea, with Asiopsocidae the sister group (Mockford & García Aldrete, 1976).
- (4) Bryopsocidae is the sister group of the clade comprising Pseudocaeciliidae and Calopsocidae (Mockford, 1984).

(5) Closer relationships between Philotarsidae and (a) Mesopsocidae or (b) Elipsocidae, are also possible (Mockford, 1984).

(6) Lachesillidae and Elipsocidae may be phylogenetic sister groups (Mockford & Sullivan, 1986).

(7) *Ectopsocus* and its close allies appear to be closer to the lachesillids than to *Peripsocus* (Mockford, 1972).

Eertmoed (1973) proposed phenetic relationships for the Epipsocetæ group – a classification which has become widely accepted.

## MATERIAL AND METHODS

Lists of the taxa examined in this study or selected from the literature are available at <http://insect3.agr.hokudai.ac.jp/psoco-web/data/index.html>. All internet resources in this paper are also available from the author on request. Terminology mainly follows Matsuda (1965, 1970, 1976) and Smithers (1991).

Dried and wet specimens were used for the study. For the observation of external structures, the material was placed in a 5% solution of KOH at 45°C for 1–3 h depending on size. It was then washed with distilled water and stored in 80% ethanol. Dissected structures were stained with Delafield's Hematoxylin, then observed and illustrated. For the study of internal structures, the wet material was dissected in 80% ethanol, and stained with methylene blue. A Leica MZ12 stereoscopic microscope was mainly used for observation and illustration. For extremely small structures, the material was slide-mounted in euparal and an Olympus BX50 compound light microscope used for observation and illustration.

As a rule, exemplars (Yeates, 1995) for the analysis were selected from all psocomorphan families based on the following criteria:

- (1) Selection to follow the taxonomic system adopted by Mockford (1993).
- (2) At least two exemplars from each family, one from the nominotypical genus and the other from a genus assumed to be distantly related to it.
- (3) Only one exemplar when the family is represented by only one genus or comprises uniform taxa.
- (4) More than two exemplars when the family is highly diverse (strategy 3 of Hills, 1998).

In some cases, exemplars and character information were selected from published descriptions and illustrations. They are listed in the next section.

The cladistic analysis was based on the external morphology and musculature or other internal structures of adults. Table 2 features the data matrix; it is also available at <http://insect3.agr.hokudai.ac.jp/psoco-web/data/index.html>. Based on this matrix, most parsimonious trees were found using PAUP\*

4.0b8 (Swofford, 2001). A heuristic search was performed with TBR and the addition sequences 'random' options (1000 replications) chosen. Character states were optimized using MacClade 4.0 (Maddison & Maddison, 2000). The cladogram was translated to a phylogenetic system following the annotated Linnaean system method (Wiley, 1981).

## CLADISTIC ANALYSIS

### EXEMPLARS

In this section, I list the criteria for selecting exemplars from each family with minimum reduction of morphological diversity.

Outgroup exemplars were selected from the remaining two psocopteran suborders, Trogiomorpha and Troctomorpha. As the former is regarded as monophyletic and apparently distantly related to Psocomorpha, only one primitive exemplar, *Echmepteryx lunulata*, was selected from it. Mockford (1967) regarded Amphientomidae of Troctomorpha as the sister group of Psocomorpha and two exemplars, *Paramphientomum yumyum* and *Tineomorpha* sp. (from Malaysia), were selected from this family because the sister group has the strongest effect upon estimating the character states of the ingroup node (Maddison *et al.*, 1984). Two other exemplars, *Tapinella* sp. (from Taiwan) and Troctopsocidae Gen. sp. (from Malaysia), were selected from other troctomorphan families, each of which is regarded as distantly related to Amphientomidae. The list, selected on the basis of the four rules in the preceding section, is as follows:

- (1) Archipsocidae: *Archipsocus* sp. (from Mexico) and *Pararchipsocus pacificus*.
- (2) Hemipsocidae: comprises two genera, *Hemipsocus* and *Anopistoscena*, the latter characterized only by autapomorphic forewing venation. In contrast, all species of *Hemipsocus* are very similar to each other except for autapomorphic modifications of the male genitalia. Thus only one exemplar, *Hemipsocus chlotriticus*, was selected.
- (3) Myopsocidae: *Myopsocus* sp. (from Japan) and *Lichenomima muscosa*.
- (4) Psilopsocidae: comprises only one genus, *Psilopsocus*; one exemplar, *Psilopsocus* sp. (from Indonesia), was selected.
- (5) Psocidae: one of the most diverse families in Psocomorpha, with many potential exemplars. However, most modifications are autapomorphic for each taxon, and provide little phylogenetic information for higher categories. Thus two exemplars, *Psocus* sp. (nr *bipunctatus*, from Japan) and *Psocidus* sp. (from Japan), were selected.
- (6) Elipsocidae: *Elipsocus abdominalis* and *Hemineura dispar*.

**Table 2.** Data matrix for phylogenetic analysis of Psocomorpha (? = missing data)

	1	2	3	4	5	6	
	0	0	0	0	0	0	
<i>Echmepteryx</i>	000000000	000000000	020?000000	000000000	000000?10	0000000110	00000000
<i>Tapinella</i>	000000000	000?000000	000?000000	0000200000	0000000100	0000000000	00000000
Troctopsocidae	000000000	000000000	100?000000	0000200000	0000000100	0000000000	00000000
<i>Tineomorpha</i>	000000000	000000000	020?000000	0000000000	000000?10	0000000000	00000000
<i>Paramphientomum</i>	000000000	000000000	020?000000	1000000000	000000?10	0000000000	00000000
<i>Archipsocus</i>	1000000010	0002100100	021?110000	1111000001	1100000102	000000001?	20000000
<i>Pararchipsocus</i>	1000000010	0002100100	021?110000	1111000001	1100000102	000000001?	00000000
<i>Hemipsocus</i>	1011000010	0010000200	0000100001	1011000001	1001000?10	0010000000	00000000
<i>Psilopsocus</i>	1010000010	0010010111	1000100000	1011200010	1001000102	001001?100	00100000
<i>Psocus</i>	1010100010	0010010111	1000100002	1011200011	0001100002	0010010100	00100001
<i>Sigmatoneura</i>	1010100010	0010010111	1000100002	1011200011	0001100002	0010010100	00100001
<i>Myopsocus</i>	1010000010	0010010111	1000100002	1011200010	1001000?10	0011010000	00000000
<i>Lichenomima</i>	1010000010	0010010111	1000100002	1011201010	1001000000	0011010000	00000000
<i>Elipsocus</i>	1000000010	0011110111	0000100000	1011100000	0000000000	0000100000	01000000
<i>Hemineura</i>	1000000010	0011110111	0000100000	1011100000	0000000000	0000100000	01000000
<i>Ectopsocus</i>	1010000010	0111110111	0000100010	1011201001	1100000000	1000200000	01000100
<i>Eolachesilla</i>	1010000010	0111110111	0000100000	1011200000	1000000000	1000000000	01000100
<i>Nanolachesilla</i>	1011100010	0111110111	0000100000	1011200001	1000000000	100030001?	1??00100
<i>Lachesilla</i> (Vietnam)	1010100010	0111110111	0000100000	1011200001	0000000?12	000000001?	1??00100
<i>Lachesilla</i>	1010100010	0111110111	0000100000	1011200001	1000000?12	000000001?	2??00100
<i>Trichopsocus</i>	1010100010	0011110211	0001100000	1011000101	1110000000	1000000100	01011000
<i>Pseudocaecilius</i>	1010100010	0011110211	0011100000	1011010001	1110111000	0000200101	01011000
<i>Ophiodopelma</i>	1010100010	0011110211	0011100000	1011010001	1100110000	1000200101	01011000
<i>Heterocaecilius</i>	1010100010	0011110211	0011100000	1011010001	1110111000	1000200101	01011000
<i>Calopsocus</i>	0010101110	0011110211	0111100000	1011010001	1010111000	1000200101	01011000
<i>Bryopsocus</i>	??????????	??????????	0100100000	1?1?0????	?0?0000000	100030?100	010?2000
<i>Kaestneriella</i>	1011000010	0011110111	0000100010	1011200001	0000000001	1100300100	01012000
<i>Peripsocus</i>	1010000010	0011111111	1000100010	1011000001	0000000001	1100300100	01012000
<i>Philotarsus</i>	1010100010	0011110111	0011100000	1111010100	0000100100	0100300100	01012000
<i>Aaroniella</i>	1010100010	0011110111	0011100000	1111010100	0000000100	1100300100	01012000
<i>Idatenopsocus</i>	1000000010	0011110111	1000100000	1011100100	0000000000	0100300102	01012000
<i>Mesopsocus</i>	1000000010	0011110111	1000100000	1011100000	0000000100	0100300102	01012000
<i>Epipsocus</i>	1011111110	1011010111	0001100100	1111020001	0000000000	000000001?	00000120
<i>Epipsocopsis</i>	1011111110	1011010111	0001100100	1111020001	0000000000	000000001?	00000120
<i>Dolabellopsocus</i>	1010111110	1011010111	0001100100	0011020001	1000000000	000000001?	00000120
<i>Isthmopsocus</i>	1010111110	1011010111	0001100100	0011020001	1000000000	000000001?	00000120
<i>Cladiopsocus</i>	1010111110	1011010111	0001100100	0011020001	0000000??	0000000000	00000120
<i>Spurostigma</i>	1010111110	1011010111	0001100000	0011020001	0000000000	0000000000	00000110
<i>Triplocania</i>	1011111110	1011010111	0001100100	0111020000	0000001?10	0000000000	00000110
<i>Ptiloneura</i>	1011111110	1011010111	0001100100	0111020000	000???????	?000000000	00000110
<i>Notiopsocus</i>	1010001111	0111111211	0000100010	1011000001	2100000000	0000000000	10000200
<i>Asiopsocus</i>	1?10?111?1	????1????1	1000100000	101?2000?1	01?0???000	000000000?	100002?0
<i>Stenopsocus</i>	1000001110	1111111111	0000101001	1011100001	1110000000	0000001000	000002?0
<i>Graphocaecilius</i>	1000001110	1111111111	0000101001	1011200001	1110000000	0000001000	00000200
<i>Amphipsocus</i>	1100001110	1111111111	0001100000	1111020001	1110000000	0000000000	000002?0
<i>Kolbia</i>	1100001110	1111111111	0001100000	1111020001	1110000000	0000000000	000002?0
<i>Matsumuraiella</i>	1100001110	1111111111	0101100000	1111100001	1110000000	0000000000	00000200
<i>Caecilius</i>	1000001110	1111111111	0000100000	1111000001	1110000000	0000000000	000002?0
<i>Kodamaius</i>	1100001110	1111111111	0001100001	1111000001	1110000000	0000000000	000002?0
<i>Dasypsocus</i>	0000001110	1111111111	0000100000	1111000001	1110000000	0000000000	000002?0



(7) Lachesillidae: exemplars selected from all three tribes of this highly diverse family. *Lachesilla pedicularia* and *L. sp.* (*pedicularia* group, from Vietnam), were chosen from the highly specialized and divergent genus *Lachesilla*. The others were *Nanolachesilla nanciae* of Graphocaeciliini and *Eolachesilla chilensis* of Eolachesillini.

(8) Ectopsocidae: only one exemplar, *Ectopsocus sp.* (from Japan), as the family consists of uniform taxa.

(9) Trichopsocidae: comprises only one genus, *Trichopsocus*; one exemplar, *T. dali*, was selected.

(10) Pseudocaeciliidae: one of the most diverse families in the Homilopsocidea both morphologically and biologically. Potential exemplars from both dead-foilage (*Ophiopelma glyptocephalus*) and living-foilage dwellers. As most taxa fall into the latter category, two exemplars, *Pseudocaecilius kagoshimensis* and *Heterocaecilius anomalis*, were selected.

(11) Calopsocidae: although the forewing characters are highly specialized and variable among genera, other morphological characters are rather similar throughout the family. Thus only one exemplar, *Calopsocus infelix*, was selected.

(12) Bryopsocidae: comprises only one species, *Bryopsocus townsendi*. Specimens were unavailable for this study and character information was extracted from the literature.

(13) Peripsocidae: *Peripsocus sp.* (from Japan) and *Kaestneriella guatemalensis*.

(14) Philotarsidae: *Philotarsus flaviceps* and *Aaroniella sp.* (from Japan).

(15) Mesopsocidae: *Mesopsocus hongkongensis* and *Idatenopsocus orientalis*.

(16) Cladiopsocidae: *Cladiopsocus garciai* and *Spurostigma epirotica*.

(17) Dolabellapsocidae: *Dolabellapsocus roseus* and *Isthmopsocus sp.* (from Mexico).

(18) Ptiloneuridae: *Triplocania spinosa* and *Ptiloneura splendida*. The male of the latter species is unknown.

(19) Epipsocidae: *Epipsocus sp.* (from Malaysia) and *Epipsocopsis sp.* (from Taiwan).

(20) Asiopsocidae: *Asiopsocus sonorensis* and *Notiopsocus aldretei*. Character information for *Asiopsocus* was selected from the literature as specimens were unavailable.

(21) Stenopsocidae: *Stenopsocus sp.* (nr *aphidiformis*, from Japan) and *Graphopsocus cruciatus*.

(22) Amphipsocidae s.s. (= *sensu* Mockford, 1993): *Amphipsocus rubrostigma* and *Kolbia fusconervosa*.

(23) Dasydemellidae: specimens of the nominotypical genus were unavailable. One exemplar, *Matsumuraiella radiopicta*, was therefore selected as, judging from descriptions and illustrations, *Matsumuraiella* is very similar to *Dasydemella*. The distinction is considered to be of little phylogenetic consequence.

(24) Caeciliusidae: one of the largest families of Psocomorpha, containing widely morphologically divergent species. Additionally, no decisive autapomorphy supporting monophyly of this family has been proposed. Thus, three exemplars, *Caecilius fuscopterus*, *Dypsocus coleopteratus*, and *Kodamaius directus*, all of which are considered distantly related, were selected.

## CHARACTERS

Of the 68 characters used in the cladistic analysis, 11 were multistate and the remainder binary. Characters were equally weighted *a priori*, but *a posteriori* weighting was applied, as discussed below. All multistate characters were initially treated as unordered for the analysis. However, if analysis and morphological observation suggested that a character was possibly ordered, it was optimized as ordered on the resultant cladogram. Descriptive or analytical information concerning characters, their states, or polarities is included in *Remarks*. Uninformative characters were excluded from the matrix but will be discussed below.

Character length (L), consistency index (CI), retention index (RI) and polarity of character states are included and were calculated using MacClade 4.0 (Maddison & Maddison, 2000).

1. *Vertex*: (0) sharply angled (Fig. 1); (1) rounded (Fig. 2). L = 3; CI = 0.33; RI = 0.67. (1) is an autapomorphy of Psocomorpha, but reversals have occurred in Calopsocidae and in a few genera of Caeciliusidae.

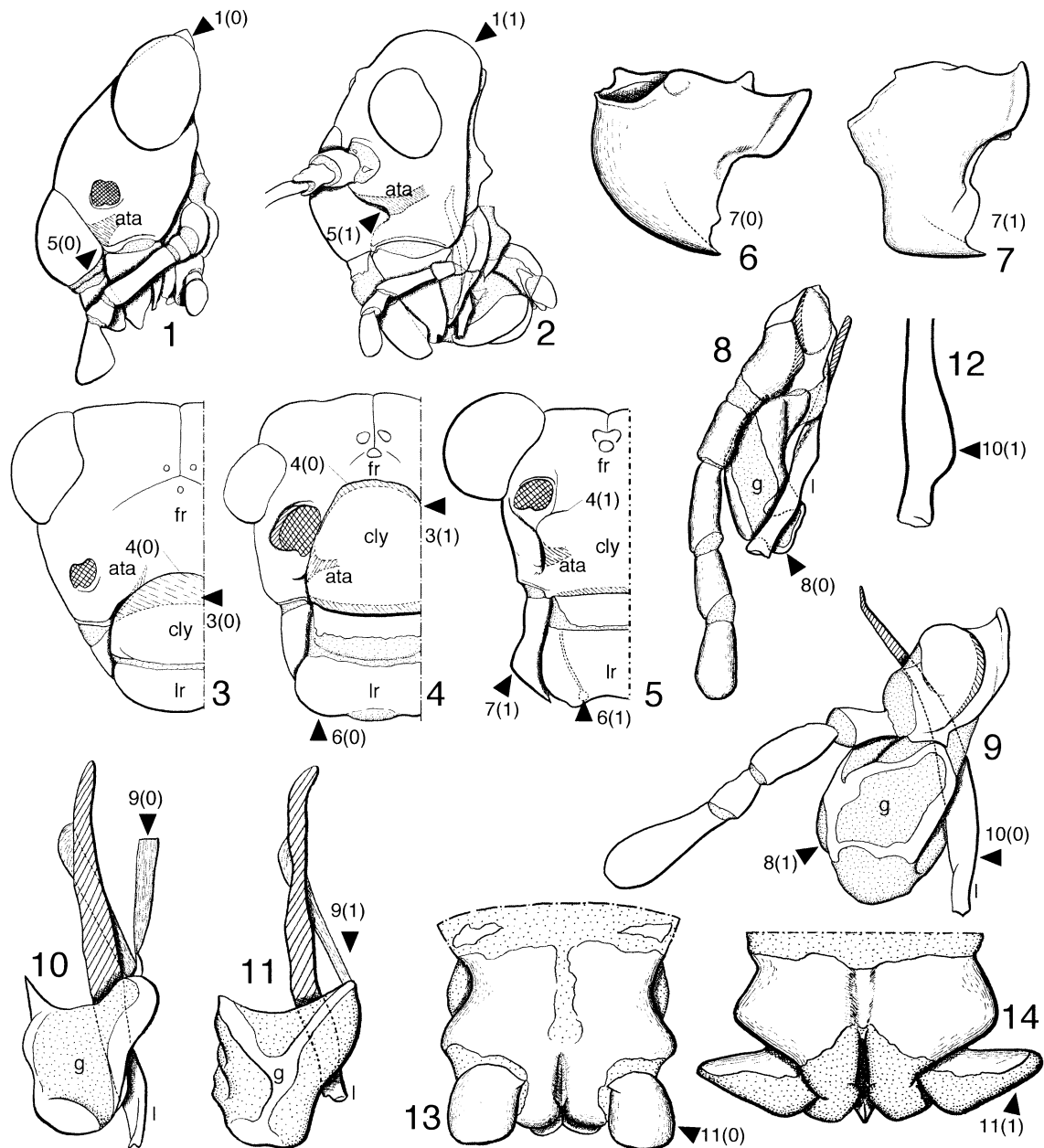
2. *Vertex*: (0) without concavity; (1) with pair of concavities. L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Amphipsocidae s.l.

3. *Internal ridge of epistomal suture*: (0) broad (Fig. 3); (1) narrow (Fig. 4). L = 4; CI = 0.25; RI = 0.83. (1) is an autapomorphy of the clade which comprises all psocomorphan families excluding Archipsocidae. However, (0) is considered secondarily derived independently in Elipsocidae, Mesopsocidae and Caeciliusoidea.

4. *Epistomal suture*: (0) complete (Figs 3, 4); (1) absent dorsally (Fig. 5). L = 4; CI = 0.20; RI = 0.33. (1) is an autapomorphy supporting the monophyly of Hemipsocidae, and has evolved independently in *Nanolachesilla* of Lachesillidae and two families in Epipsocetae.

5. *Position of anterior tentorial pit*: (0) on ventral margin of cranium (Fig. 1); (1) separated from ventral margin of cranium (Fig. 2). L = 5; CI = 0.20; RI = 0.79. (1) is regarded as the apomorphic condition in Psocomorpha, but highly homoplastic.

6. *Labrum*: (0) without paired longitudinal sclerites (Fig. 4); (1) with paired longitudinal sclerites (Fig. 5). L = 2; CI = 0.50; RI = 0.88. (1) is an autapomorphy of Epipsocetae, and was derived independently also in *Asiopsocus*. *Remarks*: within the species examined in



**Figures 1–14.** (1–5) Head of *Echmepteryx lunulata* (1) and *Psococerastis nubila* (2), lateral view; *E. lunulata* (3), *P. nubila* (4) and *Epipsocopsis* sp. (5), anterior view; (6–7) mandible of *P. nubila* (6) and *Matsumuraiella radiopicta* (7), anterior view; (8–12) maxilla of *P. nubila* (8) and *M. radiopicta* (9), lateral view; *Paramphientomum* sp. (10) and *P. nubila* (11), showing muscles attached to galea, anterior view; *Notiopsocus aldretei* (12), showing apex of lacinia; (13–14) labium of *P. nubila* (13) and *Stenopsocus* sp. (14), posterior view. Abbreviations: ata = anterior tentorial arm; cly = clypeus; fr = frons; g = galea; l = lacinia; lr = labrum.

this study, (1) is observed only in Epipsocetae and *Asiopsocus*, but Mockford (1977) and Mockford & García Aldrete (1976) noted that it is also observed in some Caeciliusoidea.

**7. Mandible:** (0) outer margin rounded and posterior margin not hollowed (Fig. 6); (1) outer margin angled

and posterior margin hollowed (Fig. 7). L = 2; CI = 0.50; RI = 0.94. (1) is an autapomorphy of the clade Epipsocetae + Caeciliusetae, and independently derived in Calopsocidae.

**8. Galea:** (0) flat (Fig. 8); (1) ball-shaped (Fig. 9). L = 2; CI = 0.50; RI = 0.94. (1) is an autapomorphy

of the clade Epipsocetae + Caeciliusetae, and was derived independently also in Calopsocidae. *Remarks:* condition of this character appears strongly correlated with character 7.

9. *Stipito-galeal muscle (s-g7)*: (0) present (Figs 10); (1) absent (Fig. 11). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Psocomorpha.

10. *Lacinia*: (0) without broadened region (Fig. 9); (1) with externally broadened subapical region (Fig. 12). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Asiopsocidae.

11. *Labial palpus*: (0) rounded (Fig. 13); (1) triangular (Fig. 14). L = 2; CI = 0.50; RI = 0.93. (1) is a possible autapomorphy of the clade Epipsocetae + Caeciliusetae. *Remarks:* Epipsocetae and Caeciliusidae have a somewhat triangular, externally expanded labial palpus. In contrast, *Notiopsocus* has a rounded labial palpus. The state of this character for *Asiopsocus* is presently unknown. Consequently, the state of this character for the common ancestor of Epipsocetae + Caeciliusetae cannot yet be determined.

12. *Preepisternum of prothorax*: (0) short (Fig. 15); (1) elongate (Fig. 16). L = 2; CI = 0.50; RI = 0.91. (1) is derived independently at least twice in Caeciliusetae and Lachesillidae + Ectopsocidae, and regarded as an autapomorphy of each clade.

13. *Mesothorax*: (0) not strongly bulged; (1) greatly bulged dorsally (Fig. 17). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of the clade which contains all psocomorphan families except Archipsocidae. *Remarks:* Mockford (1967) regarded (1) as an autapomorphy of Psocomorpha. However, the pterothorax of Archipsocidae is less developed and its dorsal margin is almost level with the vertex.

14. *Mesothoracic dorso-ventral flight muscle*: (0) comprises one or two muscles, inserted into the base of trochantin (Fig. 19); (1) divided into three muscles: external two inserted into the precoxal bridge and internal one into the trochantin (Fig. 20); (2) divided into three muscles: internal two inserted into the precoxal bridge and external one into the trochantin (Fig. 21). L = 3; CI = 1; RI = 1. (1) is derived for the clade comprising Homilopsocidea + Epipsocetae + Caeciliusetae, and regarded as autapomorphic. (2) is unique to Archipsocidae and supports its monophyly. *Remarks:* in Trogiomorpha, Troctomorpha, Hemipsocidae and Psocetae, a less developed dorso-ventral flight muscle (probably corresponding to t-p 5, 6 and t-ti 2) is inserted into the base of the trochantin (Fig. 19). In contrast, the dorso-ventral flight muscles of other psocomorphan families are split into two, one attached to the trochantin and the other to the precoxal bridge (Fig. 20). In Archipsocidae, the larger inner muscle is inserted into the precoxal bridge and the smaller outer muscle into the trochantin (Fig. 21), whereas in the other families, the smaller inner mus-

cle is inserted into the trochantin and the larger outer muscle into the precoxal bridge (Fig. 20). This suggests that splitting of the dorso-ventral flight muscles have evolved independently at least twice.

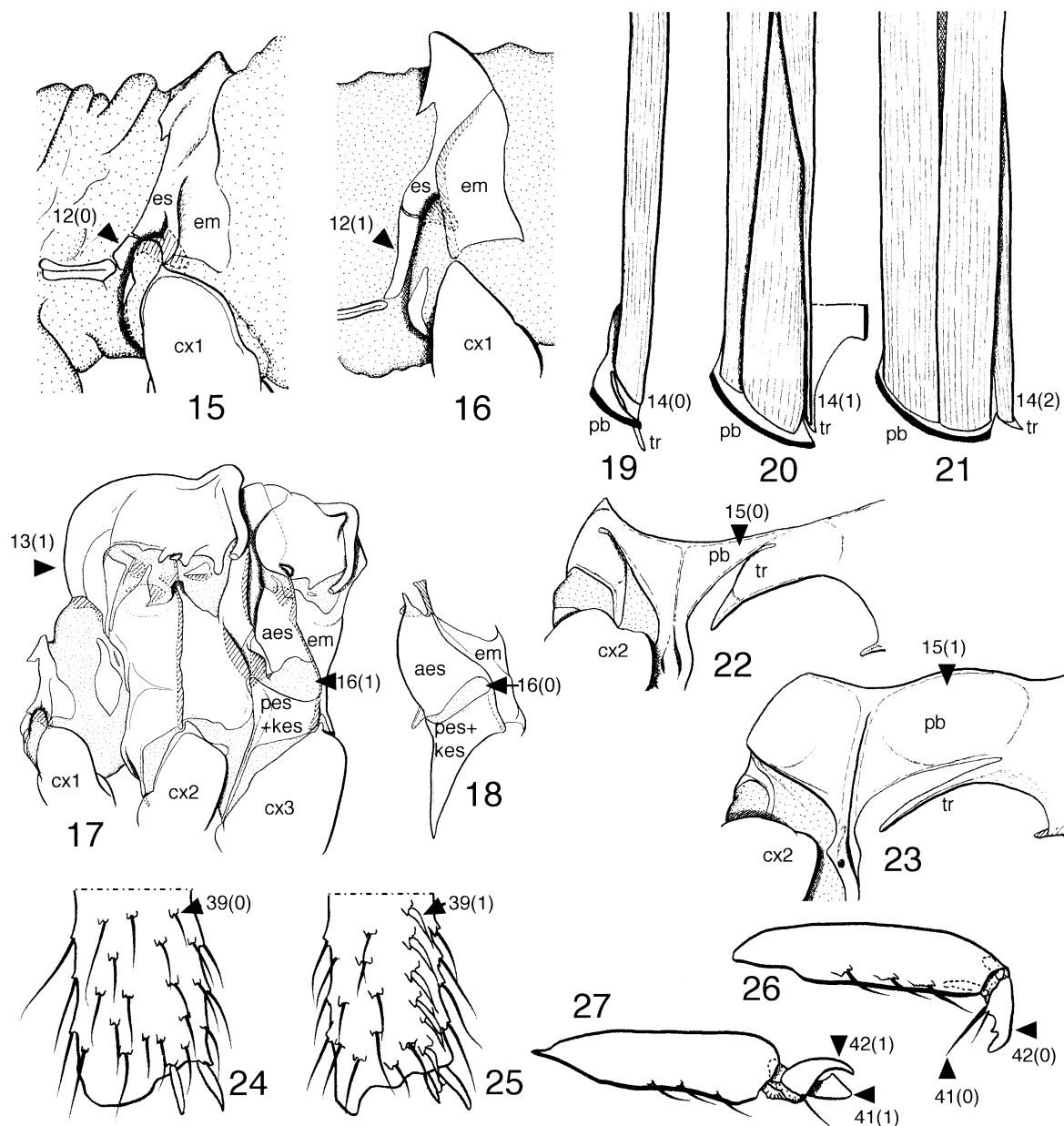
15. *Precoxal bridge*: (0) narrow (Fig. 22); (1) broad (Fig. 23). L = 3; CI = 0.33; RI = 0.89. (1) is apomorphic, and observed independently in Archipsocidae, Homilopsocidea, and Caeciliusetae. *Remarks:* see previous character and 'Monophyly of Psocomorpha and relationships of infraorders', below.

16. *Membranous region of metapleuron*: (0) narrow (Fig. 18); (1) broad (Fig. 17). L = 1; CI = 1; RI = 1. (1) is an autapomorphy supporting the clade comprising Psocetae, Homilopsocidea, Epipsocetae, and Caeciliusetae.

17. *Campaniform sensilla on forewing radius*: (0) evenly distributed; (1) divided into two groups. L = 2; CI = 0.50; RI = 0.89. (1) is an autapomorphy of Caeciliusetae, and was also derived independently in *Peripsocus*.

18. *Apex of first axillary sclerite of forewing*: (0) without minute process proximally (Fig. 28); (1) with minute process proximally (Fig. 29); (2) broadened (Fig. 30). L = 4; CI = 0.50; RI = 0.80. (1) is an autapomorphy of Psocomorpha and (2) evolved independently from (1) at least three times in Hemipsocidae, Pseudocaecilioidea, and *Notiopsocus*. *Remarks:* in most insects, the apex of first axillary sclerite (1Ax) has a long neck region that curves externally. This condition is also observed in Trogiomorpha and Troctomorpha (Fig. 28). In contrast, 1Ax of Psocomorpha is subtriangular and often has a minute process proximally. In some taxa, such as Hemipsocidae and Pseudocaeciliidae, the apex of 1Ax is broadened and the proximal minute process is inconspicuous (state 2). This character state is regarded as being derived from state 1.

19. *Second axillary sclerite (2Ax) and proximal median plate (PMP) of forewing*: (0) articulated with each other (Fig. 31); (1) fused with each other (Fig. 32). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of the clade comprising all psocomorphan families except Archipsocidae and Hemipsocidae. *Remarks:* Brodsky (1994) mentioned that the roof-like folding of the wings had presumably appeared in the common ancestors of the Paraneoptera and fusion of 2Ax and PMP was regarded as one of the most important changes for providing this folding. However, fusion of 2Ax and PMP is never observed in outgroup suborders. Apparently, Brodsky (1994) misidentified the homology of wing base structures of Hemiptera and 2Ax and PMP are articulated with each other in Thysanoptera and Hemiptera (Yoshizawa & Saigusa, 2001). Thus, fusion of 2Ax and PMP did not appear in the common ancestor of Paraneoptera but is regarded as an autapomorphy of the clade comprising all psocomorphan families



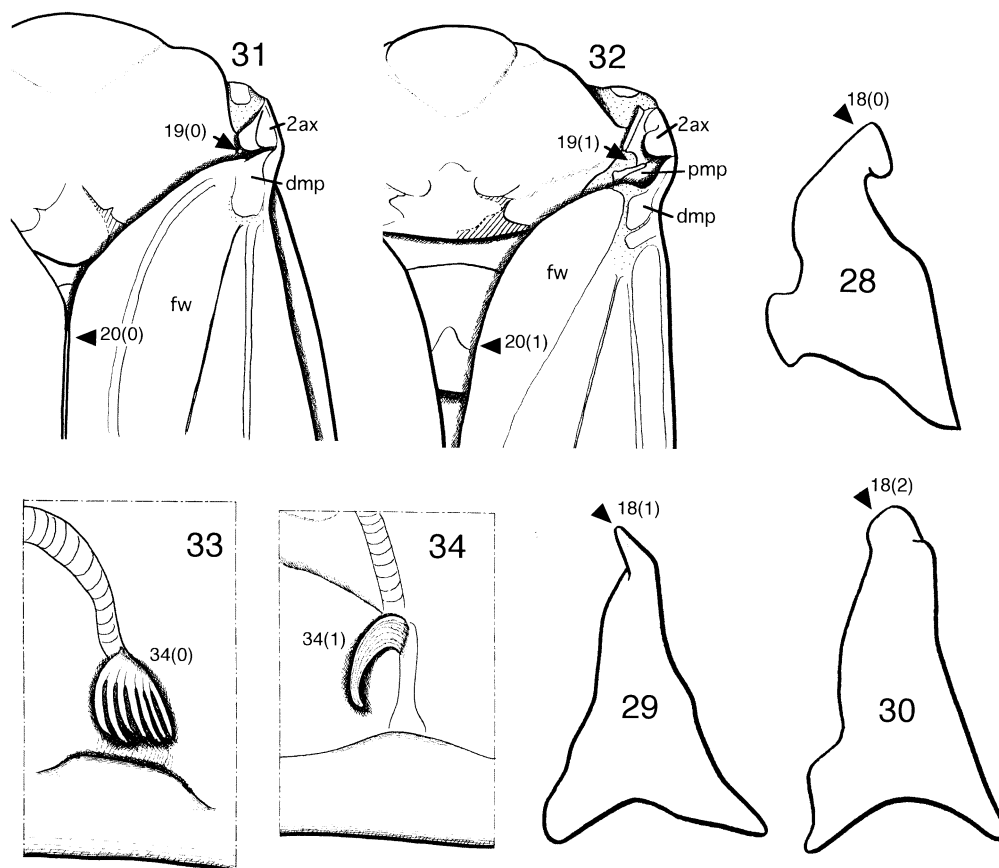
**Figures 15–27.** (15–16) prothorax of *Psococerastis nubila* (15) and *Ectopsocus* sp. (16), lateral view; (17) thorax of *P. nubila*, lateral view; (18) metapleuron of *Hemipsocus chloroticus*, lateral view; (19–21) mesothoracic dorso-ventral flight muscle of *Paramphientomum* sp. (19), *Stenopsocus* sp. (20) and *Parachipsocus pacificus* (21); (22–23) mesothoracic precoxal bridge and trochantin of *Psococerastis nubila* (22) and *S.* sp. (23); (24–25) apex of hind tibia of *S.* sp. (24) and *Psocus* sp. (25); distal tarsomere and claws of *Psocus* sp. (26) and *S.* sp. (27). Abbreviations: aes = anepisternum; cx = coxa; em = epimeron; es = episternum; kes = katepisternum; pb = precoxal bridge; pes = preepisternum; tr = trochantin.

except Archipsocidae and Hemipsocidae. (0) and (1) can be easily distinguished externally without dissection. In psocids possessing (0), the posteroproximal margin of 2Ax and the proximal margin of DMP (distal median plate) are closely approximated with each other when the wings are closed (Fig. 31). In psocids

possessing (1), 2Ax and DMP are separated by PMP when the wings are closed (Fig. 32).

20. *Posterior margin of folded forewings proximal to nodulus*: (0) closely approximated with each other (Fig. 31); (1) separated from each other (Fig. 32). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of the clade





**Figures 28–34.** (28–30) right first axillary sclerite of *Paramphientomus* sp. (28), *Peripsocus quercicola* (29) and *Pseudocaecilius kagoshimensis* (30); (31–32) mesothorax and forewing of *Hemipsocus chloroticus* (31) and *Psococerastis nubila* (32), dorsal view; (33–34) nodulus of *Paramphientomus* sp. (33) and *Psococerastis nubila* (34). Abbreviations: 2ax = second axillary sclerite; dmp = distal median plate; fw = forewing; pmp = proximal median plate.

comprising all psocomorphan families except Archipsocidae and Hemipsocidae.

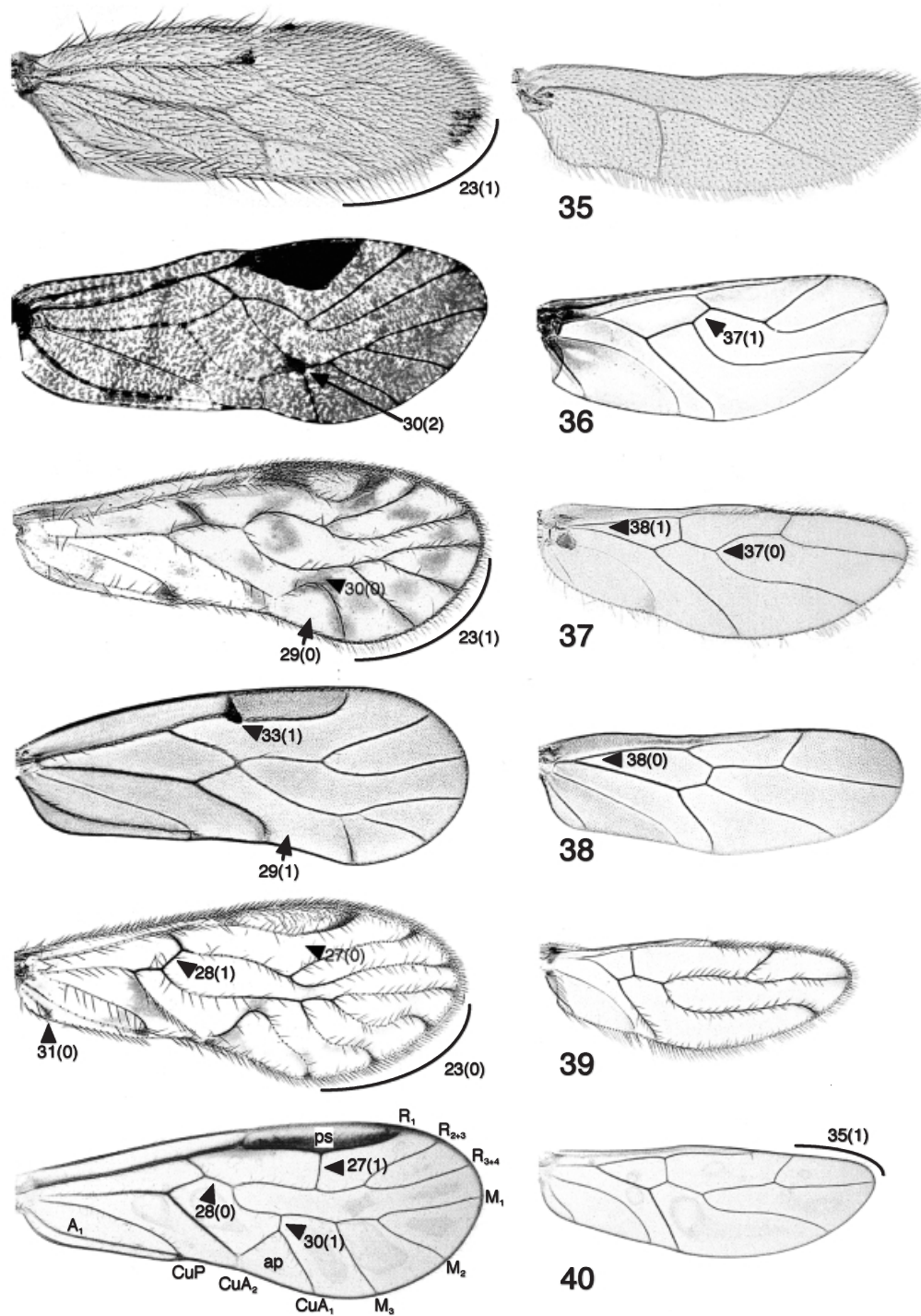
21. *Forewing margin and veins*: (0) setose (Fig. 37); (1) bare (Fig. 36). L = 5; CI = 0.20; RI = 0.56. (1) is regarded as a derived condition but highly homoplastic.

22. *Membranous region of forewing*: (0) bare (Figs 36–40); (1) sparsely setose; (2) densely setose (Fig. 35). L = 5; CI = 0.40; RI = 0.50. (1) is derived independently at least three times within Psocomorpha. (2) is considered as the most primitive condition of Psocomorpha. *Remarks*: exemplars with scaly forewing were coded as (2) because scales can be considered as modified setae. Because a possible sister group of Psocomorpha, Amphientomidae, has scaly wings and the basalmost psocomorphan clade, Archipsocidae, has a densely setose forewing, (2) is considered to be the basic condition of Psocomorpha, but further study is required.

23. *Marginal setae of forewing*: (0) not crossing (Fig. 39); (1) crossing on apical margin (Fig. 37). L = 3; CI = 0.33; RI = 0.71. (1) is apomorphic, and is derived

independently at least three times in Archipsocidae, Pseudocaecilius + Calopsocidae and Philotarsidae, and regarded as an autapomorphy of each clade. *Remarks*: exemplars with bare forewings were scored '0'.

24. *Setae on veins of forewing*: (0) 0–1 row; (1) 2 or more rows (Fig. 39). L = 4; CI = 0.25; RI = 0.83. (1) is regarded as the derived condition, and derived independently at least four times. *Remarks*: although this character is rather homoplastic, it is consistent within a family, superfamily or infraorder. (1) is regarded as autapomorphic for Pseudocaecilioidea, Philotarsidae, Epipsocetae, and Amphipsocidae *s.l.* and no reversal has been deduced. The character state of exemplars with scaly forewings (e.g. Amphientomidae) or setae (Archipsocidae) could not be determined and was scored '?'.  
25. *Pterostigma*: (0) not thickened; (1) thickened. L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Psocomorpha. *Remarks*: although a thickened pterostigma is observed in Archipsocidae, it appears to be much thinner than in other families of Psocomorpha. In this



**Figures 35–40.** Fore– (left) and hindwing (right) of *Pararchipsocus pacificus* (35), *Lichenomima muscosa* (36), *Philotarsus quercicola* (37), *Ectopsocus* sp. (38), *Triplocania spinosa* (39) and *Stenopsocus* sp. (40). Abbreviations: ap = areola postica; ps = pterostigma.

instance I did not code them separately but different degrees of thickness of the pterostigma may provide further evidence for the phylogenetic placement of Archipsocidae as the basalmost clade of Psocomorpha.

26. *Forewing veins*: (0) normal (Figs 36–40); (1) reduced (Fig. 35). L = 2; CI = 1; RI = 1. (1) is an autapomorphy of Archipsocidae.

27. *Forewing  $R_1$ – $R_{2+3}$  cross vein*: (0) absent (Fig. 39);

(1) present (Fig. 40). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Stenopsocidae.

28. *Forewing Rs and M*: (0) fused (Fig. 40); (1) connected by crossvein (Fig. 39). L = 1; CI = 1; RI = 1. (1) is regarded as the derived condition and observed in Epipsocetae only.

29. *Areola postica*: (0) present (Fig. 37); (1) absent (Fig. 38). L = 3; CI = 0.33; RI = 0.33. (1) was derived independently at least three times in Ectopsocidae, Peripsocidae, and *Notiopsocus*. *Remarks*: Ectopsocidae, Peripsocidae, and *Notiopsocus* (Asiopsocidae) had once been classified in a single family Peripsocidae based only on the absence of the areola postica (Smithers, 1972). The present analysis clearly shows that absence of the areola postica does not indicate phylogenetic affinities between families.

30. *Forewing veins CuA<sub>1</sub> and M*: (0) free from each other (Fig. 37); (1) connected by crossvein (Fig. 40); (2) fused with each other (Fig. 36). L = 5; CI = 0.40; RI = 0.50. (1) was derived independently at least three times in Hemipsocidae, Stenopsocidae, and *Kodamaius* (Amphipsocidae *s.l.*). (2) is observed in Psocetae only, but the character state of their common ancestor is unresolved. *Remarks*: Mockford (1996) reported a fossil Myopsocidae having the areola postica separated from M. If the venation of the fossil specimen represents the ancestral condition of the Myopsocidae, (0) should be assigned for the common ancestor of Psocetae.

31. *Forewing vein A<sub>2</sub>*: (0) present (Fig. 39); (1) absent (Fig. 40). L = 3; CI = 0.33; RI = 0.78. (1) is regarded as the plesiomorphic condition of Psocomorpha, and (0) as an autapomorphy of Epipsocetae but reversed to (1) in Epipsocidae. *Remarks*: Epipsocetae has been regarded as one of the most primitive groups of Psocomorpha mainly because of the presence of A<sub>2</sub> in many families of this group (Smithers, 1972). The present analysis suggests that its presence is the apomorphic condition within Psocomorpha.

32. *Ventral setae of forewing*: (0) absent; (1) present. L = 5; CI = 0.20; RI = 0.69. (1) is regarded as an apomorphic condition, but highly homoplastic.

33. *Nodus*: (0) absent; (1) present (Fig. 38). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Psocomorpha.

34. *Nodus*: (0) a set of pointed, separated spines or truncated spines set closely together (Fig. 33); (1) a hook formed by of truncated spines fused at their base (Fig. 34). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Psocomorpha, as indicated by Mockford (1967).

35. *Marginal setae of hindwing*: (0) setose all around (Fig. 39); (1) setose between R<sub>2+3</sub> and R<sub>4+5</sub> only (Fig. 40); (2) bare (Fig. 36). L = 10; CI = 0.20; RI = 0.58. (1) and (2) are regarded as derived conditions but highly homoplastic. *Remarks*: Badonnel & Lienhard (1988) regarded (1) as a synapomorphy of Elipsocidae and Mesopsocidae. However, the present analysis

shows that (1) is highly homoplastic and provides little phylogenetic information.

36. *Setae on hindwing veins*: (0) none (Fig. 36); (1) one row (Fig. 37), (2) two rows (Fig. 39). L = 4; CI = 0.50; RI = 0.86. (1) is regarded as an autapomorphy of Philotarsidae and Pseudocaeciliidae + Calopsocidae, respectively. (2) is regarded as an autapomorphy of Epipsocetae and Amphipsocinae, respectively.

37. *Hindwing Rs and M*: (0) fused (Fig. 37); (1) connected by crossvein (Fig. 36). L = 2; CI = 0.50; RI = 0. (1) is an autapomorphy of the family Ectopsocidae and was also derived independently in some genera of Myopsocidae.

38. *Hindwing Rs and M + Cu*: (0) fused with each other basally (Fig. 38); (1) separated from each other basally (Fig. 37). L = 3; CI = 0.33; RI = 0.33. (1) is regarded as the apomorphic condition and observed in Trichopsocidae, Philotarsidae, and *Idatenopsocus* (Mesopsocidae).

39. *Ctenidia of hind tibia*: (0) fine (Fig. 24); (1) broad (Fig. 25). L = 1; CI = 1; RI = 1. (1) is regarded as an autapomorphy of Psocetae.

40. *Tarsus*: (0) three-segmented; (1) two-segmented. L = 7; CI = 0.13; RI = 0.59. (1) is regarded as an autapomorphy of Psocomorpha, but this character is highly homoplastic within the suborder. *Remarks*: an early higher classification proposed by Enderlein (1903) attached great importance to the number of tarsomeres and psocids were first divided into two groups based on this feature. The phylogenetic relationship proposed by Smithers (1972) also attached importance to this character and Psocomorpha was divided into a '2-segment tarsi line' and '3-segment tarsi line' near the base of his cladogram. The present analysis clearly shows that this character is highly homoplastic and not worthy for the estimation of phylogenetic relationships in Psocomorpha.

41. *Pulvillus*: (0) fine (Fig. 26); (1) broad (Fig. 27); (2) absent. L = 9; CI = 0.22; RI = 0.68. (1) is regarded as the most plesiomorphic condition of Psocomorpha, but this character is highly homoplastic.

42. *Preapical tooth on pretarsal claw*: (0) present (Fig. 26); (1) absent (Fig. 27). L = 5; CI = 0.20; RI = 0.75. (1) is regarded as apomorphic, but highly homoplastic.

43. *Abdominal eversible vesicles*: (0) absent; (1) present. L = 3; CI = 0.33; RI = 0.82. (1) is an autapomorphy of Pseudocaecilioidea (= Trichopsocidae + Calopsocidae + Pseudocaeciliidae) and Caeciliusoidea, respectively, and a reversal has occurred in a genus of Pseudocaeciliidae. *Remarks*: the presence of abdominal eversible vesicles is often associated with living-foilage dwellers (New, 1987), and a change in habitat preference likely occurred at the basal node of Pseudocaecilioidea and Caeciliusoidea, respectively. The result of the present analysis also supports this



idea concerning the evolution of this habitat-related character.

44. *Male paraproct*: (0) rounded (Fig. 41); (1) with distal process (Fig. 42). L = 2; CI = 0.50; RI = 0.80. (1) is apomorphic, and observed in Hemipsocidae, Psilipsocidae, Myopsocidae and Psocidae. *Remarks*: (1) was not considered synapomorphic for Hemipsocidae and Psilipsocidae + Myopsocidae + Psocidae, contrary to Mockford (1993). As Hemipsocidae and Psocetae (in the present sense) branched successively, most parsimonious optimization cannot establish whether (1) is homologous or homoplastic. I think the latter is more likely because similar paraproctal processes are also observed in some species of Lachesillidae, which are apparently distantly related to Hemipsocidae and Psocetae.

45. *Hyandrium*: (0) fused with clunium laterally (Fig. 41); (1) articulated with clunium laterally (Fig. 42). L = 3; CI = 0.33; RI = 0.67. (1) is regarded as an autapomorphy of each Psocidae and Pseudocaeciliidae + Calopsocidae, and independently derived in *Philotarsus*. *Remarks*: when the hyandrium is articulated with the clunium its posterior margin always possesses processes or lobes, whereas when it is fused with the clunium the distal margin is smoothly rounded. Therefore, presence of an articulation appears to be strongly correlated with the presence of such processes or lobes. Betz (1983) studied the genital coupling mechanism of *Trichadenotecnum alexandrae*, and reported that the hyandrial distal processes and the female gonopore plates are interlocked with each other during coupling. The articulation between hyandrium and clunium probably facilitates hyandrial movement, and this morphological change may have enabled the evolution of the complicated hyandrial distal processes that lead to an interlocking mating system.

46. *Hyandrial lateral bristles*: (0) absent (Fig. 41); (1) present (Fig. 43). L = 1; CI = 1; RI = 1. (1) is regarded as an autapomorphy of clade Pseudocaeciliidae + Calopsocidae.

47. *Pair of lateral hyandrial processes*: (0) absent (Fig. 41); (1) present (Fig. 43). L = 2; CI = 0.50; RI = 0.67. (1) is regarded as an autapomorphy of clade Pseudocaeciliidae + Calopsocidae, and independently derived in Ptiloneuridae.

48. *Apex of aedeagus*: (0) pointed (Fig. 46); (1) rounded (Fig. 47). L = 4; CI = 0.25; RI = 0.57. (1) is regarded as the apomorphic condition and observed in Archipsocidae, Psilopsocidae, Philotarsidae, and *Mesopsocus* (Mesopsocidae). *Remarks*: this character is scored as unknown for exemplars which lack the aedeagus.

49. *Aedeagus*: (0) present (Fig. 46); (1) absent (Fig. 44). L = 6; CI = 0.17; RI = 0.29. (1) is regarded as a derived condition but highly homoplastic.

50. *Paramere*: (0) rod-like (Fig. 47); (1) strap-like

(Fig. 48); (2) reduced (Fig. 45). L = 4; CI = 0.50; RI = 0.71. (1) is regarded as an autapomorphy of Peripsocidae, and (2) as an autapomorphy of Archipsocidae and Psocidae + Psilopsocidae.

51. *Endophallus*: (0) without rod-like sclerites (Fig. 47); (1) with rod-like sclerites (Fig. 46). L = 5; CI = 0.20; RI = 0.60. (1) is apomorphic, supporting the clade containing homilopsocid families except Elipsocidae. These sclerites have been secondarily reduced in *Lachesilla*, *Pseudocaecilius*, Mesopsocidae, and some genera of Philotarsidae.

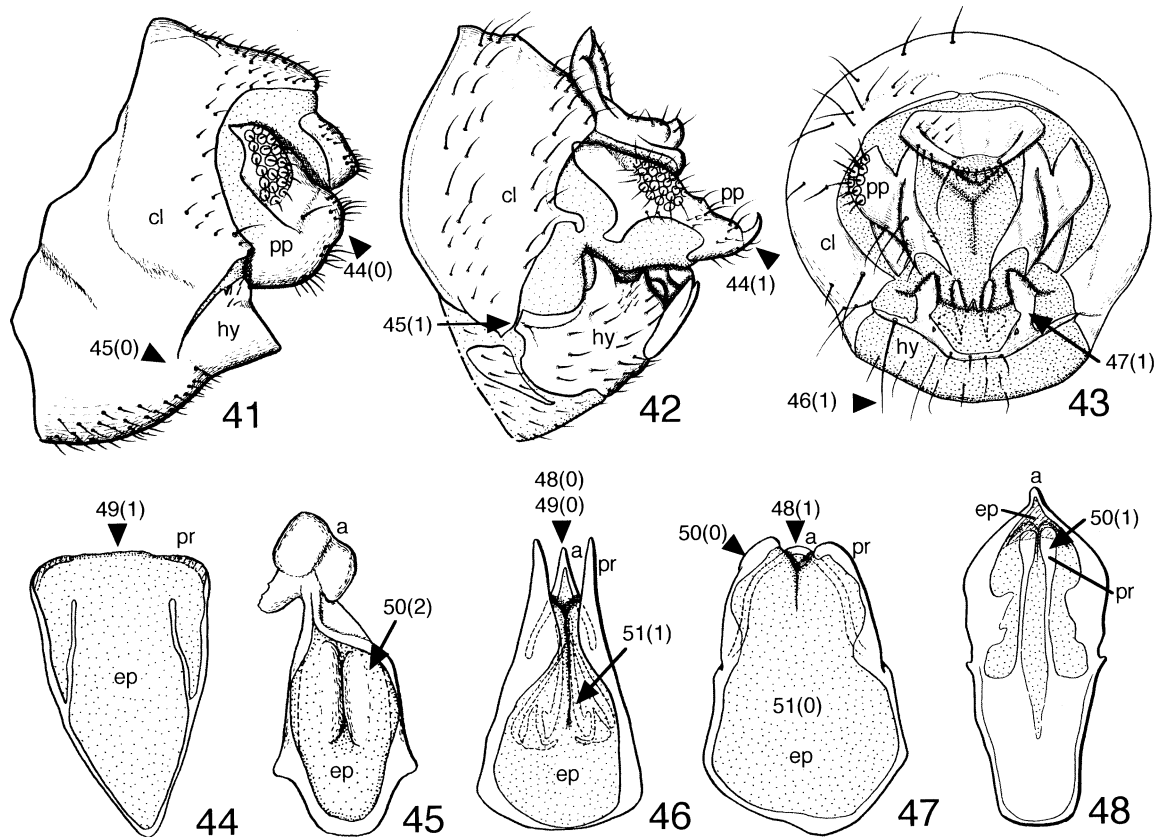
52. *Female epiproct*: (0) rounded (Fig. 49); (1) square-shaped (Fig. 50). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of the clade containing Peripsocidae, Philotarsidae and Mesopsocidae.

53. *Female paraproct*: (0) rounded (Fig. 51); (1) with conical distal projection (Fig. 52). L = 2; CI = 0.50; RI = 0.80. (1) is apomorphic, and observed in Hemipsocidae and Psocetae. *Remarks*: Hemipsocidae has been assigned to Psocetae on the basis of (1) by Mockford (1976). In the present analysis, Hemipsocidae and other families of Psocetae do not comprise a monophyletic group and Hemipsocidae and Psocetae are positioned on successive branches; most parsimonious optimization cannot therefore establish whether (1) is homologous or homoplastic.

54. *Apex of dorsal valve of gonapophyses*: (0) not strongly extended posteriorly (Fig. 55); (1) strongly extended posteriorly to reach posterior margin of paraproct (Fig. 54). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Myopsocidae.

55. *Dorsal extension of subgenital plate*: (0) absent (Fig. 53); (1) weakly projected pair of tubercles bearing a few apical setae (Fig. 56); (2) well developed, bi-lobed (Figs 57, 58); (3) well developed, single-lobed (Fig. 59). L = 10; CI = 0.30; RI = 0.79. (1) is an autapomorphy of Homilopsocidae, but reversed in Trichopsocidae and some lachesillid taxa. *Remarks*: (1–3) are only present in Homilopsocidae. The egg guide of Elipsocidae (Fig. 56) comprises a pair of small tubercles bearing apical setae (state 1), whereas those of Ectopsocidae, Pseudocaeciliidae, and Calopsocidae are well projected posteriorly, bilobed apically, with each lobe bearing apical setae (state 2) (Figs 57, 58). The structure of the egg guide's apex in (2) is basically identical to that in (1), and is therefore regarded as derived from it morphologically. The egg guide of Peripsocidae, Philotarsidae, and Mesopsocidae is well projected posteriorly, single-lobed, and usually lacks apical setae (state 3) (Fig. 59). The egg guide of some peripsocids is single-lobed but slightly hollowed apically, and somewhat intermediate between states 2 and 3. Therefore, a single-lobed egg guide is considered as being derived from state 2. To summarize, a transformation series of the egg guide from states 0 to 3 can be hypothesized. By optimizing this character as ordered on the obtained cladogram,





**Figures 41–48.** (41–43) male genitalia of *Idatenopsocus orientalis* (41) and *Trichadenotecnum sexpunctatum* (42), lateral view, and *Heterocaecilius fuscus* (43), posterior view; (44–48) phallosome of *Hemipsocus chroloticus* (44), *Psocus* sp. (45), *Het. fuscus* (46), *Haplophallus* sp. (47) and *Peripsocus quercicola* (48). Abbreviations: a = aedeagus; cl = clunium; ep = endophallus; hy = hypandrium; pp = paraprot; pr = paramere.

(1) was considered to be an additional autapomorphy of Homilopsocidea and (2) an autapomorphy of Peripsocoidea (= Bryopsocidae + Peripsocidae + Philotarsidae + Mesopsocidae).

56. *Ventral extension of subgenital plate*: (0) absent (Fig. 53); (1) present (Figs 52, 55). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Psocetae. *Remarks*: externally, (1) is similar to (3) of character 55. However, they are recognized as nonhomologous. In Psocetae, the egg guide is regarded as an extension of the ventrodistal margin of the subgenital plate, and the ventral margin of the subgenital plate (including the egg guide) is straight or smoothly arched in lateral aspect (Fig. 52). In contrast, the egg guide of Homilopsocidea is regarded as an extension of the dorsodistal margin of the subgenital plate, the ventral margin of which is strongly dorsally bent at the base of the egg guide in lateral aspect (Fig. 51).

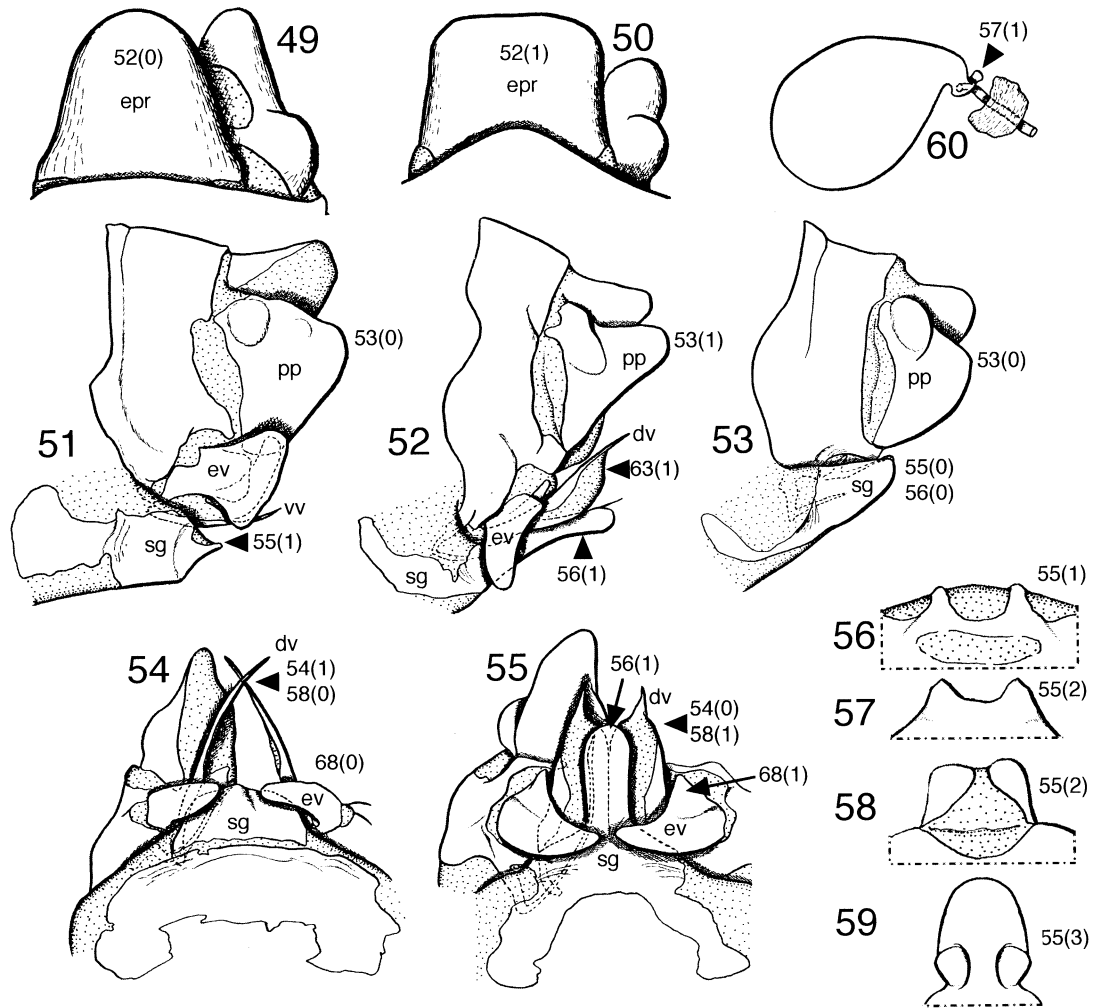
57. *Spermathecal sac*: (0) without lateral pouch; (1) with lateral pouch at junction of sac and duct (Fig. 60). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Stenopsocidae.

58. *Gonapophyses* (0) dorsal and ventral valves do not form the ovipositor (Fig. 54); (1) dorsal and ventral valves form the ovipositor together with the egg guide of the subgenital plate (Fig. 55). L = 3; CI = 0.33; RI = 0.87. (1) is regarded as an apomorphic condition, and derived independently twice within Psocomorpha. The ovipositor has also evolved at least once in the outgroup, but lacks the egg guide of the subgenital plate.

59. *Ventral valve of gonapophyses*: (0) present (Fig. 67); (1) absent (Fig. 68). L = 4; CI = 0.25; RI = 0.67. (1) is apomorphic, and derived independently four times in Psocomorpha.

60. *Apex of ventral valve of gonapophyses*: (0) tapered (Fig. 61); (1) with dorsal lobe (Fig. 66); (2) swollen (Fig. 67). L = 2; CI = 1; RI = 1. (1) is an autapomorphy of Pseudocaeciliidae + Calopscidae, and (2) is an autapomorphy of Mesopsocidae. *Remarks*: some exemplars lacked the ventral valve of the gonapophyses, and were scored ‘?’.

61. *Dorsal valve of gonapophyses*: (0) well developed (Fig. 67); (1) reduced to membranous lobe (Fig. 68); (2)



**Figures 49–60.** (49–50) female epiproct of *Elipsocus abdominalis* (49) and *Haplophallus* sp. (50), dorsal view; (51–55) female genitalia of *E. abdominalis* (51), *Psocidus* sp. (52) and *Stenopsocus* sp. (53), lateral view, *Lichenomima muscosa* (54) and *P.* sp. (55), ventral view; (56–59) apex of subgenital plate of *E. abdominalis* (56), *Ectopsocus* sp. (57), *Heterocaecilius fuscus* (58) and *Mesopsocus unipunctatus* (59); (60) spermatheca of *Stenopsocus* sp. Abbreviations: epr = epiproct; dv = dorsal valve; ev = external valve; pp = paraproct; sg = subgenital plate; vv = ventral valve.

absent. L = 4; CI = 0.50; RI = 0.50: (0) is regarded as the most primitive condition. (1) is an autapomorphy of Lachesillidae (excluding *Eolachesilla*) and Asiopsocidae, respectively. (2) was derived from (1) in some species of *Lachesilla*, and from (0) in *Archipsocus*.

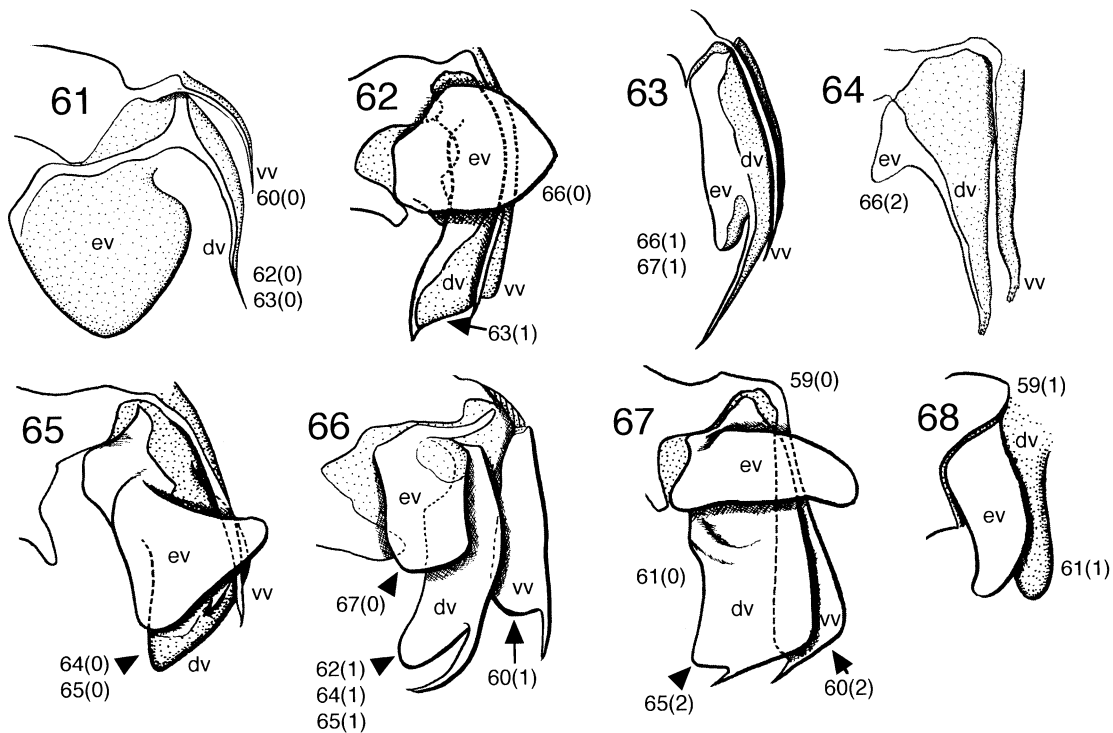
62. *Dorsal region of dorsal valve of gonapophyses*: (0) not swollen (Fig. 61); (1) swollen (Fig. 66). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Homilopsocidea. *Remarks*: See next character.

63. *Ventral region of dorsal valve of gonapophyses*: (0) without swelling (Fig. 61); (1) with swelling (Fig. 62). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of Psocetae. *Remarks*: the gonapophyses of Homilopsocidea and Psocetae both have a broad dorsal valve, and are somewhat similar to each other. However, they can be clearly distinguished by comparing them from the

lateral aspect (Figs 62, 66, 67). In Psocidae, the distal process of the dorsal valve is projected from the dorsal part of the valve (Fig. 62), whereas it is projected from the ventral part in Homilopsocidea (Figs 66, 67). This illustrates the nonhomologous condition of characters 62 and 63. In Lachesillidae, dorsal and ventral valves of the gonapophyses are reduced and thus characters 62 and 63 are scored as unknown.

64. *Dorsal swelling of dorsal valve of gonapophyses*: (0) membranous (Fig. 65); (1) sclerotized (Fig. 66). L = 1; CI = 1; RI = 1. (1) is a synapomorphy of Trichopsocidae, Pseudocaeciliidae, Calopsocidae, Bryopsocidae, Peripsocidae, Philotarsidae and Mesopsocidae.

65. *Dorsal swelling of dorsal valve of gonapophyses*: (0) lobe-like (Fig. 65); (1) forming rounded plate (Fig. 66); (2) forming square-shaped plate (Fig. 67).



**Figures 61–68.** Gonapophyses of *Hemipsocus chloroticus* (61), *Psocus* sp. (62), *Triplocania spinosa* (63), *Amphipsocus mangifera* (64), *Elipsocus abdominalis* (65), *Heterocaecilius fuscus* (66), *Mesopsocus unipunctatus* (67) and *Lachesilla* sp. (68), ventral view. Abbreviations: dv = dorsal valve; ev = external valve; vv = ventral valve.

L = 2; CI = 1; RI = 1. (1) is uniquely observed in Pseudocaecilioidea (= Trichopsocidae + Calopsocidae + Pseudocaeciliidae) and (2) is observed in Peripsocoidea (= Bryopsocidae + Peripsocidae + Philotarsidae + Mesopsocidae). *Remarks:* these superfamilies comprise a monophyletic group and thus the state of this character in their common ancestor is uncertain. In comparison with Elipsocidae, (1) could be regarded as more primitive than (2). By treating this character as ordered, (1) can be assigned to their common ancestor. (1) thus provides further evidence for the monophyly of Pseudocaecilioidea + Peripsocoidea and (2) is regarded as an autapomorphy of Peripsocoidea.

66. *External valve of gonapophyses:* (0) broad (Fig. 62); (1) narrowed (Fig. 63); (2) reduced (Fig. 64). L = 3; CI = 0.67; RI = 0.95. (1) is regarded as an autapomorphy of Lachesilloidea (= Ectopsocidae + Lachesillidae) and also observed in Epipsocetae. (2) is observed in Caeciliusetae. *Remarks:* Epipsocetae and Caeciliusetae comprise a clade and thus the state of this character in their common ancestor is ambiguous. Morphologically, the narrowed external valve can be regarded as an intermediate condition between broad and reduced external valves. By optimizing this character as ordered on the resultant cladogram, (1) can be assigned to the basal node of Epipsocetae + Caeciliusetae. (1) thus provides additional support for the

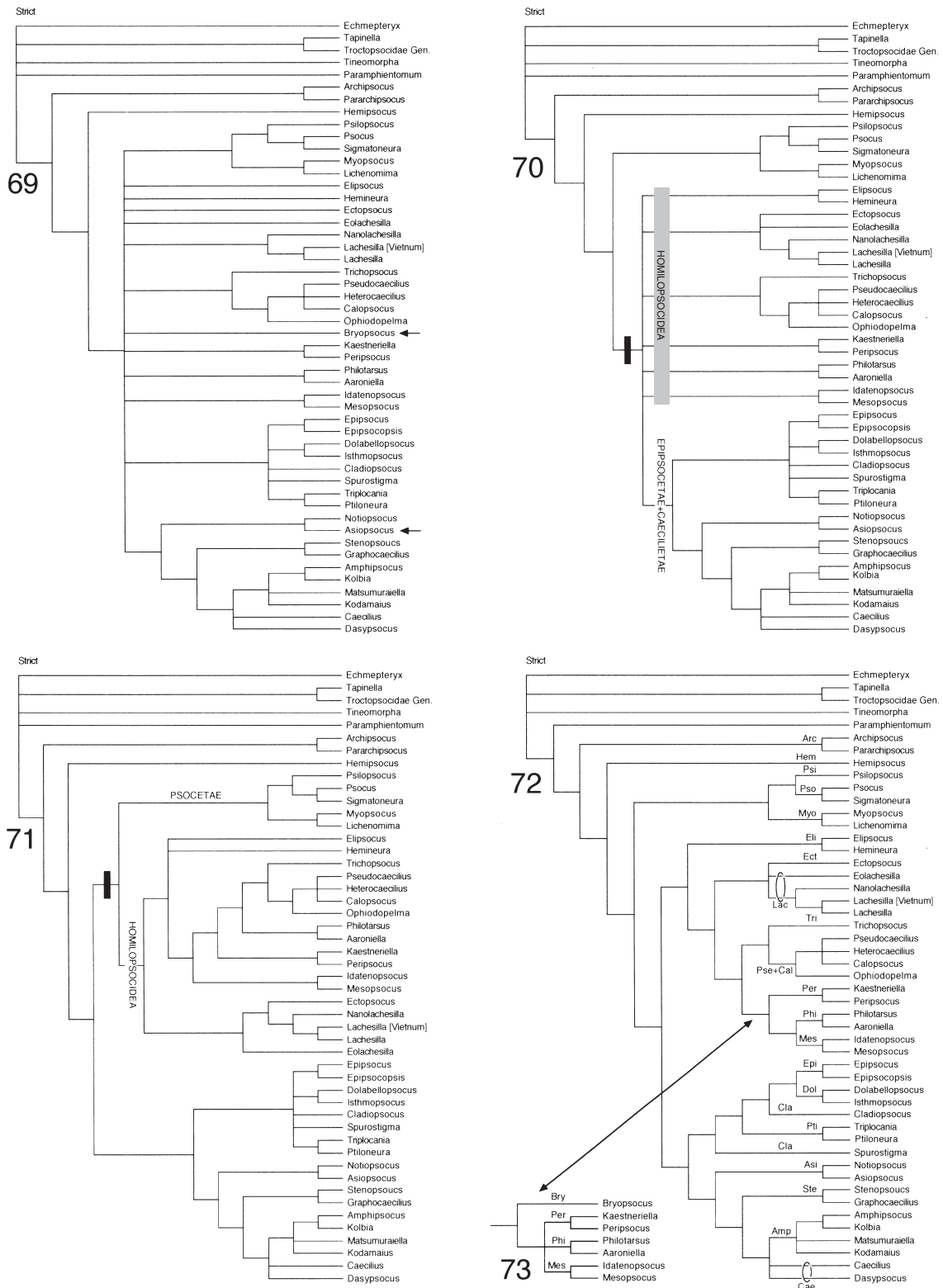
Epipsocetae + Caeciliusetae clade and (2) is considered as an autapomorphy of Caeciliusetae.

67. *Dorsal and external valves of gonapophyses:* (0) separated (Fig. 66); (1) partly fused (Fig. 63); (2) completely united. L = 2; CI = 1; RI = 1. (1) is an autapomorphy of Epipsocetae and (2) is considered as derived from (1), supporting a clade containing Epipsocidae, Dolabellopsocidae and *Cladiopsocus*.

68. *Posterior lobe of external valve:* (0) absent (Fig. 54); (1) present (Fig. 55). L = 1; CI = 1; RI = 1. (1) is an autapomorphy of the family Psocidae.

## RESULTS

The cladistic analysis including all exemplars yielded 1108 equally most parsimonious trees (L = 191). A strict consensus of the trees (Fig. 69) shows that phylogenetic relationships near the basal node are unresolved. Exemplars include two unexamined species (*Bryopsocus townsendi* and *Asiopsocus sonorensis*; Fig. 69, arrows) and the poor resolution is possibly caused by the large number of unknown characters scored in the matrix for these unexamined species (Platnick *et al.*, 1991; Novacek, 1992; Kitching *et al.*, 1998). Judging from the consensus, the phylogenetic position of *Asiopsocus* is stable (Fig. 69) and thus the exemplar used does not contribute to the poor



**Figures 69–73.** (69) generated from original data set, strict consensus of 1108 trees; (70–72) generated from new data set, strict consensus of (70) 72 trees of set 1 (71) 56 trees of set 2 (72) two trees generated using successive approximations and implied weights techniques; family names are abbreviated to first three letters. (73) 14 trees generated from original data set using successive approximations and implied weights techniques (part).



resolution. Although *Asiopsocus* contains many unknown characters, the exemplar can be considered to have enough information to decide its phylogenetic position. The lack of resolution and large number of equal length trees may be due, therefore, to the influence of *Bryopsocus*. To determine the extent of this influence, a new data set excluding *Bryopsocus* was prepared and reanalysed.

The revised data set reduced the number of equally most parsimonious trees to 128; the topology of the strict consensus tree does not differ from that of the original data set, although Ectopsocidae and Lachesilidae now constitute a monophyletic group. Trees from the new data set are assigned in two sets of trees of equal length (= islands *sensu* Maddison, 1991), containing 72 (set 1: Fig. 70) and 56 trees (set 2: Fig. 71). Set 2 differs from set 1 in making Psocetae and Homilopsocidea sister groups (Fig. 71). This relationship is supported by only one extremely homoplastic character state, a three-segmented tarsus. Alternatively, the strict consensus tree of set 1 (Fig. 70) supports a clade containing Homilopsocidea, Epipsocetae and Caeciliusetae using a reliable, nonhomoplastic character, the mesothoracic dorso-ventral flight muscle. Trees in set 1 are therefore regarded as more stable than those in set 2.

As discussed above, poor resolution may be explained by a few highly homoplastic characters. Thus, in order to assign a heavier weight to reliable characters, the characters were weighted using the successive approximations technique, based on the maximum value of RC calculated from 128 trees inferred from the new data set (Farris, 1969; Carpenter, 1988). The implied weights technique (Goloboff, 1993) was also performed with  $k = 2$  and 10 (different  $k$ -values do not alter the result). Both analyses yielded two equally parsimonious trees. The cladograms produced are identical with two of the original 72 cladograms in set 1 and are thus regarded as stable. Topologies of these two trees differ only in the relationships of outgroups.

The techniques were also applied to the original data set, reducing the number of cladograms to 14. These trees are compatible with the two cladograms estimated from the new data set. *Bryopsocus* was placed as sister group to the clade containing Peripsocidae, Philotarsidae and Mesopsocidae (Fig. 73).

Within the 14 trees, phylogenetic relationships among Peripsocidae, Philotarsidae and Mesopsocidae are unstable, although a sister-group relationship between Philotarsidae and Mesopsocidae is more likely. Badonnel & Lienhard (1988) produced a phylogeny of Mesopsocidae, and regarded state 0 of characters 38 and 48 observed in *Mesopsocus* as autapomorphies of the genus. In the present analysis, the states of these characters for the common ancestor of

Mesopsocidae could not be decided because the two exemplars have different states for them. According to Badonnel & Lienhard (1988), the basalmost taxon of the family has state 1 for both characters. This can be regarded as a ground plan for Mesopsocidae and thus they can be considered as synapomorphic for Philotarsidae and Mesopsocidae.

Polytomy is preferred for some nodes (Fig. 74: arrows) because of lack of information to resolve their relationships. Different interpretations of outgroup relationships do not alter the ingroup topology. Therefore, among 14 equal-length trees, one (Fig. 74: L = 191, CI = 0.43, RI = 0.81) was selected as providing the best estimation of the phylogenetic relationships of the psocomorphan families. Based on the monophyletic groups of families identified by the cladogram (Fig. 75), the family and higher level classification of Psocomorpha is revised (Table 1).

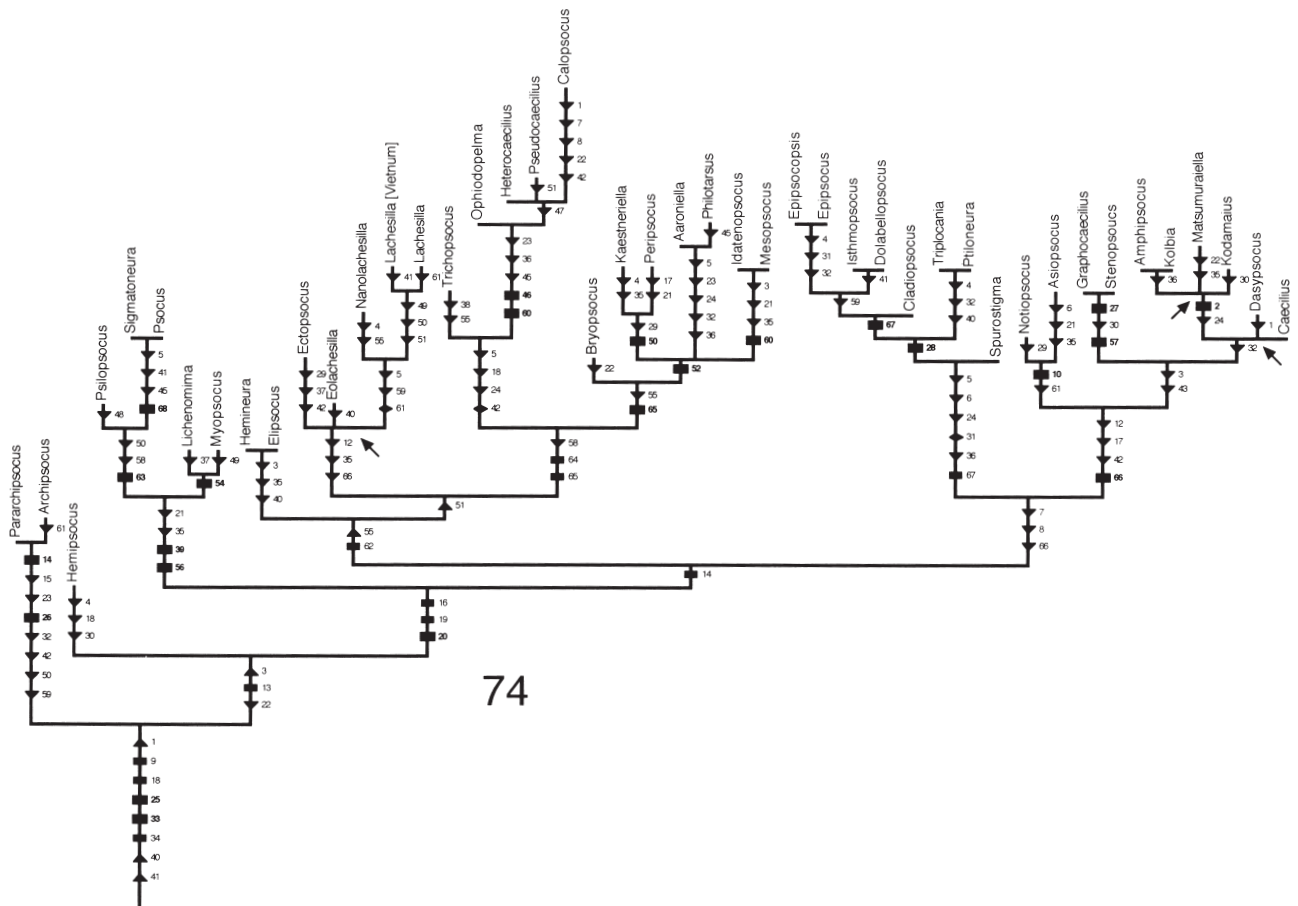
## DISCUSSION

### MONOPHYLY OF PSOCOMORPHA AND RELATIONSHIPS OF INFRAORDERS AND SUPERFAMILIES

Mockford (1967) proposed three autapomorphies supporting the monophyly of suborder Psocomorpha: a hooked nodulus formed by truncated spines fused at their base (Fig. 34); thickened pterostigma; enlargement of mesothorax (Fig. 17). The present analysis strongly supports this monophyly. However the third is not regarded as autapomorphic at the suborder level. The following additional characters were also found to support monophyly: rounded vertex (Fig. 2); absence of stipito-galeal muscle (Fig. 11); presence of proximal minute process at apex of first axillary sclerite (Figs 29, 30); presence of nodus (Fig. 38). By most parsimonious optimization of the character states, two additional character states are regarded as autapomorphies of Psocomorpha: two-segmented tarsus and broad pulvillus. However, these characters are quite variable within the suborder.

Six monophyletic infraorders are recognized in the present analysis (Table 1), four of which have been widely accepted since Pearman (1936) first established the higher taxonomic system. Two new infraorders, Archipsocetae and Hemipsocetae, are proposed. Both are represented by only one family which was formerly included in Homilopsocidea and Psocetae, respectively (Table 1).

Archipsocidae is regarded as the basalmost clade of Psocomorpha (Fig. 75). It has long been assigned to Homilopsocidea. However, it possesses the following plesiomorphic character states that exclude it from this infraorder: prothorax strongly bulged dorsally; pterothorax weakly bulged dorsally; narrow membranous region of metaepisternum; posteroproximal



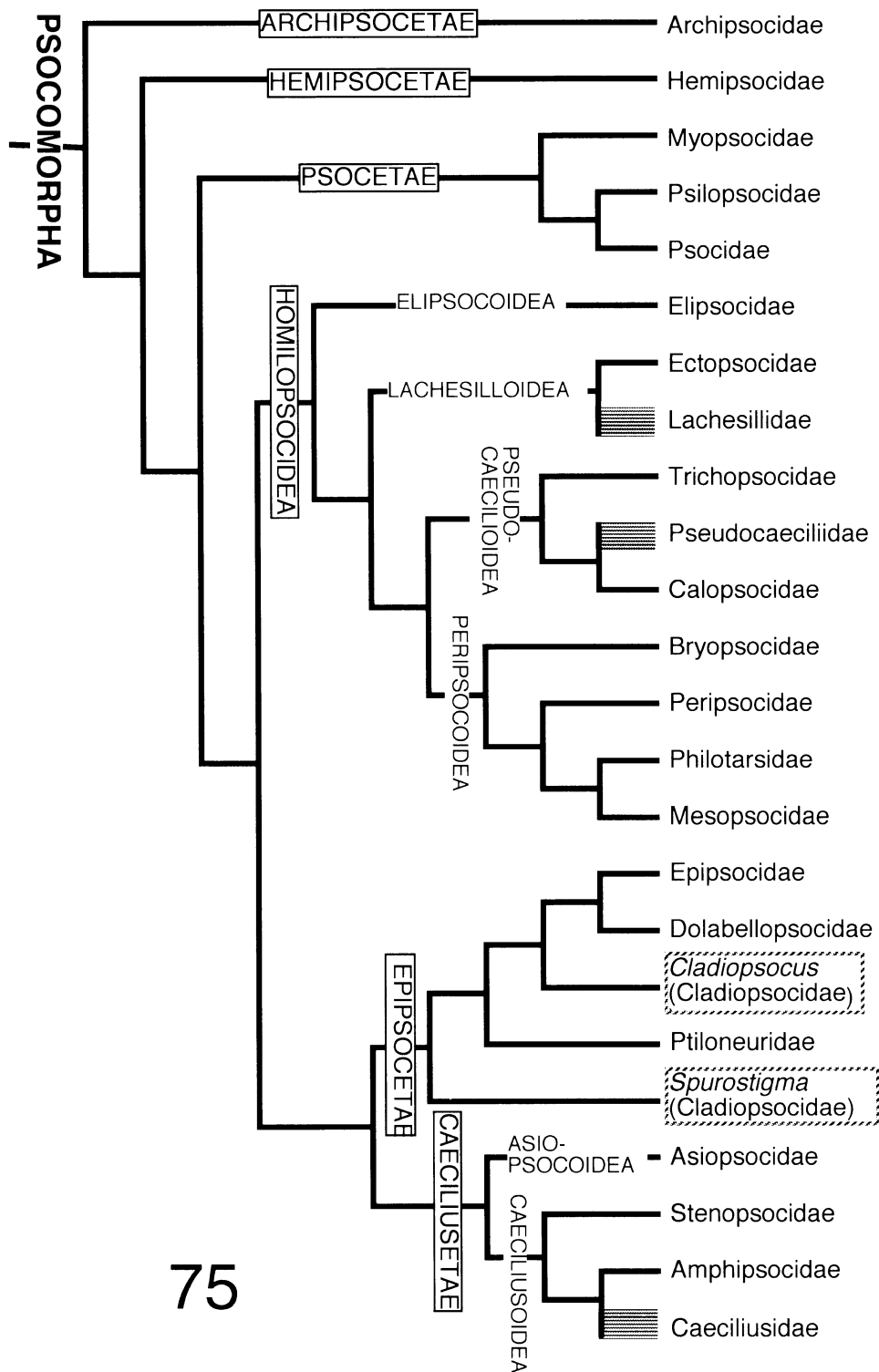
**Figure 74.** Preferred cladogram of Psocomorpha and most parsimonious reconstruction of character states. Outgroups are omitted.

corner of forewing angled; proximal median plate mobilized, not fused with second axillary sclerite. Only one derived character state, broad precoxal bridge of mesothorax (Fig. 23), is shared between Archipsocidae and families of Homilopsocidea, and possibly indicates closer relationships between them. However, the musculature associated with the precoxal bridge is completely different (Figs 20, 21) and similarity of the precoxal bridge should be regarded as convergence.

A narrow internal ridge of the epistomal suture and a strongly bulged pterothorax support the monophyly of Psocomorpha, excluding Archipsocidae. The former character is reversed in some families of the suborder (Elipsocidae, Mesopsocidae, and all families of Caeciliusoidea). Among the families of Psocomorpha (excluding Archipsocidae) Hemipsocidae is placed at the basalmost clade. It was regarded as a member of Psocetae based on the following character states: male paraprot with distal process; female paraprot with distal cylindrical projection (Fig. 54); narrow mesothoracic precoxal bridge (Fig. 22). Although the third is

plesiomorphic, the first two are apomorphic, and possibly indicate a close relationship between Hemipsocidae and Psocetae. However, as discussed in the next paragraph, monophyly of the clade containing Psocetae (excluding Hemipsocidae), Homilopsocidea, Epipsocetae, and Caeciliusetae is well supported by stable, or nonhomoplastic autapomorphies. Consequently, the similarities observed between Hemipsocidae and Psocetae are regarded as symplesiomorphies or homoplasies (ambiguous, although the latter is more likely because similar structures are independently derived in some other taxa, such as some species of *Lachesilla*).

The remaining infraorders – Psocetae, Homilopsocidea, Epipsocetae, and Caeciliusetae – comprise a monophyletic group and autapomorphies supporting this clade include: (1) the broad membranous region of the metaepisternum (Fig. 17); (2) fusion of the proximal median plate to the second axillary sclerite (Fig. 32); (3) posteroproximal margins of folded forewings separated from each other (Fig. 32). These three character states are hypothesized to have been



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**Figure 75.** Phylogenetic relationships among families of Psocomorpha. Monophyly of shaded bar is not supported.

derived only once, and no convergence or reversals were detected by the present analysis. This is especially significant where (2) is a functionally very important character state for wing folding, and

regarded as a reliable autapomorphy, strongly supporting the monophyly of Psocetae + Homilopsocidea + Epipsocetae + Caeciliusetae.

Homilopsocidea + Epipsocetae + Caeciliusetae is

supported by only one autapomorphy: divided dorsoventral flight muscle of the mesothorax (Fig. 20). In Psocetae, Hemipsocetae and outgroups, one dorsoventral flight muscle is inserted into the base of the trochantin (Fig. 19). In contrast, dorsoventral flight muscles of Homilopsocidea, Epipsocetae and Caeciliusetae are divided into two, one of which is inserted into the precoxal bridge and the other into the trochantin (Fig. 20). As already discussed above, only one highly homoplastic character may possibly contradict this clade.

Monophyly of Caeciliusetae + Epipsocetae is supported by an elongate and posteriorly hollowed mandible (Fig. 7), ball-shaped galea (Fig. 9), and narrowed or reduced external valve of the gonapophyses. A somewhat triangular labial palpus is also widely observed, possibly providing further evidence of monophyly. Since most synapomorphies supporting Caeciliusetae + Epipsocetae are presumably strongly associated with feeding behaviour, similar structures might easily have occurred independently. However, the members of Caeciliusetae are mostly living-foilage dwellers whereas those of Epipsocetae are found in leaf litter or on stone or bark surfaces. Their food sources are considered to be different, making it difficult to establish that the similarities of mouthparts are convergences associated with function. Consequently, similarities of mouthparts observed between Caeciliusetae and Epipsocetae are regarded here as synapomorphic.

#### *Infraorder Archipsocetae*

Archipsocidae is the only representative of this infraorder, distributed in tropical regions. Monophyly is strongly supported by the following autapomorphies: broad precoxal bridge and related unique musculature (Fig. 21); forewing veins and membrane covered with long setae (Fig. 35); forewing marginal crossing setae (Fig. 35); reduction of venation (Fig. 35); absence of preapical tooth on pretarsal claw (Fig. 27); lack of parameres; absence of ventral valve of gonapophyses (Fig. 68). Monophyly is also well supported by their behaviour. All known species of this family live on bark or dead leaves beneath webbing sheets in groups and subsociality is also known (New, 1987). External appearance is very similar.

#### *Infraorder Hemipsocetae*

The family Hemipsocidae is the only representative of this infraorder. It is a small family, recorded from all zoogeographical regions, but its distribution is restricted to tropical or warm areas. All species are dead-foilage dwellers. Monophyly is strongly supported by: absence of the epistomal suture; apically

broadened first axillary sclerite; two-branched M vein (not used for analysis), and  $CuA_1$ -M crossvein (Fig. 40). Although absence of aedeagus (Fig. 44) does not unambiguously support this clade, this character state is possibly an additional autapomorphy.

#### *Infraorder Psocetae*

Includes three families, Psilopsocidae, Psocidae, and Myopsocidae, all of which are bark or stone surface dwellers. Monophyly is well supported by: the ctenidia-based broad setae on the hind tibiae (Fig. 25); bare fore- and hindwings (Fig. 36), and single-lobed egg guide extended from the ventral margin of the subgenital plate (Figs 52, 55).

Mockford (1961) assigned Psilopsocidae, one of the least known and controversial families, to Psocetae. Psilopsocidae shares the above-mentioned apomorphic character states with Psocidae and Myopsocidae, and can apparently be included in this infraorder.

The areola postica of Psilopsocidae is always separate from the M vein, whereas it is connected with it in Psocidae and Myopsocidae (Fig. 36). The latter state is apomorphic, and possibly supports the monophyly of Psocidae + Myopsocidae. However, a fossil species of Myopsocidae in which the areola postica is separate is known (Mockford, 1996); if the venation of the fossil specimen represents the ancestral condition, monophyly is not justified. However, three apomorphic character states – paramere absent (Fig. 45); dorsal valve of gonapophyses with ventral swelling (Fig. 62); gonapophyses and egg guide forming the ovipositor – are shared by Psocidae and Psilopsocidae, and support their sister-group relationship.

Psilopsocidae contains only one genus and seven named species. Smithers (1995a, b, 1997) reported a unique and characteristic nymphal wood-boring behaviour in final instar nymphs of *Psilopsocus mimulus*. In addition, all psilopsocid species of which the nymphal stage is known possess a more or less sclerotized abdominal tip, and thus all are probably wood-borers (Smithers, 1995a). If this behaviour is widely observed throughout the family, monophyly is strongly supported by this highly derived behaviour and associated morphological characters. In the present analysis, a rounded aedeagus was considered to be an autapomorphy of this family.

Psocidae is one of the largest families of Psocoptera, distributed in all zoogeographical regions. Monophyly is supported by the following autapomorphic character states: presence of an articulation between hypandrium and clunium (Fig. 42); presence of the posterior lobe of the external valve of the gonapophyses (Fig. 55). Position of anterior tentorial pit and shape of pulvillus may possibly support the monophyly, but they are highly homoplastic.



Myopsocidae is distributed in all zoogeographical regions. The very long dorsal valve of the gonapophyses (Fig. 54) supports monophyly. Although forewing markings were not used for this analysis, those of this family are unique and characteristic (Fig. 36), and possibly provide further evidence supporting monophyly. Male genital characters show great diversity among genera and, as mentioned by Mockford (1961), male genital structures of some myopsocid genera are similar to those of Psilopsocidae, and may possibly support their sister-group relationship. To confirm Mockford's findings, a transformation series of male genital characters within the family must be undertaken.

#### *Infraorder Homilopsocidea*

This infraorder contains ten families assigned to four superfamilies. When Pearman (1936) first proposed Homilopsocidea, he expressed some doubts about its soundness. Badonnel (1951) also found the infraorder to be heterogeneous. Mockford (1976) transferred Hemipsocidae to Psocetae. Later, Mockford (1993) stated that "with the hemipsocids excluded, it seems to consist of a series of related families except that the peripsocid stand apart from the others, especially in structure of male genitalia" (Fig. 48).

The present cladistic analysis shows that this infraorder comprises related families except Archipsocidae which is here assigned to its own infraorder and stands apart from Homilopsocidea. Peripsocidae is here assigned to Homilopsocidea; the specialized male phallosome of the family is apparently an autapomorphic modification and thus provides no information about its phylogenetic position.

Monophyly is supported by the following two apomorphic character states: presence of egg guide extending from dorsodistal margin of the subgenital plate (Fig. 51) and the dorsal swelling of the dorsal valve of the gonapophyses (Figs 65–67).

Elipsocidae is regarded here as the sister group of all remaining homilopsocid families. Badonnel & Lienhard (1988) suggested a sister-group relationship between Elipsocidae and Mesopsocidae based on the reduction of wing setae. Specifically, hindwing margins of both families are bare except between  $R_{2+3}$  and  $R_{4+5}$  (Fig. 40). This condition is apomorphic but highly homoplastic, and similar conditions are observed also in Stenopsocidae and Dasydemellidae (Caeciliusetae). Moreover, when the entire hindwing margin is setose, marginal setae between  $R_{2+3}$  and  $R_{4+5}$  are usually stronger than those in other sections (e.g. Trichopsocidae). Forewing ciliation of Elipsocidae is plesiomorphic. Monophyly of the clade containing the remaining homilopsocid families (including Mesopsocidae) is supported by an apomorphic character state which is

more reliable than wing ciliation: presence of rod-like sclerites on the endophallus (Fig. 46). Thus, the similar condition of hindwing marginal setae observed in Elipsocidae and Mesopsocidae should be regarded as homoplasy.

The remaining families are divided into two clades: Lachesilloidea and Trichopsocidae + Pseudocaeciliidae + Calopsocidae + Bryopsocidae + Peripsocidae + Philotarsidae + Mesopsocidae. Monophyly of the latter is supported by a sclerotized dorsal valve and ventral and dorsal valves of the gonapophyses tightly united to form the ovipositor (Fig. 55). These character states are unique, and observed throughout all taxa within the clade. The latter clade also comprises two monophyletic groups, Pseudocaecilioidae and Peripsocoidae. Monophyly of each superfamily is discussed below.

#### *Superfamily Elipsocoidea*

The family Elipsocidae is the only representative of this superfamily, distributed in all zoogeographical regions, and all members are bark or stone surface dwellers.

Elipsocidae mostly retains the plesiomorphic conditions of the Homilopsocidea. Monophyly is supported by three character states: broad internal ridge of the epistomal suture (Fig. 3), hindwing marginal setae restricted between  $R_{2+3}$  and  $R_{4+5}$ , and three-segmented tarsus. The latter character state is extremely homoplastic. Male and female genital structures are very similar throughout Elipsocidae, but some are plesiomorphic and the polarity of others remains uncertain. Further study is therefore required to confirm the monophyly.

#### *Superfamily Lachesilloidea*

Monophyly is supported by three apomorphic character states: elongate preepisternum of prothorax (Fig. 16), bare hindwing margin, and narrowed external valve of gonapophyses (Fig. 68). The systematic position assigned for *Eolachesilla* by previous authors has been controversial: Lachesillidae (Badonnel, 1967; Mockford & Sullivan, 1986) or Elipsocidae (New & Thornton, 1981). The present analysis suggests a closer relationship between the genus and Lachesillidae, rather than Elipsocidae.

Ectopsocidae is distributed in all zoogeographical regions. Monophyly is strongly supported by the following autapomorphies: absence of areola postica in forewing (Fig. 38); hindwing  $R_s$  and  $M$  connected by crossvein (Fig. 38); presence of ball-shaped lobe on meta-epimeron (not used in the analysis); absence of preapical tooth of pretarsal craws.

Lachesillidae is also distributed in all zoogeographical regions. Monophyly of the family excluding *Eolachesilla* is strongly supported by: the position of anterior tentorial pit, the absence of the ventral valve of the gonapophyses and reduction of the dorsal valve of the gonapophyses (Fig. 68). *Eolachesilla* lacks these apomorphic character states and monophyly including *Eolachesilla* is therefore uncertain. In this paper, this genus is declared *incertae sedis*, and it should be noted that *Eolachesilla* may represent its own family.

#### Superfamily Pseudocaecilioidea

Monophyly of Trichopsocidae + Pseudocaeciliidae + Calopsocidae is supported by: apically broadened first axillary sclerite (Fig. 15); position of the anterior tentorial pit; forewing veins with two rows of setae, and absence of preapical tooth. The latter three characters are highly homoplastic. Presence of eversible vesicles on the abdomen may also provide further support for this superfamily, although the state of this character is ambiguous at the basal node of the clade. The male phallosome and female gonapophyses of these three families are similar but they are symplesiomorphic. Trichopsocidae, Pseudocaeciliidae, and Calopsocidae are all living-foilage dwellers. This feature is apomorphic, and provides further evidence for the monophyly of the Pseudocaecilioidea.

The present analysis posits that within Pseudocaecilioidea, Pseudocaeciliidae and Calopsocidae comprise a monophyletic group. Smithers (1967) suggested close affinity of these families but later (Thornton & Smithers, 1984) doubted this, mentioning that similarities between them were largely due to their retention of primitive features, the two synapomorphies being bilobed subgenital plate and two-segmented tarsi. Most of shared characters suggested in the earlier paper are plesiomorphic or homoplastic, including the two character states that Thornton & Smithers (1984) suggested as apomorphic. Monophyly is well supported by the following character states: crossing marginal setae of forewing (Fig. 37); hindwing veins with one row of setae; presence of an articulation between clunium and hypandrium (Fig. 43); presence of hypandrial lateral bristles (Fig. 43); ventral valve of gonapophyses with dorsal lobe (Fig. 66).

Trichopsocidae is a small family, containing one genus and eight species, distributed in all zoogeographical regions except the Orient. Monophyly is supported by secondary loss of the distal extension of the subgenital plate. An additional apomorphic feature, hindwing Rs and M + Cu separate basally (Fig. 37), is observed in one exemplar, but it is uncertain whether this character state is widely observed throughout this family.

Pseudocaeciliidae is the largest family among Homilopsocidea, and is distributed in all zoogeographical regions. No autapomorphy supporting monophyly was found in the present study. Thus, the family is regarded here as a paraphyletic group. Calopsocidae is regarded as a highly specialized clade within it. I declare the family Pseudocaeciliidae *incertae sedis*, and further phylogenetic study of Pseudocaeciliidae + Calopsocidae is required to confirm their relationships.

Calopsocidae is known only from the Oriental and Melanesian regions. Monophyly is well supported by a sharply angled vertex that is deeply emarginated medially, and presence of numerous secondary veins in the forewing (not used in the analysis). A somewhat elongate mandible, ball-shaped galea, and presence of a preapical tooth on the pretarsal claw also support monophyly.

#### Superfamily Peripsocoidea

Monophyly is supported by the following apomorphic character states: single-lobed egg guide (Fig. 59); strongly sclerotized and square-shaped dorsal valve of the gonapophyses (Fig. 67).

The family Bryopsocidae is represented by one species, *Bryopsocus townsendi* (Smithers, 1969), known from New Zealand. Smithers (1969) originally described the species under the genus *Austropsocus* of the family Philotarsidae. Thornton, Wong & Smithers (1977) subsequently erected a new genus, *Bryopsocus*, in the family Philotarsidae, designating *A. townsendi* as type species of the genus. Mockford (1984) extensively studied philotarsid and pseudocaeciliid genera, and concluded that *Bryopsocus* is intermediate between Philotarsidae and Pseudocaeciliidae. Thus, he founded the monotypic family Bryopsocidae for the genus, and considered it to be the sister group to Pseudocaeciliidae + Calopsocidae. This conclusion was based on 'extent of character sharing' (Mockford, 1984) but he did not discuss their polarity.

Judging from published descriptions and illustrations, Bryopsocidae possesses all the apomorphies supporting the monophyly of Homilopsocidea. One character state, dorsal extension of the subgenital plate (character 55), is difficult to assess from published illustrations, but a transverse line was clearly drawn near the base of the egg guide (Smithers, 1969; fig. 192) which most probably indicates that the egg guide extends from the dorsal surface. Thus, the family is regarded as a member of Homilopsocidea.

Bryopsocidae also appears to share the apomorphies of Peripsocoidea listed above. These character states are not observed in Pseudocaecilioidea. However, Bryopsocidae has long rod-like sclerites on the endophallus that are similar to those of Pseudocaeciliidae and

Calopsocidae. This may suggest closer affinities, as suggested by Mockford (1984). However, similar structures are also observed in some taxa within Lachesilloidea and Peripsocidae and, consequently, similarity of the endophallic sclerites observed in Bryopsocidae and Pseudocaeciliidae should be regarded as a symplesiomorphy. Thus, Bryopsocidae is regarded as a member of this superfamily.

Within the Peripsocoidea, Bryopsocidae occupies the basalmost clade. Monophyly of Peripsocidae + Philotarsidae + Mesopsocidae is well supported by a square-shaped female epiproct (Fig. 50). Bryopsocidae shares three-segmented tarsi with Philotarsidae and Mesopsocidae, although this character state is highly homoplastic.

In the present analysis, phylogenetic relationships among Peripsocidae, Philotarsidae, and Mesopsocidae were not resolved because no decisive autapomorphy supporting the clade comprising two of the three families was detected. However, as discussed above, state 1 of character 39 and state 1 of character 48 can be regarded as autapomorphies supporting the monophyly of Philotarsidae + Mesopsocidae.

Peripsocidae is distributed in all zoogeographical regions. Members are mostly bark or stone surface dwellers, but some are collected from dead foliage. Monophyly is well supported by absence of areola postica in the forewing (Fig. 38) and strap-like paramere (Fig. 48). Because of the first character, Peripsocidae was once classified with Ectopsocidae, but is only distantly related to it.

Philotarsidae is distributed in all zoogeographical regions. Members are all bark or stone surface dwellers. Monophyly is supported by only one decisive apomorphic character, presence of ventral setae on the forewing. Position of the anterior tentorial pit, crossing marginal setae of forewing, more than one row of setae on forewing veins, and apically rounded aedeagus possibly provide further evidence of monophyly, but they are highly homoplastic or their states at the basal node of the family are ambiguous.

Mesopsocidae is widely distributed in all zoogeographical regions and is particularly abundant in the Afrotropical and Palearctic regions. Members are mostly bark or stone surface dwellers, although one species is known to be associated with termites. Monophyly is supported by the following apomorphic character states: broad internal ridge of the epistomal suture; glabrous fore- and hindwings; apically broadened ventral valve of the gonapophyses (Fig. 67).

#### *Infraorder Epipsocetae*

Monophyly is well supported by the following apomorphic character states: anterior tentorial pit separated from ventral margin of cranium (Fig. 5); labrum with

a pair of longitudinal sclerotized lines (Fig. 5); forewing veins with more than one row of setae (Fig. 39: reversed in Epipsocidae); presence of  $A_2$  vein (Fig. 39: reversed in Epipsocidae); hindwing veins with two rows of setae (Fig. 39); dorsal and external valves of gonapophyses (partly) fused (Fig. 63). A long gena and broad lacinial tip possibly support monophyly, but these continuous, quantitative characters were not used for the analysis.

*Spurostigma* of the family Cladiopsocidae is regarded as the basalmost clade of the infraorder, and monophyly of Epipsocetae excluding *Spurostigma* is supported by one stable autapomorphy, forewing veins Rs and M connected by a crossvein.

Ptiloneuridae is regarded as the second basalmost clade of Epipsocetae. The family is known from the Afrotropical, Nearctic and Neotropical regions. Monophyly is supported by three, highly homoplastic character states: epistomal suture absent dorsally, presence of ventral setae of forewing, and three-segmented tarsus. Although not used for the cladistic analysis, highly modified male genital structures appear to be autapomorphic. However, they are extremely variable within the family and thus it is very difficult to decide their homology. I have examined only two species of this family and further morphological study of the male genitalia will provide further support for the validity of the autapomorphy.

The remaining exemplars, Epipsocidae, Dolabellopsocidae and *Cladiopsocus* of the family Cladiopsocidae, comprise a monophyletic group; a stable autapomorphy, complete fusion of external and dorsal valves of the gonapophyses, supports its monophyly. Within this clade, Epipsocidae and Dolabellopsocidae are considered to comprise a subclade, supported by only one autapomorphy: absence of ventral valve of gonapophyses. This feature is considered as derived independently three times in Psocomorpha.

Dolabellopsocidae is known only from the Neotropical region. Monophyly is supported by only one, highly homoplastic, character state, broad pulvillus. Diagnostic characters proposed by Eertmoed (1973) are mostly plesiomorphic, highly homoplastic or not consistent within the family. Further studies are required to confirm its validity.

Epipsocidae is distributed in all zoogeographical regions. Monophyly is supported by three autapomorphies: epistomal suture absent dorsally, absence of  $A_2$  vein in forewing, and presence of ventral setae of forewing.

Cladiopsocidae also is known only from the Neotropical region. As discussed above, the family is regarded as polyphyletic in the present analysis and character states suggesting nonmonophyly can be regarded as stable. In contrast, diagnostic characters proposed by Eertmoed (1973) are mostly plesiomor-



phic, highly homoplastic or not consistent within the family. As the present analysis strongly suggests polyphyly I postpone division and declare it *incertae sedis* because I have examined only two species. Cladiopsocidae probably will be divided into at least two independent families in a future study.

#### *Infraorder Caeciliusetae*

Monophyly is supported by the following apomorphic character states: elongate preepisternum of prothorax (Fig. 16); campaniform sensilla on the radius divided into two groups; absence of preapical tooth of the pretarsal claw; reduction of external valve of the gonapophyses.

#### *Superfamily Asiopsocoidea*

This superfamily is represented by only one bark dwelling family, Asiopsocidae, known from the Nearctic, Neotropical and Palearctic regions. Although it does not have to be established to translate the cladogram to the Linnaean system, I herein maintain this widely accepted superfamily. Monophyly is supported by two unique apomorphic character states, broadened subapical region of the lacinia (Fig. 12) and reduced and membranous dorsal valve of the gonapophyses.

#### *Superfamily Caeciliusoidea*

This superfamily comprises three families: Stenopsocidae, Amphipsocidae, and Caeciliusidae. A well-developed internal ridge of the epistomal suture and presence of abdominal eversible vesicles support monophyly. The derived male and female external genitalia are remarkably uniform throughout, and most possibly indicate closer relationships among caeciliusoid families. Members are living-foliage dwellers, providings further evidence of monophyly.

Phylogenetic relationships are very difficult to establish because of uniformity of external characters throughout the superfamily. As mentioned by Mockford (1978), the external genitalia are remarkably uniform. However, the external valve of the gonapophyses of Dasydemellinae is rather well developed, whereas it is greatly reduced in the other taxa. The former character state is regarded as autapomorphic in the present analysis, although it does not, unfortunately, provide information about interfamilial phylogenetic relationships. Only one highly homoplastic character state, presence of ventral setae on the forewing, supports the monophyly of Amphipsocidae *s.l.* + Caeciliusidae.

Stenopsocidae is distributed in the Afrotropical, Palearctic, Oriental, and Australian regions. Monophyly is well supported by the presence of the  $R_1$ – $R_{2+3}$

crossvein (Fig. 40),  $M$ – $CuA_1$  crossvein (Fig. 40), and lateral pouch of the spermathecal sac (Fig. 40).

Mockford (1993) raised the status of Dasydemellidae from subfamilial level within the Amphipsocidae. Monophyly of Amphipsocidae *s.l.* is supported by apomorphic ciliation of the forewing and a pair of concavities on the vertex. Autapomorphy was found for Dasydemellinae and monophyly of Amphipsocinae is also supported by apomorphic ciliation of the hindwing. In the present analysis, *Kodamaius*, which has been assigned at various times to Amphipsocidae (Smithers, 1990), Stenopsocidae (Smithers, 1972; Badonnel, 1981) and Caeciliusidae (Mockford, 1993, 1999; Yoshizawa, 1997), is assigned to the clade comprising Dasydemellinae and Amphipsocinae but included in neither. Thus, there are two options for the taxonomic treatment of these taxa: either all three should be placed within a single family or treated as independent. A morphological gap is observed between Dasydemellinae and the other taxa, especially in the shape of the external valve of the gonapophyses. As mentioned above, the taxonomic position of *Kodamaius* was ambiguous due to its unique forewing venation. However, these morphological gaps cannot be considered as evidence of family level hierarchy, because the external valve, similar to that of Dasydemellinae, is also observed in some species of Stenopsocidae and forewing venation is variable within Amphipsocinae. Therefore, it is more practical to treat the taxa as a single family, Amphipsocidae *s.l.* (Yoshizawa, 2001). Members are widely distributed in all zoogeographical regions.

Caeciliusidae is the largest family of Psocomorpha, and is widely distributed in all zoogeographical regions. Monophyly was not supported by any autapomorphy. Mockford (1978, 1999) proposed some apomorphic character states but they were not confirmed in the present study or are too homoplasious. The family is possibly paraphyletic. I declare it *incertae sedis* until the phylogenetic relationships within it can be established.

## DIAGNOSES OF PSOCOMORPHA, INCLUDING INFRAORDERS AND SUPERFAMILIES

### SUBORDER PSOCOMORPHA

Head usually with rounded vertex; antennae 13-segmented; flagellomeres never annulated; maxilla without stipito-galeal muscle; hypopharyngeal filaments fused for most of their length; labial palpus 1-segmented. Forewing with nodus and thickened pterostigma; nodulus hook-shaped, formed by truncated spines fused at their base;  $CuP$  ending together with  $A_1$  at wing margin. Apex of first axillary sclerite usually with minute proximal process. Subgenital plate lacking median sclerite.



## ARCHIPSOCETAE, INFRAORDER NOV.

Small to medium in size, about 1–3 mm in length (from head to tips of closed wings). Brown to reddish-brown in colour. Almost all body surfaces densely covered with long hyaline setae. Members mostly bark dwellers, living within dense silk nests.

Head with rounded vertex; postclypeus strongly convex, epistomal suture with broad internal ridge; anteclypeus weakly sclerotized; eyes small, no sexual size dimorphism; ocelli usually present, not clustered on small tubercle; antennae short; mandible short, with rounded outer margin; lacinial tip bicuspid; galea flattened; labial palpus rounded. Prothorax well developed, bulged dorsally. Pterothorax not strongly bulged dorsally, dorsal margin almost same level with vertex; median part of mesoscutellum triangular; precoxal bridge of mesothorax broad; meso-trochantin narrow; second phragma strongly swollen posteriorly; membranous region of metaepisternum narrow. Wing polymorphism present: macropterous, micropterous, or apterous. Forewing almost uniformly brown, posteroproximal corner strongly angled; veins, membrane, and wing margin densely clothed with long, hyaline setae; veins faint; pterostigma shallow, weakly thickened; M unbranched; areola postica flattened. Hindwing hyaline, narrow in shape, posteroproximal corner slightly extended posteriorly; veins and membrane covered with minute setae, distal and posterior margins with longer setae; veins faint and reduced to unbranched Rs, M, CuA, and CuP; Sc, R<sub>1</sub>, and A almost indistinguishable. Tarsi 2-segmented; preapical tooth of pretarsal claw absent; pulvillus broad. Abdomen lacking eversible vesicles ventrally. Male genitalia: hypandrium simply rounded posteriorly. Phallosome: aedeagus rounded or pointed apically; parameres weakly sclerotized or more often completely absent; aedeagus and phallobase sometimes detached; phallobase closed or opened apically; endophallus without sclerite. Female genitalia: Subgenital plate simply rounded or slightly flattened distally. Gonapophyses modified, ventral valve absent; dorsal valve present or absent, narrow and short if present; external valve large, with long marginal bristles. All valves absent in viviparous species.

*Included family:* Archipsocidae.

## HEMIPSOCETAE, INFRAORDER NOV.

Medium-sized, about 2.5–3.5 mm. Usually whitish to pale brown in coloration, with blackish bristles. Dead-foilage dwellers.

Head with rounded vertex; clypeus not strongly bulged, epistomal suture reduced; anteclypeus sclerotized; eyes rather small, no sexual size dimorphism; ocelli complete, not clustered on small tubercle;

mandible short, with smoothly rounded outer margin; lacinial tip bicuspid; galea flattened; labial palpus rounded. Prothorax rather well developed. Pterothorax strongly bulged dorsally, its dorsal margin higher than vertex; mesoscutellum somewhat pentagonal medially; precoxal bridge of mesothorax narrow; mesotrochantin broad basally; membranous region of metaepisternum narrow. Forewing hyaline to very pale brown in ground colour, bearing marginal setae; posteroproximal corner strongly angled; pterostigma shallow; veins and wing margin setose, veins with one row of setae except CuP bare; Rs and M joined at point; M 2-branched; areola postica low; CuA<sub>1</sub> connected with stem of M by crossvein; A<sub>2</sub> absent. Hindwing glabrous, posteroproximal corner angled; Sc strong basally but faint distally; Rs and M + Cu fused for long distance basally; Rs and M fused for short distance. Tarsi 2-segmented; preapical tooth of pretarsal claw present; pulvillus broad. Abdomen lacking eversible vesicles ventrally. Male genitalia: paraproct with distal process directed posteriorly to dorsally. Hypandrium simple. Phallosome triangular, consisting of thin phallobase and paramere; aedeagus absent; parameres strongly bent internally, supporting posterior margin of endophallus; endophallus with or without sclerotized portion. Female genitalia: subgenital plate simple, posterior margin smoothly rounded or slightly hollowed at middle. Gonapophyses complete; ventral valve and dorsal valve simple, narrow, pointed apically; external valve large.

*Included family:* Hemipsocidae.

## INFRAORDER PSOCETAE

Medium to large in size, about 3–10 mm. Coloration variable, but usually whitish in ground colour and with dark brown markings. All bark or stone surface dwellers.

Head with rounded vertex; postclypeus not strongly bulged; internal ridge of epistomal suture narrow; anteclypeus sclerotized; male eyes usually much larger than female's; ocelli complete, not clustered on small tubercle; mandible short, outer margin smoothly rounded, posterolateral margin not hollowed; lacinial tip variable; galea flattened; labial palpus rounded. Prothorax less bulged dorsally. Pterothorax greatly bulged dorsally; median part of mesoscutellum pentagonal; mesothorax with narrow precoxal bridge and broad trochantin; membranous region of metaepisternum broad. Forewing often with dark brown markings; posteroproximal corner smoothly rounded; veins and wing margin glabrous; top of CuA<sub>1</sub> usually connected with M except free in Psilopsocidae; A<sub>2</sub> never present. Hindwing glabrous, posteroproximal corner smoothly rounded; Sc clear; Rs

and M + Cu fused for long distance basally; Rs and M fused or connected by crossvein (some genera in Myopsocidae). Hind tarsus with row of broad ctenidia based setae (condition of this character in Psilopsocidae not examined or documented); tarsi 2- or 3-segmented; claws with preapical tooth; pulvillus broad or narrow (Psocidae). Abdomen without eversible vesicles ventrally. Male genitalia: paraproct with process on distal margin. Hypandrium usually with complex distal processes or lobes. Phallosome variable; internal valve present or absent; external valve often absent; endophallus lacking sclerotized portion. Female genitalia: paraproct with cylindrical distal projection. Subgenital plate with 1-lobed egg guide extending from ventral margin; apex of egg guide usually bearing setae. Gonapophyses complete and variable in structure; external valve internally expanded.

*Included families:* Psilopsocidae, Myopsocidae, Psocidae.

#### INFRAORDER HOMILOPSOCIDEA

This infraorder contains a great diversity of taxa, both morphologically and biologically.

Head usually with rounded vertex except sharply pointed in Calopsocidae; postclypeus usually well bulged; epistomal suture with or without well-developed internal ridge; anteclypeus variable; male eyes usually much larger than female's; ocelli complete, usually clustered on weakly developed tubercle; mandible short, with rounded outer margin except Calopsocidae with somewhat angled outer margin; lacinial tip usually bicuspid; galea usually flattened; labial palpus rounded. Prothorax less bulged dorsally; pterothorax strongly bulged dorsally; mesothorax with broad precoxal bridge and narrow trochantin; metaepisternum with broad membranous region. Forewing with various coloration and markings; posteroproximal corner smoothly rounded; venation generally of *Caecilius*-type. Hindwing with rounded posteroproximal corner; Sc faint. Male genitalia variable; phallosome complete. Female genitalia: subgenital plate usually with distal projection extended from dorsal margin. Gonapophyses usually complete; dorsal valve swollen dorsally, usually with subapical ventral process.

#### ELIPSOCOIDEA, SUPERFAM. NOV.

Small to medium in size, about 1–4 mm in length. Body generally brown to blackish brown. Bark or stone surface dwellers.

Head with rounded vertex; postclypeus well bulged; epistomal suture with broad internal ridge; anteclypeus membranous or sclerotized narrowly. Wing

polymorphism present, macropterous or apterous. Macropterous forewing venation of *Caecilius*-type; veins and wing margin with one row of setae, CuP sometimes bare. Hindwing scarcely setose; marginal setae present between  $R_{2+3}$  and  $R_{4+5}$  only; Rs and M + Cu separate or fused for short distance basally; Rs and M fused. Tarsi 3-segmented; claws with preapical tooth; pulvillus narrow. Abdomen without eversible vesicles ventrally. Male genitalia: Hypandrium simply rounded posteriorly. Phallosome simple; aedeagus pointed apically; parameres extended distally far beyond aedeagus; endophallus without rod-like sclerite. Female genitalia: Subgenital plate with less developed pair of tubercles on distal margin, each bearing some apical setae. Gonapophyses complete; ventral valve simple; dorsal valve narrowed apically, with or without subapical process; external valve enlarged.

*Type genus:* *Elipsocus* Hagen, 1866.

*Included family:* Elipsocidae.

#### LACHESILLOIDEA SUPERFAM. NOV.

Lachesillidae Badonnel (1951); emended from Pterodelidae Pearman, 1936, is the oldest family group name within the superfamily.

Small in size, about 1.5–4 mm in length. Body generally pale brown to blackish-brown. Mostly collected from dead-foilage, ground litter, bird's nests, and from bark.

Head with rounded vertex; postclypeus less bulged; epistomal suture sometimes reduced, always without broad internal ridge; anteclypeus usually not sclerotized. Pre-episternum of prothorax elongate. Metaepimeron of Ectopsocidae with ball-shaped lobe laterally. Forewing hyaline, sometimes with blackish-brown markings; pterostigma usually shallow; areola postica, if present, usually free from M, absent in Ectopsocidae, and fused with M in some Lachesillidae. Hindwing veins and margin glabrous; Rs and M + Cu fused for long distance basally; Rs and M fused (Lachesillidae) or connected by crossvein (Ectopsocidae). Tarsi 2- or 3- (*Eolachesilla*) segmented; claws with or without (Ectopsocidae) preapical tooth; pulvillus broad or narrow. Abdomen without eversible vesicles ventrally. Male genitalia: variable; clunium, epiproct, paraproct, and hypandrium often with various processes. Phallosome variable; endophallus usually with sclerites but absent in some genera of Lachesillidae. Female genitalia: subgenital plate with (Ectopsocidae and some genera of Lachesillidae) or without distal projection extended from dorsal margin. Dorsal and ventral valves of gonapophyses often reduced; external valve narrowed, bearing long setae.

*Type genus:* *Lachesilla* Westwood, 1840.

*Included families:* Lachesillidae, Ectopsocidae.

#### PSEUDOCAECILIOIDEA, SUPERFAM. NOV.

All three included families of this superfamily were simultaneously established by Pearman (1936) and a name could not be decided by the principle of priority. I propose Pseudocaecilioidea since *Pseudocaecilius* has the widest distributional range among the type genera of the three families.

Small to middle in size, about 2–4 mm. Coloration variable. Usually living-foliage dwellers, except for some genera of Pseudocaeciliidae (e.g. *Ophiodopelma*).

Vertex generally rounded but strongly angled in Calopsocidae; postclypeus not strongly bulged; epistomal suture faint dorsally, without broad internal ridge; anteclypeus sclerotized. Forewing veins with more than one row of setae; marginal setae crossing on anterior margin or not (Trichopsocidae). Apex of first axillary sclerite broadened. Hindwing veins and margins setose; Rs and M + Cu separate or fused for short distance basally; Rs and M fused. Tarsi usually 2-segmented; claws with or without preapical tooth; pluvillus broad. Abdomen with eversible vesicles ventrally except some dead-foliage dwelling taxa in Pseudocaeciliidae. Male genitalia: hypandrium articulated laterally with clunium or not (Trichopsocidae); with or without (Trichopsocidae) lateral projection and lateral bristle. Phallosome: aedeagus pointed apically; parameres long, extending far beyond aedeagus; endophallus with or without (Trichopsocidae and some genera of Pseudocaeciliidae) rod-like sclerites. Female genitalia: subgenital plate with well-developed egg guide extending from dorsal margin; egg guide 2-lobed, each bearing 1 or 2 apical setae. Gonapophyses complete; ventral valve usually with dorsal lobe apically; dorsal valve with dorsal lobe and subapical process; external valve variable, bearing many long bristles.

*Type genus:* *Pseudocaecilius* Enderlein, 1903.

*Included families:* Trichopsocidae, Calopsocidae, Pseudocaeciliidae.

#### PERIPSOCOIDEA, SUPERFAM. NOV.

Peripsocinae Kolbe 1880, is the oldest family group name within the superfamily.

Small to large in size, about 2–5 mm in length. Body whitish in ground colour with blackish-brown markings or wholly blackish-brown. All bark dwellers.

Head with rounded vertex; postclypeus well bulged; epicranial suture with (Mesopsocidae) or without broad internal ridge; anteclypeus sclerotized or not (Mesopsocidae). Forewing coloration, venation, and ciliation variable. Hindwing ciliation variable; Rs and M + Cu separate (most Mesopsocidae), or fused for

short (Philotarsidae) or long (Peripsocidae) distance basally; Rs and M fused. Tarsi 2- (Peripsocidae) or 3-segmented; claws with preapical tooth; pulvillus narrow. Abdomen without eversible vesicles ventrally. Male genitalia: hypandrium usually simple except *Philotarsus*. Phallosome variable; aedeagus rounded (most of Mesopsocidae and Philotarsidae) or pointed apically; phallobase united and rounded apically; endophallus with (Bryopsocidae, Peripsocidae, and some Philotarsidae) or without sclerites. Female genitalia: epiproct usually rectangular in dorsal aspect except rounded in Bryopsocidae. Subgenital plate with 1-lobed egg guide extended from dorsal margin. Gonapophyses complete; ventral valve and dorsal valve strongly united, forming ovipositor; dorsal valve strongly sclerotized, somewhat rectangular in lateral aspect, with or without (Peripsocidae) subapical process; external valve variable.

*Type genus:* *Peripsocus* Kolbe, 1866.

*Included families:* Bryopsocidae, Peripsocidae, Philotarsidae, Mesopsocidae.

#### INFRAORDER EIPSOCETAE

Medium to large in size, about 3–7 mm in length. Coloration variable. Collected from dead foliage, leaf litter, or bark and stone surfaces.

Head with rounded vertex; gena elongate; postclypeus less bulged; epistomal suture often reduced, always without well-developed internal ridge; anteclypeus broadly sclerotized; anterior tentorial pit separate from ventral margin of cranium; male eyes much larger than female's; ocelli complete or absent dorsally, clustered on small tubercle; labrum with pair of longitudinal sclerotized lines; mandible elongate, its outer margin strongly angled and posterolateral margin deeply hollowed; maxilla with ball-shaped galea; labial palpus somewhat triangular. Prothorax less bulged dorsally. Pterothorax well bulged dorsally; mesoscutellum pentagonal medially; mesothorax with narrow precoxal bridge and trochantin; metaepisternum with broad membranous region. Forewing setose, veins often with more than 1 row of setae; postero-proximal corner smoothly rounded; Rs and M usually fused by crossvein;  $A_2$  usually present but absent in Epipsocidae. Hindwing with smoothly rounded postero-proximal corner; veins setose, often with more than 1 row of setae in distal half; margins wholly setose except anterior margin proximal to marginal end of  $R_1$ ; Rs and M + Cu fused for long distance basally; Rs and M fused. Tarsi 2- or 3-segmented; claws with preapical tooth; pulvillus narrow. Abdomen without eversible vesicles ventrally. Male genitalia: phallosome variable; phallobase usually open apically. Female genitalia: subgenital plate usually simple.



Gonapophyses: ventral valve present or absent; dorsal valve narrowed to pointed apex; external valve narrowed; dorsal and external valve fused with each other.

*Included families:* Cladiopsocidae, Ptiloneuridae, Dolabellapsocidae, Epipsocidae.

#### INFRAORDER CAECILIUSETAE

Small to large in size, about 2–10 mm in length. Sexual dimorphism present.

Head with rounded vertex; eyes variable; ocelli complete, clustered on small tubercle; mandible more or less elongate, outer margin angled; galea ball-shaped; labial palpus somewhat triangular. Prothorax less bulged dorsally; preepisternum of prothorax elongate. Pterothorax greatly bulged dorsally in winged form; mesothorax with broad precoxal bridge and narrow trochantin; metathorax with broad membranous region. Forewing variable in venation, size, shape, and colour; posteroproximal corner smoothly rounded. Hindwing with smoothly rounded posteroproximal corner; ciliation variable; Sc clear; Rs and M + Cu fused for long distance basally; Rs and M fused. Tarsi 2-segmented; claws without preapical tooth. Male genitalia: Hypandrium simple, posterior margin smoothly rounded. Phallosome: aedeagus pointed apically, strongly arched in lateral aspect; paramere extended along aedeagus, strongly arched in lateral aspect; phallobase simple and narrow, anterior margin not divided; endophallus usually with weakly sclerotized region but never with rod-like sclerites. Female genitalia: Subgenital plate simply rounded or slightly hollowed posteriorly. Gonapophyses variable; external valve more or less reduced.

#### SUPERFAMILY ASIOPSOCOIDEA

Small to medium in size, about 2–3 mm in length. Generally brownish in colour. Bark dwellers. Sexual dimorphism present, male (*Notiopsocus*) or female (*Asiopsocus*) often apterous.

Head: clypeus less bulged; epistomal suture without broad internal ridge; anteclypeus desclerotized; distal margin of labrum with small projections laterally; mandible variable, its outer margin more or less angled; lacinia with subapical broadened region, lacinial tip broad with denticle. Forewing as for Caeciliusetae; pterostigma shallow; areola postica present or absent (*Notiopsocus*). Hindwing veins glabrous; wing margin glabrous or setose from apex to posterior margin. Pulvillus variable, sometimes absent. Abdomen without eversible vesicles on ventral surface. Male genitalia: as for Caeciliusetae. Female genitalia: gonapophyses reduced; ventral valve more or less

reduced; dorsal valve reduced to membranous lobe; external valve reduced but somewhat narrowed.

*Type genus:* *Asiopsocus* Günther, 1968.

*Included family:* Asiopsocidae.

#### SUPERFAMILY CAECILIUISOIDEA

Small to large in size, about 3–10 mm in length. Coloration of body and wings greatly diverse. All living-foilage dwellers.

Head capsule somewhat elongate, parallel sided; vertex usually rounded; anteclypeus narrowly sclerotized; male eyes always much larger than female's; ocelli complete, clustered on well-developed small tubercle; mandible elongate, external margin strongly angled, posterior margin deeply hollowed. Maxilla with ball-shaped galea; lacinial tip usually narrow, not denticulated; labium with well-developed salivary duct; labial palpus triangular. Forewing venation, coloration, and ciliation variable; veins and wing margin always setose. Hindwing variable. Pulvillus broad. Abdomen with eversible vesicles on ventral surface. Male genitalia as in Caeciliusetae. Female genitalia: Subgenital plate simple, its posterior margin smoothly rounded or slightly hollowed medially. Gonapophyses simple; ventral and dorsal valves narrow and pointed apically; external valve reduced, sometimes almost indistinguishable, with or without few setae.

*Type genus:* *Caecilius* Curtis, 1837.

*Included families:* Stenopsocidae, Amphipsocidae, Caeciliusidae.

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