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Phylogeny of the suborder Psocomorpha: congruence and incongruence between morphology and molecular data (Insecta: Psocodea: 'Psocoptera')

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1 The largest suborder of bark lice (Insecta: Psocodea: "Psocoptera") is Psocomorpha,
2 which includes over 3600 described species. We estimated the phylogeny of this major
3 group with family level taxon sampling using multiple gene markers, including both
4 nuclear and mitochondrial ribosomal RNA and protein coding genes. Monophyly of the
5 suborder was strongly supported, and monophyly of three of four previously recognized
6 infraorders (Caeciliusetae, Epipsocetae and Psocetae) was also strongly supported. In
7 contrast, monophyly of the infraorder Homilopsocidea was not supported. Based on the
8 phylogeny, we divided Homilopsocidea into three independent infraorders: Archipsocetae,
9 Philotarsetae and Homilopsocidea. Except for a few cases, previously recognized families
10 were recovered as monophyletic. To establish a classification more congruent with the
11 phylogeny, we synonymized the families Bryopsocidae (with Zelandopsocinae of
12 Pseudocaeciliidae), Calopsocidae (with Pseudocaeciliidae), and Neurostigmatidae (with
13 Epipsocidae). Monophyly of Elipsocidae, Lachesillidae, and Mesopsocidae was not
14 supported, but the monophyly of these families could not be rejected statistically, so that
15 they are tentatively maintained as valid families. The molecular tree was compared with a
16 morphological phylogeny estimated previously. Sources of congruence and incongruence
17 exist and the utility of the morphological data for phylogenetic estimation is evaluated.

18
19 ADDITIONAL KEYWORDS: higher level classification - infraorder - Archipsocetae -
20 Philotarsetae - synonym - Bryopsocidae - Calopsocidae - Neurostigmatidae

21 INTRODUCTION

22 The insect suborder Psocomorpha is the largest within Psocodea (book lice, bark
23 lice and parasitic lice) with over 3600 species in 25 families (Lienhard & Smithers 2002).
24 The suborder was first established by Pearman (1936) who also recognized four
25 infraorders within it: Epipsocetae, Caecilietae (= present Caeciliusetae), Homilopsocidea
26 and Psocetae. This taxonomic arrangement has long been accepted with some minor
27 modifications (Roesler 1944; Badonnel 1951; Smithers 1996; Lienhard & Smithers 2002;
28 Li 2002: see Yoshizawa 2002 for review). However, until recently, no formal test of this
29 classification had been performed.

30 Phylogenetic analysis based on morphological data by Yoshizawa (2002) was the
31 first formal cladistic test of Pearman's system. The resulting trees were largely congruent
32 with the classification established by Pearman (1936), but the following modifications
33 were also proposed: two additional infraorders, each represented by a single family,
34 Archipsocetae for Archipsocidae and Hemipsocetae for Hemipsocidae, were proposed,
35 which were formerly classified under Homilopsocidea and Psocetae, respectively.
36 Yoshizawa (2002) also recognized four superfamilies within Homilopsocidea. In addition
37 to these suprafamilial rearrangements, results from the morphological analyses also cast
38 doubt on monophyly of the families Lachesillidae, Pseudocaeciliidae (Homilopsocidea),
39 Cladiopsocidae (Epipsocetae) (see also Casasola González 2006) and Caeciliusidae
40 (Caeciliusetae).

41 However, the results from the morphological phylogeny were far from decisive.
42 First, a large number of equally parsimonious trees (1108) resulted when the
43 morphological data were analyzed with an equal weighting scheme (Yoshizawa 2002).
44 Under the equally weighted analysis, the deepest relationships among infraorders and
45 homilopsocid families are almost completely unresolved, and highly resolved trees were
46 only obtained by applying successive weighting (Farris 1969; Carpenter 1988) or implied
47 weighting methods (Goloboff, 1993). Therefore, a test of the morphology-based
48 phylogeny is needed using molecular data to obtain a robust classification for
49 Psocomorpha and also to reevaluate utility and transformation of morphological
50 characters.

51 A number of prior molecular phylogenetic studies have included representatives of

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2
3 52 Psocomorpha. However, each of these studies either had limited taxon sampling or a
4
5 53 small number of genes analyzed. A molecular phylogeny for Psocomorpha was estimated
6
7 54 previously with limited taxon sampling and multiple gene markers (Johnson & Mockford
8
9 55 2003). Only 17 species from 12 of 25 families (Lienhard & Smithers 2002) were included.
10
11 56 A molecular phylogeny of Psocodea based on more extensive taxon sampling, including
12
13 57 wide range of psocomorphan taxa, was estimated by Johnson, Yoshizawa & Smith (2004),
14
15 58 but this analysis only used a single gene marker, 18S rDNA. A considerable number of
16
17 59 psocomorphan taxa were also analyzed by Yoshizawa & Johnson (2010) using four gene
18
19 60 markers. However, the emphasis of these prior studies (Johnson, Yoshizawa & Smith
20
21 61 2004; Yoshizawa & Johnson 2010) was on the origins of parasitic lice, and no
22
23 62 comparison has been made between the results from the molecular- and morphology-
24
25 63 based trees for the phylogeny of Psocomorpha.

26
27 64 In this study, we estimated the phylogeny of the suborder Psocomorpha using data
28
29 65 from four gene markers selected from nuclear and mitochondrial genomes, and both
30
31 66 protein coding and ribosomal RNA genes. The gene markers employed in the present
32
33 67 analyses are identical with those used in Yoshizawa & Johnson (2010), but taxon
34
35 68 coverage for Psocomorpha is greatly expanded: i.e., 77 genera and 100 species of
36
37 69 Psocomorpha covering all families recognized by Lienhard & Smithers (2002), except for
38
39 70 Ptiloneuridae. The analyses resulted in a highly resolved and well supported tree for the
40
41 71 suborder. Based on this tree, we propose a revised classification of Psocomorpha. In
42
43 72 addition, we also compared the trees estimated from the molecular and morphological
44
45 73 data and re-evaluate the phylogenetic utility and transformation series of the
46
47 74 morphological characters.

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49 75

46 76 MATERIAL AND METHODS

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48 77 Samples were selected from all extant families of Psocomorpha listed in Lienhard
49
50 78 & Smithers (2002), except for Ptiloneuridae. Although some new classification schemes
51
52 79 have been proposed subsequently (Li 2002; Yoshizawa 2002; Schmidt & New 2004;
53
54 80 Casasola González 2006; Yoshizawa, Mockford & Johnson 2014), the family group or
55
56 81 higher names listed in Lienhard & Smithers (2002) were adopted in the following unless
57
58 82 specified. A total of 24 families, 77 genera and 100 species were sampled for ingroup

1
2
3 83 taxa (Table 1). Outgroups were selected from suborders Trogiomorpha (root of the tree)
4
5 84 and Troctomorpha (sister of Psocomorpha) (Johnson, Yoshizawa & Smith 2004;
6
7 85 Yoshizawa, Lienhard & Johnson 2006). Samples were not included from Phthiraptera
8
9 86 (parasitic lice: subgroup of Troctomorpha) and its close relatives (Liposcelididae and
10
11 87 Pachytroctidae) because of the presence of long molecular branches and other unusual
12
13 88 molecular evolutionary processes in these taxa that may confound phylogenetic analysis
14
15 89 (Yoshizawa & Johnson 2003, 2010, 2013; Johnson, Yoshizawa & Smith 2004).

16 90 Partial sequences of the nuclear 18S rDNA and Histone3 and mitochondrial 16S
17
18 91 rDNA and COI genes were used for analyses. Methods for DNA extraction, PCR
19
20 92 amplification, sequencing and alignment followed Yoshizawa & Johnson (2010). The
21
22 93 aligned data set is available as a Supplementary Data of the journal's website or at
23
24 94 <http://insect3.agr.hokudai.ac.jp/psoco-web/data/psocomorpha/>.

25 95 Using the aligned data set, maximum-likelihood (ML) and Bayesian analyses were
26
27 96 conducted. The best fit model for the ML analysis was estimated using the hierarchical
28
29 97 likelihood ratio test (hLRT) as implemented in jModelTest 2.1.1 (Darriba et al. 2012).
30
31 98 The best model was selected based on a BioNJ tree. As a result, the GTR + Gamma +
32
33 99 Invariable site model was selected (detailed parameters were described in the
34
35 100 Supplementary Data matrix). ML tree searches were conducted using PAUP* 4b10
36
37 101 (Swofford 2002). NJ, MP, and Bayesian trees were used as starting trees and TBR branch
38
39 102 swapping was conducted. The most likely tree was found when Bayesian tree was
40
41 103 designated as the starting tree. Likelihood-based bootstrap support values were calculated
42
43 104 using PhyML 3.0 (Guindon et al. 2010) with 500 bootstrap replicates. NNI branch
44
45 105 swapping was performed for each replicate, with GTR + Gamma + Invariable sites model
46
47 106 (all parameters estimated from the data set).

48 107 We used MrBayes 3.2.1 (Ronquist et al. 2012) for Bayesian MCMC analyses. For
49
50 108 Bayesian analyses, data were subdivided into eight categories (18S, 16S, first, second and
51
52 109 third codon positions of Histone 3 and COI), and the substitution models for the analysis
53
54 110 were estimated separately for each data category using hLRT as implemented in
55
56 111 MrModeltest 2.3 (Nylander 2004). Detailed settings for Bayesian analyses are described
57
58 112 in the data matrix (Supplementary Data). We performed two runs each with four chains
59
60 113 for 2,000,000 generations and trees were sampled every 1,000 generations. The first 50%

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3 114 of the sampled trees were excluded for burn-in, and a 50% majority consensus tree was
4
5 115 computed to estimate Bayesian posterior probabilities. In addition to the bootstrap
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7 116 support and posterior probabilities, robustness of the tree was tested using an
8
9 117 approximately unbiased test (AU test: Shimodaira 2002), by contrasting the best ML tree
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11 118 with those estimated by constraining some alternative relationships (e.g., monophyly of
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13 119 Homilopsocidea: see below).

14 To examine the sources of congruence versus incongruence between the
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16 121 morphological and molecular trees and also to examine the phylogenetic utility of
17
18 122 morphological data, we re-analyzed the morphological data scored by Yoshizawa (2002).
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20 123 We reanalyzed only the genera sampled in the molecular data set, and other taxa included
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22 124 in Yoshizawa (2002) were omitted from the data set. In the original data set, Yoshizawa
23
24 125 (2002) coded the number and condition of the mesothoracic muscles as a single character
25
26 126 (Character 14). However, this character is now re-coded as two separate characters:
27
28 127 number of muscles (Character 14) and their conditions (Characters 69 and 70) to clarify
29
30 128 ancestral state reconstructions. See Yoshizawa (2002) for description of other
31
32 129 morphological characters selected for phylogenetic analyses. The final data set contained
33
34 130 39 taxa (34 for ingroup) and 70 characters. Phylogenetic analyses were conducted using
35
36 131 maximum parsimony in PAUP* 4b10 as described in Yoshizawa (2002). For evaluating
37
38 132 various morphological features, the morphological data set was categorized into 6
39
40 133 categories (head, thorax, wings, legs and male and female genitalia). The phylogenetic
41
42 134 congruence of each category was examined by comparing the homology indices
43
44 135 (consistency and retention indices) derived from the MP morphology and ML molecular
45
46 136 enforced trees using MacClade 4.08 (Maddison & Maddison 2000).

47 137

48 138 **RESULTS**

49 139 *Molecular Phylogenetics*

50 Both the ML and Bayesian analyses resulted in nearly identical trees, and the ML
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52 141 trees are presented in Figs 1 and 2. Monophyly of Psocomorpha was consistently and
53
54 142 robustly supported by all analyses. The family Archipsocidae is sister to the remainder of
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56 143 Psocomorpha with 100% bootstrap support (bs) and Bayesian posterior probability (pp).

57 144 Excluding Archipsocidae, the remainder of the psocomorphan families clustered

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3 145 into two clades: one composed of Caeciliusetae and a part of Homilopsocidea (Homilo1:
4 146 Lachesillidae, Peripsocidae, Ectopsocidae, Elipsocidae and Mesopsocidae) (100% pp and
5 147 98% bs) and the other composed of Epipsocetae, Psocetae and the remaining
6
7
8 148 Homilopsocidea (Homilo2: Philotarsidae, Trichopsocidae, Pseudocaeciliidae and
9 149 Calopsocidae) (91% pp and 83% bs). Monophyly of each of the infraorders Caeciliusetae,
10 150 Epipsocetae, and Psocetae (including Hemipsocidae) was all strongly supported (all
11 151 100% pp and bs). Monophyly of Homilopsocidea was not supported by ML and Bayesian
12 152 analyses. Monophyly of Homilopsocidea could also be rejected by the AU test ($P < 0.001$
13 153 using *Lachesilla*-excluded data set: see below), even in the case where the separate
14 154 placement of Archipsocidae from the rest of Homilopsocidea was allowed.

15 155 When all the taxa were included in the analyses (Fig. 1), the clade composed of
16 156 Peripsocidae and *Lachesilla* of Lachesillidae (moderately to weakly supported: 95% pp
17 157 and 64% bs) was placed to the sister of Caeciliusetae. However, placement of the clade
18 158 was highly unstable (53% pp and $< 50\%$ bs). Detailed examination of the trees resulting
19 159 from Bayesian and bootstrap analyses revealed that *Lachesilla* is the major source of this
20 160 instability. Therefore, we also prepared a data set excluding *Lachesilla*, which was used
21 161 for subsequent analyses. In analyses excluding *Lachesilla*, monophyly of Homilo1
22 162 including Peripsocidae and the rest of Lachesillidae (*Anomopsocus* and *Eolachesilla*) was
23 163 supported strongly (99% pp and 72% bs) (Fig. 2). Regardless of the inclusion/exclusion
24 164 of *Lachesilla*, monophyly of the clade composed of Caeciliusetae and Homilo1 was
25 165 strongly supported (100% pp and 98-99% bs). Relationships within Caeciliusetae have
26 166 been discussed before (Yoshizawa, Mockford & Johnson 2014), and the present results
27 167 were in complete agreement with the previous study. Relationships within Homilo1 were
28 168 only poorly resolved, but monophyly of Elipsocidae and Mesopsocidae was not
29 169 recovered. However, the monophyly of these two families could not be rejected
30 170 statistically ($P = 0.327$ and 0.461 from AU test, respectively). As already mentioned,
31 171 monophyly of Lachesillidae was not recovered but could not be rejected statistically ($P =$
32 172 0.194 from AU test of all included data set).

33 173 Monophyly of a clade comprising Psocetae + Epipsocetae + Homilo2 was
34 174 supported by both data sets, but support values were improved by excluding *Lachesilla*
35 175 (91% → 94% pp and 83% → 87% bs). Monophyly of Homilo2 was also strongly and
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3 176 consistently supported. Within the clade, Philotarsidae branched off first, and monophyly
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5 177 of a group comprising the remaining taxa was strongly supported (99% pp and 74-77%
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7 178 bs). Trichopsocidae branched off next, but this branching order was only poorly
8
9 179 supported (<50% pp and bs). The rest of the families in this group are divided into two
10
11 180 clades. The first was Calopsocidae + Pseudocaeciliinae of Pseudocaeciliidae, which was
12
13 181 very strongly supported (100% pp and bs), and the second was composed of
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15 182 Bryopsocidae and Zelandopsocinae of Pseudocaeciliidae, which was moderately to
16
17 183 strongly supported (91-97% pp and 68-71% bs). A sister relationship between
18
19 184 Bryopsocidae and *Zelandopsocus* was very strongly supported (100% pp and bs).

20 185 A sister group relationship between Epipsocetae and Psocetae received only
21
22 186 moderate support (83-94% pp and 62% bs). Relationships within Epipsocetae were only
23
24 187 poorly resolved, but Neurostigmatidae was embedded within Epipsocidae (100% pp and
25
26 188 96-98% bs) and placed sister to *Mesepipsocus* (100% pp and bs). Within Psocetae, a
27
28 189 sister group relationship between Psilopsocidae and Hemipsocidae was strongly
29
30 190 supported (100% pp and 99% bs). Myopsocidae and Psocidae composed a clade, but their
31
32 191 relationship was only moderately supported (88-90% pp and 68-70% bs).

33 193 *Comparison with Morphology*

34
35 194 Maximum parsimony analysis of the morphological data set produced 154 equal
36
37 195 length trees, with $L = 175$, $CI = 0.49$ and $RI = 0.81$ (Table 2). Application of successive
38
39 196 (6 trees) and implied weighting (12 trees under $K = 2$ and 10) greatly reduced the number
40
41 197 of most parsimonious trees. These trees are all included in the original 154 trees, and the
42
43 198 strict consensus of the trees estimated from each analysis are all identical (Fig. 3 above).
44
45 199 Female genitalic characters ($CI = 0.8$, $RI = 0.94$) and thoracic characters ($CI = 0.67$, $RI =$
46
47 200 0.92) were more congruent with the MP tree compared to the average homology index
48
49 201 values of the total morphological data set ($CI = 0.49$, $RI = 0.81$). In contrast, characters
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51 202 from the wings ($CI = 0.44$, $RI = 0.73$), legs ($CI = 0.20$, $RI = 0.66$), and male genitalia (CI
52
53 203 $= 0.43$, $RI = 0.70$) were less congruent with the morphological MP tree.

54 204 When the topology obtained from the ML analysis of the molecular data was
55
56 205 constrained (Fig. 3 bottom), tree scores from the morphological data set became $L = 212$,
57
58 206 $CI = 0.41$, and $RI = 0.73$ (Table 2). Comparisons of consistency and retention indices of
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3 207 morphological data reconstructed on MP and ML trees showed increased amount of
4
5 208 homoplasy for almost all data categories (Table 2). In particular, more homoplasy was
6
7 209 detected in female genitalic characters on the molecular ML tree (range of reduction of
8
9 210 homology index values was 0.08 on average whereas 0.24-0.35 in female genitalia). In
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11 211 contrast, thoracic character showed identical homology index values on both the
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13 212 molecular and morphological trees.
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15 213

16 214 **DISCUSSION**

17 215 RELATIONSHIPS AND VALIDITY OF INFRAORDERS

18
19 216 DNA sequences from four gene regions produced a generally well-resolved and
20
21 217 supported tree for the bark louse suborder, Psocomorpha. The sister relationship between
22
23 218 Archipsocidae and the rest of Psocomorpha is strongly supported (100% bs and pp).
24
25 219 Archipsocidae had long been placed in Homilopsocidea (from Pearman 1936). However,
26
27 220 more recent cladistic analyses of morphological data have already identified a sister
28
29 221 relationship between Archipsocidae and the remainder of Homilopsocidea (Yoshizawa
30
31 222 2002). Previous molecular analyses with smaller gene and taxon sampling also supported
32
33 223 the basal divergence of Archipsocidae (Johnson & Mockford 2003; Johnson, Yoshizawa
34
35 224 & Smith 2004; Yoshizawa & Johnson 2010). Therefore, an independent infraordinal
36
37 225 status for the family as proposed by Yoshizawa (2002), i.e., Archipsocetae, can be
38
39 226 strongly recommended.

40
41 227 In contrast, an independent infraordinal status for Hemipsocidae, as suggested by
42
43 228 morphological analysis (Yoshizawa 2002), is not supported by molecular data, and the
44
45 229 family falls within Psocetae. Support values for the monophyly of Psocetae including
46
47 230 Hemipsocidae and close relationship between Hemipsocidae and Psilopsocidae are both
48
49 231 very high (99-100% bs; 100% pp). Therefore, the placement of Hemipsocidae within
50
51 232 Psocetae is robust. Placement of Hemipsocidae within Psocetae has also been previously
52
53 233 recovered in other molecular studies (Johnson & Mockford 2003; Johnson, Yoshizawa &
54
55 234 Smith 2004; Yoshizawa & Johnson 2010); thus this placement is robust to the taxon and
56
57 235 gene sampling. Using morphological characters, the placement of Hemipsocidae within
58
59 236 Psocetae has also previously been suggested, based on a shared distal process of the male
60
237 paraproct, a potential synapomorphy (Mockford 1976, 1993). This relationship was also

1
2
3 238 recovered in the parsimonious trees estimated from a reanalysis of morphological data
4
5 239 with successive weighting (Fig. 3). In contrast, the analyses of Yoshizawa (2002)
6
7 240 suggested that Hemipsocidae is one of the earliest diverging lineages within
8
9 241 Psocomorpha, and a condition of the wing base (separated 2Ax and proximal median
10
11 242 plate) was suggested to be the plesiomorphic condition excluding this family and
12
13 243 Archipsocidae from the rest of Psocomorpha. Given the strong molecular support and
14
15 244 presence of morphological evidence for the placement of Hemipsocidae within Psocetae,
16
17 245 the condition of the wing base structures should be regarded as secondary reversal
18
19 246 occurring in the common ancestor of Hemipsocidae.

20
21 247 Monophyly of all the infraorders accepted by Lienhard & Smithers (2002), except
22
23 248 for Homilopsocidea, was supported strongly (99-100% bs and 100% pp). Monophyly of
24
25 249 Homilopsocidea was not supported by analyses of the molecular data even if
26
27 250 Archipsocetae is excluded from the infraorder. This result is also congruent with the
28
29 251 previous morphology-based phylogeny, because monophyly of Caeciliusetae,
30
31 252 Epipsocetae, and Psocetae (except for the placement of Hemipsocidae mentioned above)
32
33 253 was all consistently supported based on morphological data, whereas monophyly of
34
35 254 Homilopsocidea was only recovered after the application of successive weighting
36
37 255 (Yoshizawa 2002). Apart from the separate placement of Archipsocidae, analysis of the
38
39 256 molecular data divided the infraorder into two major groups. Monophyly of
40
41 257 Homilopsocidea (excluding Archipsocidae) was also rejected by the AU test ($P < 0.001$),
42
43 258 justifying naming of an independent infraorder for one of two clades of Homilopsocidea.

44
45 259 The first group of Homilopsocidea (Homilo1) is composed Peripsocidae,
46
47 260 Ectopsocidae, Elipsocidae, Mesopsocidae, and Lachesillidae, but relationships among
48
49 261 these families are highly unstable depending on taxon sampling. When the genus
50
51 262 *Lachesilla* was included in the analysis, the first group (Homilo1) was divided into two
52
53 263 groups that are not sister taxa: one composed of the family Peripsocidae and the genus
54
55 264 *Lachesilla* of the Lachesillidae (Lachesillinae) and the other containing Ectopsocidae,
56
57 265 Elipsocidae, Mesopsocidae, and a part of Lachesillidae (*Anomopsocus* and *Eolachesilla*:
58
59 266 *Eolachesillinae*). However, as mentioned above, placement of the first clade, especially
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267 the placement of *Lachesilla*, is highly unstable, as also evident by the long branch leading
268 to the genus compared to the other homilopsocid taxa. After removing *Lachesilla* from

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2
3 269 the analysis, Peripsocidae was placed sister to the remainder of Homilo1, and this
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5 270 relationship received high support values (72% bs and 99% pp). Exclusion of *Lachesilla*
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7 271 from the analyses also stabilizes some other branches (Figs 1 and 2). Therefore, we
8
9 272 consider the separation of *Lachesilla* + Peripsocidae from the remainder of Homilo1 may
10
11 273 be an artifact caused by unusual substitution properties and long branches for *Lachesilla*.
12
13 274 Monophyly of Homilo1 excluding *Lachesilla* is also supported by two morphological
14
15 275 character states, but they are either highly homoplasious (Character 55: single-lobed egg
16
17 276 guide) or also observed in the second homilopsocid clade (Character 62: dorsally
18
19 277 swelling dorsal valve of gonapophyses). Regardless of the inclusion or exclusion of
20
21 278 *Lachesilla*, members of Homilo1 are placed in a clade together with Caeciliusetae, and
22
23 279 this relationship received strong support (98-99% bs and 100% pp). However, no
24
25 280 unambiguous morphological apomorphies supporting this relationship occurs among the
26
27 281 characters coded by Yoshizawa (2002).

28 282 The second group of Homilopsocidea (Homilo2) is composed of Philotarsidae,
29
30 283 Trichopsocidae, Bryopsocidae, Calopsocidae, and Pseudocaeciliidae. The monophyly of
31
32 284 this group is strongly supported in all analyses (99% bs and 100% pp). Some
33
34 285 synapomorphies can be identified in morphological characters, but all are homoplasious:
35
36 286 i.e., gonapophyses and egg guide tightly associated, together forming ovipositor
37
38 287 (Character 58), and dorsal region of dorsal valve of gonapophyses swollen (Character 62)
39
40 288 and sclerotized (Character 64). This clade (Homilo2) is sister to a clade comprising
41
42 289 Epipsocetae + Psocetae, and this relationship is modestly well supported (83% bs and
43
44 290 91% pp), although no unambiguous morphological apomorphy supporting this
45
46 291 relationship occurs among the characters coded by Yoshizawa (2002). One possible
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48 292 character supporting this clade is the position of the anterior tentorial pit separated from
49
50 293 the ventral margin of cranium (Character 5). However, this character state is variable
51
52 294 within Psocetae, and the plesiomorphic state within this group cannot be unambiguously
53
54 295 reconstructed.

55 296 Most of the recent classification schemes have placed Epipsocetae as the most basal
56
57 297 group within Psocomorpha (e.g., Smithers 1972, 1996; Mockford 1993; Lienhard 1998;
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59 298 Li 2002; Lienhard & Smithers 2002; New & Lienhard 2007). One reason for this is
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299 because, among Psocomorpha, the second anal vein is only observed in Epipsocetae,

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3 300 which was suggested to be the plesiomorphic condition within the suborder. Alternatively,
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5 301 Yoshizawa (2002) placed this infraorder as the sister of Caeciliusetae, and concluded that
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7 302 the presence of A2 vein in this infraorder represents a secondary reversal. The
8
9 303 secondarily reversed condition of the A2 vein is not observed in earliest diverging family
10
11 304 of Epipsocetae: Dolabellopsocidae (Yoshizawa 2002; Casasola González 2006). The
12
13 305 present results, on the other hand, placed Epipsocetae as sister to Psocetae. Although the
14
15 306 support values for this relationship are not high (62% bs and 94% pp when *Lachesilla* is
16
17 307 excluded from the analyses), a sister relationship of Epipsocetae with the remainder of
18
19 308 Psocomorpha can be rejected by the AU test ($P < 0.001$). Therefore, the secondary reversal
20
21 309 in the condition of the A2 vein is evident also suggested by the molecular phylogeny. The
22
23 310 reanalysis of the morphological data set suggested that there are a couple of potential
24
25 311 synapomorphies between Epipsocetae and Psocetae: narrow precoxal bridge (Character
26
27 312 15) and the two muscles inserted to the trochantin (Character 69) (Yoshizawa 2002,
28
29 313 2005).

314

315 VALIDITY OF SUPERFAMILIES

316 Several superfamilies have been recognized within Caeciliusetae (Lienhard &
317 Smithers 2002) and Homilopsocidea (Yoshizawa 2002). Within Caeciliusetae, two
318 superfamilies have been recognized: Asiopsocoidea and Caeciliusoidea. The present
319 analyses rejected the monophyly of Caeciliusoidea (Caeciliusidae, Amphipsocidae,
320 Stenopsocidae and Dasydemeridae), and Asiopsocidae (only the representative of
321 Asiopsocoidea) was placed sister to Paracaeciliusinae, supporting the results presented by
322 Yoshizawa, Mockford & Johnson (2014).

323 Yoshizawa (2002) recognized four superfamilies within Homilopsocidea based on
324 the phylogenetic analyses of morphological data. However, the validity of all these
325 superfamilies can be rejected by the molecular data. Monophyly of Pseudocaecilioidea
326 (composed of the Trichopsocidae, Pseudocaeciliidae, and Calopsocidae) was nearly
327 supported, but the family Bryopsocidae was also imbedded within this clade. See below
328 for further discussion regarding the monophyly of Pseudocaeciliidae. The other three
329 superfamilies recognized on the basis of morphological data but rejected by the molecular
330 data are Lachesilloidea (Ectopsocidae + Lachesillidae), Peripsocoidea (Bryopsocidae +

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2
3 331 Peripsocidae + Philotarsidae + Mesopsocidae), and Elipsocoidea (Elipsocidae). Validity
4
5 332 of the monotypic Elipsocoidea is also brought into question (see below).
6

7 333

8
9 334 RELATIONSHIPS AND VALIDITY OF FAMILIES

10 335 Monophyly was confirmed for most of the psocomorphan families recognized
11
12 336 previously (Lienhard & Smithers 2002). Although monophyly of Cladiopsocidae was
13
14 337 questioned on the basis of morphology (Yoshizawa 2002; Casasola González 2006), the
15
16 338 family was recovered to be monophyletic with moderate to high support values (87-89%
17
18 339 pp and 84% bs). However, the family Ptiloneuridae was not sampled here, which is
19
20 340 potentially embedded within Cladiopsocidae (Yoshizawa 2002; Casasola González 2006).
21
22 341 This family should be analyzed before making firm conclusions regarding the monophyly
23
24 342 of Cladiopsocidae. The following families were not recovered as monophyletic:
25
26 343 Caeciliusidae, Lachesillidae, Elipsocidae, Mesopsocidae, Pseudocaeciliidae, and
27
28 344 Epipsocidae. Monophyly of Caeciliusidae, Lachesillidae, and Pseudocaeciliidae has also
29
30 345 been questioned by Yoshizawa (2002), and monophyly of Epipsocidae was questioned by
31
32 346 Casasola González (2006). Monophyly of Caeciliusidae has already been discussed based
33
34 347 on a recent molecular phylogeny (Yoshizawa, Mockford & Johnson 2014). Therefore, the
35
36 348 following discussion focuses on the status of the other families.

37 349 Lachesillidae is divided into two different groups when all taxa were included in the
38
39 350 analyses: *Lachesilla* versus *Anomopsocus* + *Eolachesilla*. These clades correspond to the
40
41 351 subfamilies Lachesillinae and Eolachesillinae, respectively (Mockford & Sullivan 1986;
42
43 352 Lienhard & Smithers 2002). In the morphological phylogeny, monophyly of *Lachesilla* +
44
45 353 *Nanolachesilla* (the latter belong to Eolachesillinae) was supported, but *Eolachesilla* did
46
47 354 not compose a monophyletic group together with them (Yoshizawa 2002). The placement
48
49 355 of *Lachesilla* was highly unstable based on the analysis of the molecular data and its
50
51 356 close affinity with *Anomopsocus* + *Eolachesilla* could not be rejected statistically (AU
52
53 357 test, $P = 0.182$). Therefore, we tentatively retain the family "Lachesillidae", but
54
55 358 highlighting the possibility of its paraphyly.

56 359 Monophyly of Elipsocidae was not supported by the present analyses, and this
57
58 360 family is divided into three clades: *Propsocus* (Propsocinae), *Kilauella* (Elipsocinae), and
59
60 361 *Nepiomorpha* (Nepiomorphinae) + *Reuterella* (Pseudopsocinae) + *Cuneopalpus* +

1
2
3 362 *Elipsocus* (both Elipsocinae). This division of the family does not even reflect the current
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5 363 subfamilial classification system (Lienhard & Smithers 2002). Elipsocidae was recovered
6
7 364 to be monophyletic based on analysis of morphological data (Yoshizawa 2002), but, in
8
9 365 that study, taxonomic sampling was restricted to two genera both representing the
10
11 366 subfamily Elipsocinae. The phylogeny of Elipsocidae was extensively studied by Schmidt
12
13 367 & New (2004), in which monophyly of Elipsocidae was accepted. In their revised system,
14
15 368 the family was subdivided into two subfamilies and, according to their classification
16
17 369 system, all genera of the latter clade are classified into Elipsocinae, and *Propsocus* and
18
19 370 *Kilauella* are in Propsocinae. Therefore, the classification system proposed by Schmidt &
20
21 371 New (2004) is more congruent with the results from the molecular phylogeny, except for
22
23 372 the non-monophyly of the family. However, in the molecular phylogeny, the placement
24
25 373 of the members of this family is far from stable, and monophyly of Elipsocidae could not
26
27 374 be rejected statistically (AU test, $P = 0.327$). Therefore, we tentatively accept the family
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29 375 Elipsocidae.

30
31 376 Monophyly of Mesopsocidae was strongly supported based on morphological data
32
33 377 (Badonnel & Lienhard 1988; Yoshizawa & Lienhard 1997; Yoshizawa 2002) but was not
34
35 378 supported by the present molecular analyses. The morphological phylogeny of
36
37 379 Yoshizawa & Lienhard (1997) and Yoshizawa (2002) sampled *Idatenopsocus* and
38
39 380 *Mesopsocus*, taxa analyzed in the present study, and identified several synapomorphies
40
41 381 between them. In the present analyses, *Idatenopsocus* was placed sister to *Kilauella*, but
42
43 382 this relationship received marginal support values only (91% pp and 72% bs). Monophyly
44
45 383 of Mesopsocidae could not be rejected statistically using the AU test ($P = 0.461$), so that
46
47 384 this family should be retained until more taxa and genes are analyzed.

48
49 385 Pseudocaeciliidae was shown to be paraphyletic for two reasons: Bryopsocidae was
50
51 386 placed within the subfamily Zelandopsocinae; and Calopsocidae was placed within the
52
53 387 subfamily Pseudocaeciliinae. Placement of Calopsocidae within Pseudocaeciliidae has
54
55 388 already been strongly suggested using morphological data (Smithers 1967; Thornton &
56
57 389 Smithers 1984; Yoshizawa 2002). Therefore, the present analyses corroborate this
58
59 390 suggestion. Given the strong morphological and molecular support, Calopsocidae should
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391 be synonymized with Pseudocaeciliidae (see below). The placement of Bryopsocidae as
392 close to Pseudocaeciliidae, concordant to the present result, has also been proposed based

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2
3 393 on morphological data (Mockford, 1984). Furthermore, *Bryopsocus townsendi*, the type
4
5 394 species of the genus, was originally described under the genus *Austropsocus* (Smithers
6
7 395 1969; Thorngon, Wong & Smithers 1977), which closely matches to the present result. In
8
9 396 contrast, the phylogeny based on morphological data places Bryopsocidae distant to
10
11 397 Pseudocaeciliidae (Fig. 3) (Yoshizawa 2002). However, in the previous morphological
12
13 398 analyses, no taxa were sampled from Zelandopsocinae, and morphological information of
14
15 399 Bryopsocidae was only scored based on published literatures (Thornton, Wong &
16
17 400 Smithers 1977; Mockford 1984). Support values for the placement of Bryopsocidae as
18
19 401 sister to *Zelandopsocus* based on the molecular data are high (100% pp and bs for
20
21 402 Bryopsocidae + *Zelandopsocus* and 97% pp and 67% bs for Bryopsocidae within
22
23 403 Zelandopsocinae). Monophyly of Pseudocaeciliidae + Calopsocidae, excluding
24
25 404 Bryopsocidae, was also rejected using the AU test ($P = 0.006$), providing strong support
26
27 405 for the placement of Bryopsocidae within the Pseudocaeciliidae + Calopsocidae clade.

28 406 Non-monophyly of Epipsocidae and the placement of Neurostigmatidae within the
29
30 407 family have already been suggested by Casasola González (2006) and accepted by
31
32 408 Lienhard (2007). However, because the placement of *Neurostigma* (monotypic genus of
33
34 409 Neurostigmatidae) was not stable based on morphological data, no official nomenclatural
35
36 410 change was proposed to date (Casasola González 2006). This arrangement received
37
38 411 strong support from the present molecular data, and *Neurostigma* is placed to the sister of
39
40 412 *Mesepipsocus* with strong support values (100% pp and bs).

41 414 TAXONOMIC SUMMARY

42 415 In conclusion, based on the molecular phylogenetic results, we propose several
43
44 416 novel taxonomic arrangements (Table 3). The validity of Psocomorpha receives strong
45
46 417 support from both molecular and morphological data (Yoshizawa 2002). Six infraorders
47
48 418 are proposed within Psocomorpha, of which five are proposed previously (Pearman 1936;
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50 419 Yoshizawa 2002), and one (Philotarsetae) is newly proposed here. The infraorder
51
52 420 Hemipsocetae proposed by Yoshizawa (2002) is unjustified. Superfamilies proposed
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54 421 within Caeciliusetae (Mockford & García Aldrete 1976) and Homilopsocidea (Yoshizawa
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56 422 2002) are all rejected (see also Yoshizawa, Mockford & Johnson 2014). At the family
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58 423 level, monophyly of Elipsocidae, Lachesillidae, and Mesopsocidae are questionable, but

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3 424 additional gene and taxon sampling is needed to draw more finalized conclusions about
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5 425 the status of these families. The family Bryopsocidae (Mockford 1984) is treated as a new
6
7 426 junior synonym of Zelandopsocinae within Pseudocaeciliidae, and the family
8
9 427 Calopsocidae is newly synonymized with Pseudocaeciliidae. The family
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11 428 Neurostigmatidae is treated as a junior synonym of Epipsocidae, as proposed by Casasola
12
13 429 González (2006).

14 430

15 431 REEVALUATION OF MORPHOLOGICAL CHARACTERS

16
17 432 Results from the morphological phylogeny presented in Yoshizawa (2002) were
18
19 433 largely congruent with the ML tree estimated from the molecular data in the current study.
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21 434 This clearly shows that the morphological data contains a considerable amount of
22
23 435 phylogenetic signal congruent with the molecular information. However, some significant
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25 436 incongruence is also identified between the morphological and molecular phylogenies.
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27 437 Comparisons of consistency and retention indices of the morphological data
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29 438 reconstructed on the molecular and morphological trees enable us to identify the source
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31 439 of congruence and incongruence between two data sets and to reevaluate the importance
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33 440 of the morphological data for phylogenetic reconstruction of this group.

34 441 Comparisons of the consistency and retention indices of each morphological
35
36 442 category on the molecular MP trees show that the thoracic and female genital characters
37
38 443 are more congruent with these tree topologies; whereas those from the wings, legs, and
39
40 444 male genitalia are less congruent with the MP molecular tree (Table 2). When
41
42 445 morphological characters were reconstructed over the constrained ML tree, consistency
43
44 446 and retention indices decreased for most morphological categories, but the degree of
45
46 447 decrease is largest for female genital characters (0.35 for CI, whereas 0-0.07 for other
47
48 448 categories; 0.24 for RI, in contrast to 0-0.10 for other categories). This clearly shows that
49
50 449 the characters coded from the female genitalia are the main source of the conflict between
51
52 450 the morphological and molecular trees. For example, monophyly of Homilopsocidea
53
54 451 excluding Archipsocidae was supported by the morphological phylogeny, and the
55
56 452 characters supporting this clade were both selected from female genitalia (Yoshizawa
57
58 453 2002: see above). Monophyly of Homilopsocidea was strongly rejected by the molecular
59
60 454 data, which is one of the most substantial differences between the morphological and

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2
3 455 molecular phylogeny.
4

5 456 Characters from the thorax were also more congruent with molecular phylogeny, as
6
7 457 was the case for female genital characters. However, in contrast to the female genital
8
9 458 characters, no decrease of consistency and retention indices was detected when the
10
11 459 characters were reconstructed on the constrained ML tree. As discussed above, the
12
13 460 molecular and morphological phylogenies were almost completely concordant
14
15 461 concerning the major clades of Psocomorpha, and thoracic characters contributed mostly
16
17 462 to the resolution of the deep level phylogeny. Genital characters are known to evolve very
18
19 463 rapidly, frequently utilized for delimitating closely related species (Song & Bucheli 2010,
20
21 464 but they also argued that male genitalia are potentially useful in resolving a variety of
22
23 465 levels in a phylogeny), whereas useful signal for deeper phylogenetic scales have been
24
25 466 detected from more slowly evolving thoracic characters for many insect groups (e.g.,
26
27 467 Friedrich & Beutel 2010a b). The present results are also congruent with these previous
28
29 468 suggestions. In contrast, the thoracic characters do not contain any signal in resolving
30
31 469 shallower clades, and inclusion of both rapidly and slowly evolving characters are
32
33 470 important in obtaining a fully resolved phylogeny. To avoid the negative effects from the
34
35 471 rapidly evolving morphological characters, information as presented in Table 2 may be
36
37 472 useful for establishing an empirical scheme of character weighting.

38
39 473 Except for the basal split of Archipsocetae and sister relationship between
40
41 474 Epipsocetae + Psocetae, no unambiguous morphological apomorphies are identified for
42
43 475 the relationships among infraorders in the constrained ML tree (Fig. 3). Further
44
45 476 morphological investigation of Psocomorpha is required to test or verify the molecular
46
47 477 phylogeny presented here and to provide new apomorphies for the major groups we
48
49 478 identified.

50 479

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5 589 **Figure captions**6
7 590 **Figure 1.** Maximum likelihood tree estimated from the data set with all taxa included.8
9 591 Branch lengths are proportional to ML estimated branch length. Numbers
10 592 associated with the branches are Bayesian posterior probabilities (above) and ML
11 593 bootstrap support values (below). See text for dotted circle.12
13 59414
15 595 **Figure 2.** Maximum likelihood tree estimated from the data set excluding *Lachesilla*.16
17 596 Branch lengths are proportional to ML estimated branch length. Numbers
18 597 associated with the branches are Bayesian posterior probabilities (above) and ML
19 598 bootstrap support values (below). See text for dotted circle.20
21 59922
23 600 **Figure 3.** Most parsimonious reconstruction of morphological characters on the MP tree24
25 601 (above: strict consensus of trees obtained by successive and implied weighting
26 602 schemes) and ML topology (bottom). Black and gray bars on branches indicate
27 603 non-homoplasious and homoplasious character states supporting the branch,
28 604 respectively. Numbers associated with character bar indicate character number and
29 605 its state (see Online Supplement). Characters supporting interfamilial relationships
30 606 only are indicated, but lengths for intrafamilial branches are also proportional to the
31 607 number of characters supporting the branch.32
33 60834
35 609 **Table 1.** Taxa examined in the study. Families and higher level taxon names of36
37 610 Psocomorpha and Troctomorpha followed Lienhard & Smithers (2002). Infraorders
38 611 for Troctomorpha followed Yoshizawa, Lienhard and Johnson (2006).39
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613 **Table 2.** Comparisons of homology indices calculated on MP trees and ML topology.

614 Numbers of characters included in each morphological category are follow: head 11,
 615 thorax 6, wings 22, legs 4, male (M.) genitalia 8, and female (F.) genitalia 17.

616

| | ML constrained | MP trees | Δ ML–MP |
|------------------------------|----------------|----------|----------------|
| 617 <u>Tree Length</u> | 212 | 175 | 37 |
| 619 <u>Consistency Index</u> | | | |
| 620 Total | 0.41 | 0.49 | -0.08 |
| 621 Head | 0.41 | 0.48 | -0.07 |
| 622 Thorax | 0.67 | 0.67 | 0.00 |
| 623 Wings | 0.40 | 0.44 | -0.04 |
| 624 Legs | 0.18 | 0.20 | -0.02 |
| 625 M. genitalia | 0.36 | 0.43 | -0.07 |
| 626 F. genitalia | 0.45 | 0.80 | -0.35 |
| 628 <u>Retention Index</u> | | | |
| 629 Total | 0.73 | 0.81 | -0.08 |
| 630 Head | 0.80 | 0.85 | -0.05 |
| 631 Thorax | 0.92 | 0.92 | 0.00 |
| 632 Wings | 0.69 | 0.73 | -0.04 |
| 633 Legs | 0.62 | 0.66 | -0.04 |
| 634 M. genitalia | 0.60 | 0.70 | -0.10 |
| 635 F. genitalia | 0.70 | 0.94 | -0.24 |

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3 637 **Table 3.** Higher level classification of Psocomorpha based on this study. Families
4 638 marked with "" indicate their monophyly was not supported, but could also not be
5 639 rejected statistically.
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8 641 ARCHIPSOCETAE

9 642 Archipsocidae

10 643 CAECILIUSETAE (see Yoshizawa, Mockford & Johnson 2014 for detail)

11 644 Amphipsocidae

12 645 Stenopsocidae

13 646 Dasydemellidae

14 647 Asiopsocidae

15 648 Paracaeciliidae

16 649 Caeciliusidae

17 650 HOMILOPSOCIDEA

18 651 Peripsocidae

19 652 Ectopsocidae

20 653 "Elipsocidae"

21 654 "Lachesillidae"

22 655 "Mesopsocidae"

23 656 PHILOTARSETAE

24 657 Philotarsidae

25 658 Trichopsocidae

26 659 Pseudocaeciliidae (including Calopsocidae and Bryopsocidae as new synonym
27 660 of Pseudocaeciliidae and Zelandpsocinae, respectively)

28 661 EIPSOCETAE

29 662 Dolabellopsocidae

30 663 Cladiopsocidae

31 664 Ptiloneuridae

32 665 Epipsocidae (including Neurostigmatidae as a new synonym)

33 666 PSOCETAE

34 667 Psilopsocidae

35 668 Hemipsocidae

36 669 Myopsocidae

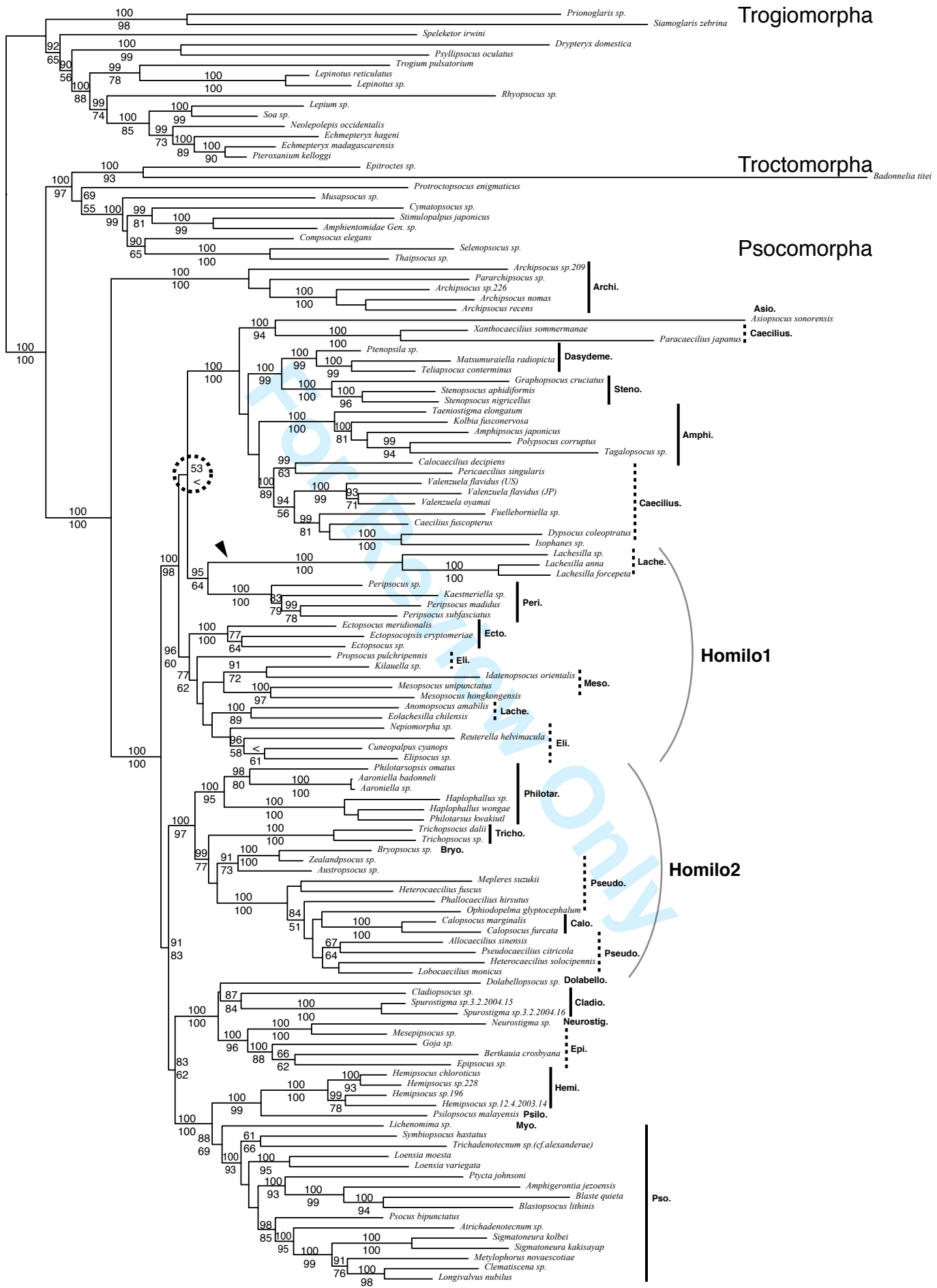
37 670 Psocidae
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| Suborder | Infraorder | Family | Genus | Species | Locality | Extract Code | 18S | 16S | COI | |
|--------------|------------------|-------------------|-------------------------|------------------------|---------------|---------------------|----------|-----------|----------|----------|
| Trogiomorpha | Prionoglaridetae | Prionoglaridae | <i>Prionoglaris</i> | <i>sp. 1</i> | Greece | KY249 | AY630456 | DQ104773 | DQ104745 | - |
| Trogiomorpha | Prionoglaridetae | Prionoglaridae | <i>Siamoglaris</i> | <i>zebrina</i> | Thailand | KY255 | DQ104798 | - | DQ104746 | AB918973 |
| Trogiomorpha | Prionoglaridetae | Prionoglaridae | <i>Speleketor</i> | <i>irwini</i> | USA | KY308 | DQ104799 | DQ104774 | DQ104747 | - |
| Trogiomorpha | Psylliposocetae | Psylliposocidae | <i>Dorypteryx</i> | <i>domestica</i> | Czech Rep. | KY97, KY253 | AY630454 | DQ104777 | DQ104749 | - |
| Trogiomorpha | Psylliposocetae | Psylliposocidae | <i>Psylliposoc</i> | <i>oculatus</i> | Mexico | Pscou.2.4.2002.12 | AY630455 | DQ104776 | DQ104748 | GU569242 |
| Trogiomorpha | Atropetae | Psocillidae | <i>Rhoposocus</i> | <i>sp.</i> | USA | KY297 | DQ104801 | DQ104778 | DQ104750 | - |
| Trogiomorpha | Atropetae | Trogiidae | <i>Lepinotus</i> | <i>reticulatus</i> | UK | Leret.11.17.2003.5 | AY630452 | - | DQ104756 | AB918974 |
| Trogiomorpha | Atropetae | Trogiidae | <i>Lepinotus</i> | <i>sp.</i> | USA | Lesp.11.2.2001.6 | AY630451 | DQ104783/ | DQ104755 | - |
| Trogiomorpha | Atropetae | Trogiidae | <i>Trogium</i> | <i>pulsatorium</i> | UK | Tgpul.11.17.2003.4 | AY630453 | DQ104786 | DQ104759 | GU569243 |
| Trogiomorpha | Atropetae | Lepidosopocidae | <i>Echmepteryx</i> | <i>hageni</i> | USA | Echag.1.16.2001.1 | AY630448 | DQ104782 | DQ104754 | GU569245 |
| Trogiomorpha | Atropetae | Lepidosopocidae | <i>Echmepteryx</i> | <i>madagascarensis</i> | Japan | KY61, KY246 | AY630447 | DQ104781 | DQ104753 | AB918975 |
| Trogiomorpha | Atropetae | Lepidosopocidae | <i>Lepium</i> | <i>sp.</i> | PNG | Lpsp.11.17.2003.11 | AY630451 | GU569312 | GU569187 | GU569244 |
| Trogiomorpha | Atropetae | Lepidosopocidae | <i>Neolepoplepis</i> | <i>occidentalis</i> | USA | Neocc.8.31.2001.13 | AY630446 | DQ104779 | DQ104751 | GU569246 |
| Trogiomorpha | Atropetae | Lepidosopocidae | <i>Pteroxaniam</i> | <i>kelloggi</i> | USA | Pxkel.12.4.2003.7 | AY630449 | DQ104784 | DQ104757 | - |
| Trogiomorpha | Atropetae | Lepidosopocidae | <i>Soa</i> | <i>sp.</i> | PNG | KY323 | DQ104802 | DQ104780 | DQ104752 | - |
| Troctomorpha | Amphientometae | Amphientomidae | <i>Stimulopalpus</i> | <i>japonicus</i> | USA | Stjap.8.31.2001.15 | AY630459 | GU569345 | GU569220 | GU569286 |
| Troctomorpha | Amphientometae | Amphientomidae | <i>Cymatopsocus</i> | <i>sp.</i> | Malaysia | KY200 | AY630460 | AB919021 | AB918935 | AB918976 |
| Troctomorpha | Amphientometae | Amphientomidae | <i>Genus</i> | <i>sp.</i> | Malaysia | KY197, KY256 | AY630458 | AB919022 | AB918936 | - |
| Troctomorpha | Amphientometae | Compsoecidae | <i>Compsoec</i> | <i>elegans</i> | Costa Rica | Coele.3.24.2001.14 | AY630462 | DQ104790 | DQ104763 | GU569287 |
| Troctomorpha | Amphientometae | Electrentomidae | <i>Epitroctes</i> | <i>sp.</i> | Mexico | Eisp.11.17.2003.6 | AY630463 | AB919023 | AB918937 | - |
| Troctomorpha | Amphientometae | Musapsocidae | <i>Musapsocus</i> | <i>sp.</i> | Mexico | Musp.2.4.2002.13 | AY630461 | DQ104789 | DQ104762 | GU569285 |
| Troctomorpha | Amphientometae | Protroctosocidae | <i>Protroctosocus</i> | <i>enigmaticus</i> | Mexico | Preni.3.2.2004.10 | AB919004 | AB919024 | AB918938 | - |
| Troctomorpha | Amphientometae | Troctosopocidae | <i>Selenosocus</i> | <i>sp.</i> | Malaysia | KY198 | AY630457 | AB919025 | AB918939 | - |
| Troctomorpha | Amphientometae | Troctosopocidae | <i>Thaiposocus</i> | <i>sp.</i> | Malaysia | KY258 | AB919005 | AB919026 | AB918940 | AB918977 |
| Troctomorpha | Nanopsocetae | Sphaeropsocidae | <i>Badonnella</i> | <i>titei</i> | Switzerland | Batt.12.4.2003.12 | AY630464 | GU569346 | GU569221 | GU569288 |
| Psocomorpha | Episocetae | Cliadopsocidae | <i>Spurostigma</i> | <i>sp.</i> | Mexico | Sssp.3.2.2004.16 | AB919008 | AB919028 | AB918942 | - |
| Psocomorpha | Episocetae | Cliadopsocidae | <i>Spurostigma</i> | <i>sp.</i> | Dominica | Sssp.3.2.2004.15 | AB919007 | AB919027 | AB918941 | - |
| Psocomorpha | Episocetae | Cliadopsocidae | <i>Cliadopsocus</i> | <i>sp.</i> | Mexico | Cloco.3.2.2004.14 | AB919009 | AB919029 | AB918943 | - |
| Psocomorpha | Episocetae | Dolabellopsocidae | <i>Dolabellopsocus</i> | <i>sp.</i> | Costa Rica | Dosp.3.2.2004.6 | AB919010 | AB919030 | AB918944 | AB918978 |
| Psocomorpha | Episocetae | Episocidae | <i>Berkauia</i> | <i>crossbyana</i> | USA | Becro.8.31.2001.14 | AY630537 | DQ104793 | DQ104766 | GU569250 |
| Psocomorpha | Episocetae | Episocidae | <i>Goja</i> | <i>sp.</i> | Costa Rica | Gosp.12.4.2003.3 | AY630538 | GU569315 | GU569191 | GU569251 |
| Psocomorpha | Episocetae | Episocidae | <i>Episocus</i> | <i>sp.</i> | Malaysia | KY205 | AY630539 | GU569314 | GU569189 | GU569249 |
| Psocomorpha | Episocetae | Episocidae | <i>Mesepisocus</i> | <i>sp.</i> | Dominica | Mmsp.3.2.2004.13 | AB919011 | AB919031 | AB918945 | AB918979 |
| Psocomorpha | Episocetae | Neurostigmatidae | <i>Neurostigma</i> | <i>sp.</i> | Peru | KY471 | AB919012 | AB919032 | AB918946 | - |
| Psocomorpha | Caeciliusetae | Amphipsocidae | <i>Polypsocus</i> | <i>corruptus</i> | USA | Pocor.8.31.2001.6 | AY630488 | GU569334 | GU569209 | GU569273 |
| Psocomorpha | Caeciliusetae | Amphipsocidae | <i>Kolbia</i> | <i>fusconervosa</i> | Japan | KY208 | AY630487 | GU569333 | GU569208 | GU569272 |
| Psocomorpha | Caeciliusetae | Amphipsocidae | <i>Japonosocus</i> | <i>japonicus</i> | Japan | KY211 | AY630489 | GU569331 | AB918947 | AB918980 |
| Psocomorpha | Caeciliusetae | Amphipsocidae | <i>Taeniostrongylus</i> | <i>elongatum</i> | Malaysia | KY221 | AY630486 | GU569335 | GU569210 | GU569274 |
| Psocomorpha | Caeciliusetae | Amphipsocidae | <i>Calocaccilius</i> | <i>deciplens</i> | Malaysia | KY201 | AY630485 | GU569332 | GU569207 | GU569271 |
| Psocomorpha | Caeciliusetae | Amphipsocidae | <i>Tagalopsocus</i> | <i>sp.</i> | Malaysia | KY257 | AB856949 | AB856968 | - | AB918981 |
| Psocomorpha | Caeciliusetae | Asiopsocidae | <i>sonorensis</i> | <i>sp.</i> | USA | Assp.11.17.2003.3 | AY630481 | GU569330 | GU569205 | GU569269 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Valenzuela</i> | <i>flavidus</i> | USA | Vafia.8.31.2001.5 | AY630499 | GU569343 | GU569218 | GU569283 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Valenzuela</i> | <i>flavidus</i> | Japan | KY223 | AY630498 | AB919033 | AB918948 | AB918982 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Valenzuela</i> | <i>cyamai</i> | Japan | KY210 | AY630497 | AB856966 | AB856930 | - |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Xanthocaecilius</i> | <i>sommermanae</i> | USA | Xasom.8.31.2001.4 | AY630500 | GU569344 | GU569219 | GU569284 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Caecilius</i> | <i>fuscoperus</i> | Japan | KY227 | AY630484 | AB856969 | AB856933 | - |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Dypsocus</i> | <i>coleopratus</i> | Japan | KY202 | AY630482 | GU569341 | GU569216 | GU569281 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Fuelleborniella</i> | <i>sp.</i> | Ghana | Fusp.11.24.2003.6 | AY630496 | GU569339 | GU569214 | GU569279 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Isophanes</i> | <i>sp.</i> | Japan | KY230 | AY630483 | GU569342 | GU569217 | GU569282 |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Paracaecilius</i> | <i>japanus</i> | Japan | KY233 | AY630501 | AB856970 | AB856934 | - |
| Psocomorpha | Caeciliusetae | Caeciliusidae | <i>Pericaecilius</i> | <i>sp.</i> | Taiwan | KY239 | AY630495 | GU569340 | GU569215 | GU569280 |
| Psocomorpha | Caeciliusetae | Dasydemellidae | <i>Matsumuraella</i> | <i>radiopicta</i> | Japan | KY236 | AY630493 | DQ104797 | DQ104770 | GU569275 |
| Psocomorpha | Caeciliusetae | Dasydemellidae | <i>Ptenopsis</i> | <i>sp.</i> | Chile | KY243 | AY630494 | - | AB856929 | - |
| Psocomorpha | Caeciliusetae | Dasydemellidae | <i>Teliapsocus</i> | <i>conterminus</i> | USA | Tecon.3.2.2004.1 | AB856951 | AB856972 | AB856936 | AB918983 |
| Psocomorpha | Caeciliusetae | Stenopsocidae | <i>Grathopsocus</i> | <i>cruciatius</i> | USA | Grcru.11.2.2001.5 | AY630490 | GU569336 | GU569211 | GU569276 |
| Psocomorpha | Caeciliusetae | Stenopsocidae | <i>Stenopsocus</i> | <i>nigridiformis</i> | Japan | KY219 | AY630491 | GU569337 | GU569212 | GU569277 |
| Psocomorpha | Caeciliusetae | Stenopsocidae | <i>Stenopsocus</i> | <i>aphricellus</i> | Japan | KY241 | AY630492 | GU569338 | GU569213 | GU569278 |
| Psocomorpha | Homilopsocidae | Archipsocidae | <i>Archipsocus</i> | <i>nomas</i> | USA | Arnom.3.16.2001.2 | AY900133 | AB919034 | AY275354 | AY275279 |
| Psocomorpha | Homilopsocidae | Archipsocidae | <i>Archipsocus</i> | <i>recens</i> | Taiwan | KY206 | AY630480 | AB919035 | AB918949 | - |
| Psocomorpha | Homilopsocidae | Archipsocidae | <i>Archipsocus</i> | <i>sp. 1</i> | Malaysia | KY209 | GU569164 | GU569313 | GU569188 | GU569247 |
| Psocomorpha | Homilopsocidae | Archipsocidae | <i>Archipsocus</i> | <i>sp. 2</i> | Malaysia | KY226 | AY630478 | DQ104791 | DQ104764 | GU569248 |
| Psocomorpha | Homilopsocidae | Archipsocidae | <i>Pararchipsocus</i> | <i>sp.</i> | Costa Rica | Pasp.3.2.2004.5 | AB919006 | AB919036 | AB918950 | AB918984 |
| Psocomorpha | Homilopsocidae | Phliotarsidae | <i>Aaroniella</i> | <i>badonneli</i> | USA | Aaad.8.31.2001.8 | AY630532 | GU569317 | GU569192 | GU569253 |
| Psocomorpha | Homilopsocidae | Phliotarsidae | <i>Aaroniella</i> | <i>sp.</i> | Japan | KY216 | AY630533 | AB919037 | AB918951 | AB918985 |
| Psocomorpha | Homilopsocidae | Phliotarsidae | <i>Haplophallus</i> | <i>wongae</i> | Australia | Hawon.12.4.2003.5 | AY630528 | - | AB918952 | AB918986 |
| Psocomorpha | Homilopsocidae | Phliotarsidae | <i>Haplophallus</i> | <i>sp.</i> | Japan | KY204 | AY630529 | AB919038 | AB918953 | AB918987 |
| Psocomorpha | Homilopsocidae | Phliotarsidae | <i>Phliotarsopsis</i> | <i>ornatus</i> | Australia | Prsp.12.4.2003.6 | AY630531 | - | AB918954 | AB918988 |
| Psocomorpha | Homilopsocidae | Phliotarsidae | <i>Phliotarsus</i> | <i>kwakutl</i> | USA | Phkwa.11.17.2003. | AY630530 | GU569318 | GU569193 | GU569254 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Allocaecilius</i> | <i>sinensis</i> | Japan | KY232 | AY630526 | DQ104796 | DQ104769 | GU569258 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Phalocaecilius</i> | <i>hirsutus</i> | Japan | KY217 | AY630523 | GU569320 | GU569195 | GU569256 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Mepleres</i> | <i>suzukii</i> | Japan | KY242 | AY630525 | AB919039 | AB918955 | AB918989 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Ophiopelma</i> | <i>glyptocephalum</i> | Japan | KY234 | AY630524 | AB919040 | AB918956 | - |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Heterocaecilius</i> | <i>solocipennis</i> | Japan | Hcsol.12.4.2003.8 | AY630521 | AB919041 | AB918957 | AB918990 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Heterocaecilius</i> | <i>fuscus</i> | Japan | KY237 | AY630520 | DQ104795 | DQ104768 | GU569257 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Lobocaecilius</i> | <i>monicus</i> | Australia | Lomon.12.4.2003.1 | AY630522 | AB919042 | AB918958 | - |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Pseudocaecilius</i> | <i>clitricola</i> | Australia | Pccit.11.17.2003.12 | AY630527 | GU569321 | GU569196 | GU569259 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Austratopsocus</i> | <i>sp.</i> | New Caledonia | Ausp.12.4.2003.9 | AY630534 | AB919043 | AB918959 | AB918991 |
| Psocomorpha | Homilopsocidae | Pseudocaeciliidae | <i>Zelandopsocus</i> | <i>sp.</i> | New Caledonia | Zesp.11.24.2003.9 | AY630535 | AB919044 | AB918960 | - |
| Psocomorpha | Homilopsocidae | Bryopsocidae | <i>Bryopsocus</i> | <i>sp.</i> | New Zealand | KY470 | AB919013 | AB919045 | AB918961 | - |
| Psocomorpha | Homilopsocidae | Trichopsocidae | <i>Trichopsocus</i> | <i>dalii</i> | Switzerland | KY248 | AY630536 | AB919046 | AB918962 | - |
| Psocomorpha | Homilopsocidae | Trichopsocidae | <i>Trichopsocus</i> | <i>sp.</i> | USA | KY322 | AB919014 | AB919047 | AB918963 | AB918992 |
| Psocomorpha | Homilopsocidae | Calopsocidae | <i>Calopsocus</i> | <i>marginalis</i> | PNG | Camar.12.4.2003.1 | AB919015 | AB919048 | AB918964 | AB918993 |
| Psocomorpha | Homilopsocidae | Calopsocidae | <i>Calopsocus</i> | <i>furcata</i> | Malaysia | KY199 | AY630519 | GU569319 | GU569194 | GU569255 |
| Psocomorpha | Homilopsocidae | Ectopsocidae | <i>Ectopsocus</i> | <i>cryptomeriae</i> | USA | Etcry.11.17.2003.2 | AY630511 | GU569323 | GU569198 | GU569261 |
| Psocomorpha | Homilopsocidae | Ectopsocidae | <i>Ectopsocus</i> | <i>meridionalis</i> | USA | Epmer.2.3.2001.4 | AY630512 | GU569322 | GU569197 | GU569260 |
| Psocomorpha | Homilopsocidae | Ectopsocidae | <i>Ectopsocus</i> | <i>sp.</i> | Japan | KY212 | AY630510 | AB919049 | AB918965 | AB918994 |
| Psocomorpha | Homilopsocidae | Elipsocidae | <i>Kilauella</i> | <i>sp.</i> | Hawaii | Kisp.11.24.2003.10 | AY630517 | GU569329 | GU569204 | GU569267 |
| Psocomorpha | Homilopsocidae | Elipsocidae | <i>Cuneopalpus</i> | <i>cyanops</i> | USA | KY318 | AB919016 | AB919050 | AB918966 | AB918995 |
| Psocomorpha | Homilopsocidae | Elipsocidae | <i>Elipsocus</i> | <i>sp.</i> | USA | KY319 | AB919017 | AB919051 | AB91 | |

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|----|-------------|----------------|---------------|---------------------------|----------------------------|---------------|--------------------|----------|----------|----------|----------|
| 1 | Psocomorpha | Homilopsocidea | Peripsocidae | <i>Peripsocus</i> | <i>subfasciatus</i> | USA | Pesub.2.3.2001.2 | AY630507 | GU569325 | GU569200 | GU569263 |
| 2 | Psocomorpha | Homilopsocidea | Peripsocidae | <i>Peripsocus</i> | <i>sp.</i> | New Caledonia | Pesp.3.2.2004.4 | AB919020 | - | AB918972 | AB919001 |
| 3 | Psocomorpha | Homilopsocidea | Lachesillidae | <i>Anomopsocus</i> | <i>amabilis</i> | USA | Anama.11.17.2003 | AY630509 | GU569326 | GU569201 | GU569264 |
| 4 | Psocomorpha | Homilopsocidea | Lachesillidae | <i>Eolachesilla</i> | <i>chilensis</i> | Chile | KY214 | AY630514 | GU569328 | GU569203 | GU569266 |
| 5 | Psocomorpha | Homilopsocidea | Lachesillidae | <i>Lachesilla</i> | <i>sp.</i> | Malaysia | KY229 | AB856947 | AB856964 | AB856925 | AB919002 |
| 6 | Psocomorpha | Homilopsocidea | Lachesillidae | <i>Lachesilla</i> | <i>anna</i> | USA | Laann.1.16.2001.2 | AY630504 | - | AY275351 | AB919003 |
| 7 | Psocomorpha | Homilopsocidea | Lachesillidae | <i>Lachesilla</i> | <i>forcepeta</i> | USA | Lafor.8.31.2001.10 | AY630503 | GU569327 | GU569202 | GU569265 |
| 8 | Psocomorpha | Psocetae | Hemipsocidae | <i>Hemipsocus</i> | <i>chloroticus</i> | Japan | Hechl.5.16.2002.6 | AY630545 | - | AY139957 | AY275290 |
| 9 | Psocomorpha | Psocetae | Hemipsocidae | <i>Hemipsocus</i> | <i>sp. 1</i> | Malaysia | KY196 | AY630543 | EF662139 | EF662100 | GU569252 |
| 10 | Psocomorpha | Psocetae | Hemipsocidae | <i>Hemipsocus</i> | <i>sp. 2</i> | Malaysia | KY228 | AY630544 | DQ104792 | DQ104765 | EF662063 |
| 11 | Psocomorpha | Psocetae | Hemipsocidae | <i>Hemipsocus</i> | <i>sp.</i> | Ghana | Hesp.12.4.2003.14 | AY630542 | AB919055 | - | - |
| 12 | Psocomorpha | Psocetae | Myopsocidae | <i>Lichenomima</i> | <i>sp.</i> | Japan | KY231 | AY630540 | EF662142 | EF662103 | EF662066 |
| 13 | Psocomorpha | Psocetae | Psilopsocidae | <i>Psilopsocus</i> | <i>malayensis</i> | Malaysia | KY195 | AY630541 | EF662140 | EF662101 | EF662064 |
| 14 | Psocomorpha | Psocetae | Psocidae | <i>Amphigerontia</i> | <i>jezoensis</i> | Japan | KY213 | AY630546 | EF662143 | EF662104 | EF662067 |
| 15 | Psocomorpha | Psocetae | Psocidae | <i>Blaste</i> | <i>quieta</i> | USA | Blqui.2.3.2001.5 | AY630547 | EF662145 | EF662106 | EF662069 |
| 16 | Psocomorpha | Psocetae | Psocidae | <i>Blastopsocus</i> | <i>lithinis</i> | USA | Blili.8.31.2001.11 | AY630548 | EF662147 | AY275363 | AY275288 |
| 17 | Psocomorpha | Psocetae | Psocidae | <i>Loensia</i> | <i>moesta</i> | USA | Lomoe.8.31.2001.2 | AY630550 | EF662169 | AY275360 | AY275285 |
| 18 | Psocomorpha | Psocetae | Psocidae | <i>Loensia</i> | <i>vanegata</i> | France | KY179 | AY630549 | EF662170 | AY139953 | AY374556 |
| 19 | Psocomorpha | Psocetae | Psocidae | <i>Ptycta</i> | <i>johnsoni</i> | Japan | KY235 | AY630553 | EF662175 | AY139954 | EF662093 |
| 20 | Psocomorpha | Psocetae | Psocidae | <i>Symbiopsocus</i> | <i>hastatus</i> | Japan | KY180 | AY630552 | EF662178 | AY374575 | AY374559 |
| 21 | Psocomorpha | Psocetae | Psocidae | <i>Trichadenotecnurr</i> | <i>sp. cf. alexanderax</i> | USA | Trale.1.16.2001.3 | AY630554 | - | AY275362 | AY275287 |
| 22 | Psocomorpha | Psocetae | Psocidae | <i>Psocus</i> | <i>bipunctatus</i> | Japan | KY225 | AY630555 | EF662162 | EF662121 | EF662084 |
| 23 | Psocomorpha | Psocetae | Psocidae | <i>Atrichadenotecnurr</i> | <i>sp.</i> | Malaysia | KY238 | EF662274 | EF662156 | EF662116 | EF662079 |
| 24 | Psocomorpha | Psocetae | Psocidae | <i>Metylophorus</i> | <i>novaescotiae</i> | USA | Menov.2.3.2001.3 | AY630558 | EF662154 | AY275361 | AY275286 |
| 25 | Psocomorpha | Psocetae | Psocidae | <i>Sigmatoneura</i> | <i>kolbei</i> | Japan | KY181 | AY630556 | - | EF662115 | EF662078 |
| 26 | Psocomorpha | Psocetae | Psocidae | <i>Sigmatoneura</i> | <i>kakisayap</i> | Malaysia | KY240 | AY630557 | GU569316 | EF662112 | EF662076 |
| 27 | Psocomorpha | Psocetae | Psocidae | <i>Clematoscenea</i> | <i>sp.</i> | Malaysia | KY215 | AY630560 | EF662151 | EF662111 | EF662074 |
| 28 | Psocomorpha | Psocetae | Psocidae | <i>Longivalvus</i> | <i>nubilus</i> | Japan | KY218 | AY630559 | EF662152 | AY139952 | EF662075 |

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