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

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

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

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INTRODUCTION

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

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

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

A number of prior molecular phylogenetic studies have included representatives of

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Psocomorpha. However, each of these studies either had limited taxon sampling or a small number of genes analyzed. A molecular phylogeny for Psocomorpha was estimated previously with limited taxon sampling and multiple gene markers (Johnson & Mockford 2003). Only 17 species from 12 of 25 families (Lienhard & Smithers 2002) were included. A molecular phylogeny of Psocodea based on more extensive taxon sampling, including wide range of psocomorphan taxa, was estimated by Johnson, Yoshizawa & Smith (2004), but this analysis only used a single gene marker, 18S rDNA. A considerable number of psocomorphan taxa were also analyzed by Yoshizawa & Johnson (2010) using four gene markers. However, the emphasis of these prior studies (Johnson, Yoshizawa & Smith 2004; Yoshizawa & Johnson 2010) was on the origins of parasitic lice, and no comparison has been made between the results from the molecular- and morphology-based trees for the phylogeny of Psocomorpha.

In this study, we estimated the phylogeny of the suborder Psocomorpha using data from four gene markers selected from nuclear and mitochondrial genomes, and both protein coding and ribosomal RNA genes. The gene markers employed in the present analyses are identical with those used in Yoshizawa & Johnson (2010), but taxon coverage for Psocomorpha is greatly expanded: i.e., 77 genera and 100 species of Psocomorpha covering all families recognized by Lienhard & Smithers (2002), except for Ptiloneuridae. The analyses resulted in a highly resolved and well supported tree for the suborder. Based on this tree, we propose a revised classification of Psocomorpha. In addition, we also compared the trees estimated from the molecular and morphological data and re-evaluate the phylogenetic utility and transformation series of the morphological characters.

MATERIAL AND METHODS

Samples were selected from all extant families of Psocomorpha listed in Lienhard & Smithers (2002), except for Ptiloneuridae. Although some new classification schemes have been proposed subsequently (Li 2002; Yoshizawa 2002; Schmidt & New 2004; Casasola González 2006; Yoshizawa, Mockford & Johnson 2014), the family group or higher names listed in Lienhard & Smithers (2002) were adopted in the following unless specified. A total of 24 families, 77 genera and 100 species were sampled for ingroup

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taxa (Table 1). Outgroups were selected from suborders Trogiomorpha (root of the tree) and Troctomorpha (sister of Psocomorpha) (Johnson, Yoshizawa & Smith 2004; Yoshizawa, Lienhard & Johnson 2006). Samples were not included from Phthiraptera (parasitic lice: subgroup of Troctomorpha) and its close relatives (Liposcelididae and Pachytroctidae) because of the presence of long molecular branches and other unusual molecular evolutionary processes in these taxa that may confound phylogenetic analysis (Yoshizawa & Johnson 2003, 2010, 2013; Johnson, Yoshizawa & Smith 2004).

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

Using the aligned data set, maximum-likelihood (ML) and Bayesian analyses were conducted. The best fit model for the ML analysis was estimated using the hierarchical likelihood ratio test (hLRT) as implemented in jModelTest 2.1.1 (Darriba et al. 2012). The best model was selected based on a BioNJ tree. As a result, the GTR + Gamma + Invariable site model was selected (detailed parameters were described in the Supplementary Data matrix). ML tree searches were conducted using PAUP* 4b10 (Swofford 2002). NJ, MP, and Bayesian trees were used as starting trees and TBR branch swapping was conducted. The most likely tree was found when Bayesian tree was designated as the starting tree. Likelihood-based bootstrap support values were calculated using PhyML 3.0 (Guindon et al. 2010) with 500 bootstrap replicates. NNI branch swapping was performed for each replicate, with GTR + Gamma + Invariable sites model (all parameters estimated from the data set).

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

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

To examine the sources of congruence versus incongruence between the morphological and molecular trees and also to examine the phylogenetic utility of morphological data, we re-analyzed the morphological data scored by Yoshizawa (2002). We reanalyzed only the genera sampled in the molecular data set, and other taxa included in Yoshizawa (2002) were omitted from the data set. In the original data set, Yoshizawa (2002) coded the number and condition of the mesothoracic muscles as a single character (Character 14). However, this character is now re-coded as two separate characters: number of muscles (Character 14) and their conditions (Characters 69 and 70) to clarify ancestral state reconstructions. See Yoshizawa (2002) for description of other morphological characters selected for phylogenetic analyses. The final data set contained 39 taxa (34 for ingroup) and 70 characters. Phylogenetic analyses were conducted using maximum parsimony in PAUP* 4b10 as described in Yoshizawa (2002). For evaluating various morphological features, the morphological data set was categorized into 6 categories (head, thorax, wings, legs and male and female genitalia). The phylogenetic congruence of each category was examined by comparing the homology indices (consistency and retention indices) derived from the MP morphology and ML molecular enforced trees using MacClade 4.08 (Maddison & Maddison 2000).

RESULTS

Molecular Phylogenetics

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

Excluding Archipsocidae, the remainder of the psocomorphan families clustered

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into two clades: one composed of Caeciliusetae and a part of Homilopsocidea (Homilo1: Lachesillidae, Peripsocidae, Ectopsocidae, Elipsocidae and Mesopsocidae) (100% pp and 98% bs) and the other composed of Epipsocetae, Psocetae and the remaining Homilopsocidea (Homilo2: Philotarsidae, Trichopsocidae, Pseudocaeciliidae and Calopsocidae) (91% pp and 83% bs). Monophyly of each of the infraorders Caeciliusetae, Epipsocetae, and Psocetae (including Hemipsocidae) was all strongly supported (all 100% pp and bs). Monophyly of Homilopsocidea was not supported by ML and Bayesian analyses. Monophyly of Homilopsocidea could also be rejected by the AU test ($P<0.001$ using *Lachesilla*-excluded data set: see below), even in the case where the separate placement of Archipsocidae from the rest of Homilopsocidea was allowed.

When all the taxa were included in the analyses (Fig. 1), the clade composed of Peripsocidae and *Lachesilla* of Lachesillidae (moderately to weakly supported: 95% pp and 64% bs) was placed to the sister of Caeciliusetae. However, placement of the clade was highly unstable (53% pp and <50% bs). Detailed examination of the trees resulting from Bayesian and bootstrap analyses revealed that *Lachesilla* is the major source of this instability. Therefore, we also prepared a data set excluding *Lachesilla*, which was used for subsequent analyses. In analyses excluding *Lachesilla*, monophyly of Homilo1 including Peripsocidae and the rest of Lachesillidae (*Anomopsocus* and *Eolachesilla*) was supported strongly (99% pp and 72% bs) (Fig. 2). Regardless of the inclusion/exclusion of *Lachesilla*, monophyly of the clade composed of Caeciliusetae and Homilo1 was strongly supported (100% pp and 98-99% bs). Relationships within Caeciliusetae have been discussed before (Yoshizawa, Mockford & Johnson 2014), and the present results were in complete agreement with the previous study. Relationships within Homilo1 were only poorly resolved, but monophyly of Elipsocidae and Mesopsocidae was not recovered. However, the monophyly of these two families could not be rejected statistically ($P = 0.327$ and 0.461 from AU test, respectively). As already mentioned, monophyly of Lachesillidae was not recovered but could not be rejected statistically ($P = 0.194$ from AU test of all included data set).

Monophyly of a clade comprising Psocetae + Epipsocetae + Homilo2 was supported by both data sets, but support values were improved by excluding *Lachesilla* (91%->94% pp and 83%->87% bs). Monophyly of Homilo2 was also strongly and

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consistently supported. Within the clade, Philotarsidae branched off first, and monophyly of a group comprising the remaining taxa was strongly supported (99% pp and 74-77% bs). Trichopsocidae branched off next, but this branching order was only poorly supported (<50% pp and bs). The rest of the families in this group are divided into two clades. The first was Calopsocidae + Pseudocaeciliinae of Pseudocaeciliidae, which was very strongly supported (100% pp and bs), and the second was composed of Bryopsocidae and Zelandopsocinae of Pseudocaeciliidae, which was moderately to strongly supported (91-97% pp and 68-71% bs). A sister relationship between Bryopsocidae and *Zelandopsocus* was very strongly supported (100% pp and bs).

A sister group relationship between Epipsocetae and Psocetae received only moderate support (83-94% pp and 62% bs). Relationships within Epipsocetae were only poorly resolved, but Neurostigmatidae was embedded within Epipsocidae (100% pp and 96-98% bs) and placed sister to *Mesepipsocus* (100% pp and bs). Within Psocetae, a sister group relationship between Psilopsocidae and Hemipsocidae was strongly supported (100% pp and 99% bs). Myopsocidae and Psocidae composed a clade, but their relationship was only moderately supported (88-90% pp and 68-70% bs).

Comparison with Morphology

Maximum parsimony analysis of the morphological data set produced 154 equal length trees, with L = 175, CI = 0.49 and RI = 0.81 (Table 2). Application of successive (6 trees) and implied weighting (12 trees under K = 2 and 10) greatly reduced the number of most parsimonious trees. These trees are all included in the original 154 trees, and the strict consensus of the trees estimated from each analysis are all identical (Fig. 3 above). Female genitalic characters (CI = 0.8, RI = 0.94) and thoracic characters (CI = 0.67, RI = 0.92) were more congruent with the MP tree compared to the average homology index values of the total morphological data set (CI = 0.49, RI = 0.81). In contrast, characters from the wings (CI = 0.44, RI = 0.73), legs (CI = 0.20, RI = 0.66), and male genitalia (CI = 0.43, RI = 0.70) were less congruent with the morphological MP tree.

When the topology obtained from the ML analysis of the molecular data was constrained (Fig. 3 bottom), tree scores from the morphological data set became L = 212, CI = 0.41, and RI = 0.73 (Table 2). Comparisons of consistency and retention indices of

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morphological data reconstructed on MP and ML trees showed increased amount of homoplasy for almost all data categories (Table 2). In particular, more homoplasy was detected in female genitalic characters on the molecular ML tree (range of reduction of homology index values was 0.08 on average whereas 0.24-0.35 in female genitalia). In contrast, thoracic character showed identical homology index values on both the molecular and morphological trees.

DISCUSSION

RELATIONSHIPS AND VALIDITY OF INFRAORDERS

DNA sequences from four gene regions produced a generally well-resolved and supported tree for the bark louse suborder, Psocomorpha. The sister relationship between Archipsocidae and the rest of Psocomorpha is strongly supported (100% bs and pp). Archipsocidae had long been placed in Homilopsocidea (from Pearman 1936). However, more recent cladistic analyses of morphological data have already identified a sister relationship between Archipsocidae and the remainder of Homilopsocidea (Yoshizawa 2002). Previous molecular analyses with smaller gene and taxon sampling also supported the basal divergence of Archipsocidae (Johnson & Mockford 2003; Johnson, Yoshizawa & Smith 2004; Yoshizawa & Johnson 2010). Therefore, an independent infraordinal status for the family as proposed by Yoshizawa (2002), i.e., Archipsocetae, can be strongly recommended.

In contrast, an independent infraordinal status for Hemipsocidae, as suggested by morphological analysis (Yoshizawa 2002), is not supported by molecular data, and the family falls within Psocetae. Support values for the monophyly of Psocetae including Hemipsocidae and close relationship between Hemipsocidae and Psilopsocidae are both very high (99-100% bs; 100% pp). Therefore, the placement of Hemipsocidae within Psocetae is robust. Placement of Hemipsocidae within Psocetae has also been previously recovered in other molecular studies (Johnson & Mockford 2003; Johnson, Yoshizawa & Smith 2004; Yoshizawa & Johnson 2010); thus this placement is robust to the taxon and gene sampling. Using morphological characters, the placement of Hemipsocidae within Psocetae has also previously been suggested, based on a shared distal process of the male paraproct, a potential synapomorphy (Mockford 1976, 1993). This relationship was also

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recovered in the parsimonious trees estimated from a reanalysis of morphological data with successive weighting (Fig. 3). In contrast, the analyses of Yoshizawa (2002) suggested that Hemipsocidae is one of the earliest diverging lineages within Psocomorpha, and a condition of the wing base (separated 2Ax and proximal median plate) was suggested to be the plesiomorphic condition excluding this family and Archipsocidae from the rest of Psocomorpha. Given the strong molecular support and presence of morphological evidence for the placement of Hemipsocidae within Psocetae, the condition of the wing base structures should be regarded as secondary reversal occurring in the common ancestor of Hemipsocidae.

Monophyly of all the infraorders accepted by Lienhard & Smithers (2002), except for Homilopsocidea, was supported strongly (99-100% bs and 100% pp). Monophyly of Homilopsocidea was not supported by analyses of the molecular data even if Archipsocetae is excluded from the infraorder. This result is also congruent with the previous morphology-based phylogeny, because monophyly of Caeciliusetae, Epipsocetae, and Psocetae (except for the placement of Hemipsocidae mentioned above) was all consistently supported based on morphological data, whereas monophyly of Homilopsocidea was only recovered after the application of successive weighting (Yoshizawa 2002). Apart from the separate placement of Archipsocidae, analysis of the molecular data divided the infraorder into two major groups. Monophyly of Homilopsocidea (excluding Archipsocidae) was also rejected by the AU test ($P<0.001$), justifying naming of an independent infraorder for one of two clades of Homilopsocidea.

The first group of Homilopsocidea (Homilo1) is composed Peripsocidae, Ectopsocidae, Elipsocidae, Mesopsociae, and Lachesillidae, but relationships among these families are highly unstable depending on taxon sampling. When the genus *Lachesilla* was included in the analysis, the first group (Homilo1) was divided into two groups that are not sister taxa: one composed of the family Peripsocidae and the genus *Lachesilla* of the Lachesillidae (Lachesillinae) and the other containing Ectopsocidae, Elipsocidae, Mesopsocidae, and a part of Lachesillidae (*Anomopsocus* and *Eolachesilla*: Eolachesillinae). However, as mentioned above, placement of the first clade, especially the placement of *Lachesilla*, is highly unstable, as also evident by the long branch leading to the genus compared to the other homilopsocid taxa. After removing *Lachesilla* from

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the analysis, Peripsocidae was placed sister to the remainder of Homilo1, and this relationship received high support values (72% bs and 99% pp). Exclusion of *Lachesilla* from the analyses also stabilizes some other branches (Figs 1 and 2). Therefore, we consider the separation of *Lachesilla* + Peripsocidae from the remainder of Homilo1 may be an artifact caused by unusual substitution properties and long branches for *Lachesilla*. Monophyly of Homilo1 excluding *Lachesilla* is also supported by two morphological character states, but they are either highly homoplasious (Character 55: single-lobed egg guide) or also observed in the second homilopsocid clade (Character 62: dorsally swelling dorsal valve of gonapophyses). Regardless of the inclusion or exclusion of *Lachesilla*, members of Homilo1 are placed in a clade together with Caeciliusetae, and this relationship received strong support (98-99% bs and 100% pp). However, no unambiguous morphological apomorphies supporting this relationship occurs among the characters coded by Yoshizawa (2002).

The second group of Homilopsocidea (Homilo2) is composed of Philotarsidae, Trichopsocidae, Bryopsocidae, Calopsocidae, and Pseudocaeciliidae. The monophyly of this group is strongly supported in all analyses (99% bs and 100% pp). Some synapomorphies can be identified in morphological characters, but all are homoplasious: i.e., gonapophyses and egg guide tightly associated, together forming ovipositor (Character 58), and dorsal region of dorsal valve of gonapophyses swollen (Character 62) and sclerotized (Character 64). This clade (Homilo2) is sister to a clade comprising Epipsocetae + Psocetae, and this relationship is modestly well supported (83% bs and 91% pp), although no unambiguous morphological apomorphy supporting this relationship occurs among the characters coded by Yoshizawa (2002). One possible character supporting this clade is the position of the anterior tentorial pit separated from the ventral margin of cranium (Character 5). However, this character state is variable within Psocetae, and the plesiomorphic state within this group cannot be unambiguously reconstructed.

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

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which was suggested to be the plesiomorphic condition within the suborder. Alternatively, Yoshizawa (2002) placed this infraorder as the sister of Caeciliusetae, and concluded that the presence of A2 vein in this infraorder represents a secondary reversal. The secondarily reversed condition of the A2 vein is not observed in earliest diverging family of Epipsocetae: Dolabellopsocidae (Yoshizawa 2002; Casasola González 2006). The present results, on the other hand, placed Epipsocetae as sister to Psocetae. Although the support values for this relationship are not high (62% bs and 94% pp when *Lachesilla* is excluded from the analyses), a sister relationship of Epipsocetae with the remainder of Psocomorpha can be rejected by the AU test ($P<0.001$). Therefore, the secondary reversal in the condition of the A2 vein is evident also suggested by the molecular phylogeny. The reanalysis of the morphological data set suggested that there are a couple of potential synapomorphies between Epipsocetae and Psocetae: narrow precoxal bridge (Character 15) and the two muscles inserted to the trochantin (Character 69) (Yoshizawa 2002, 2005).

VALIDITY OF SUPERFAMILIES

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

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

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Peripsocidae + Philotarsidae + Mesopsocidae), and Elipsocoidea (Elipsocidae). Validity of the monotypic Elipsocoidea is also brought into question (see below).

RELATIONSHIPS AND VALIDITY OF FAMILIES

Monophyly was confirmed for most of the psocomorphan families recognized previously (Lienhard & Smithers 2002). Although monophyly of Cladiopsocidae was questioned on the basis of morphology (Yoshizawa 2002; Casasola González 2006), the family was recovered to be monophyletic with moderate to high support values (87-89% pp and 84% bs). However, the family Ptiloneuridae was not sampled here, which is potentially embedded within Cladiopsocidae (Yoshizawa 2002; Casasola González 2006). This family should be analyzed before making firm conclusions regarding the monophyly of Cladiopsocidae. The following families were not recovered as monophyletic: Caeciliusidae, Lachesillidae, Elipsocidae, Mesopsocidae, Pseudocaeciliidae, and Epipsocidae. Monophyly of Caeciliusidae, Lachesillidae, and Pseudocaeciliidae has also been questioned by Yoshizawa (2002), and monophyly of Epipsocidae was questioned by Casasola González (2006). Monophyly of Caeciliusidae has already been discussed based on a recent molecular phylogeny (Yoshizawa, Mockford & Johnson 2014). Therefore, the following discussion focuses on the status of the other families.

Lachesillidae is divided into two different groups when all taxa were included in the analyses: *Lachesilla* versus *Anomopsocus* + *Eolachesilla*. These clades correspond to the subfamilies Lachesillinae and Eolachesillinae, respectively (Mockford & Sullivan 1986; Lienhard & Smithers 2002). In the morphological phylogeny, monophyly of *Lachesilla* + *Nanolachesilla* (the latter belong to Eolachesillinae) was supported, but *Eolachesilla* did not compose a monophyletic group together with them (Yoshizawa 2002). The placement of *Lachesilla* was highly unstable based on the analysis of the molecular data and its close affinity with *Anomopsocus* + *Eolachesilla* could not be rejected statistically (AU test, $P = 0.182$). Therefore, we tentatively retain the family "Lachesillidae", but highlighting the possibility of its paraphyly.

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

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Elipsocus (both Elipsocinae). This division of the family does not even reflect the current subfamilial classification system (Lienhard & Smithers 2002). Elipsocidae was recovered to be monophyletic based on analysis of morphological data (Yoshizawa 2002), but, in that study, taxonomic sampling was restricted to two genera both representing the subfamily Elipsocinae. The phylogeny of Elipsocidae was extensively studied by Schmidt & New (2004), in which monophyly of Elipsocidae was accepted. In their revised system, the family was subdivided into two subfamilies and, according to their classification system, all genera of the latter clade are classified into Elipsocinae, and *Propsocus* and *Kilauella* are in Propsocinae. Therefore, the classification system proposed by Schmidt & New (2004) is more congruent with the results from the molecular phylogeny, except for the non-monophyly of the family. However, in the molecular phylogeny, the placement of the members of this family is far from stable, and monophyly of Elipsocidae could not be rejected statistically (AU test, P = 0.327). Therefore, we tentatively accept the family Elipsocidae.

Monophyly of Mesopsocidae was strongly supported based on morphological data (Badonnel & Lienhard 1988; Yoshizawa & Lienhard 1997; Yoshizawa 2002) but was not supported by the present molecular analyses. The morphological phylogeny of Yoshizawa & Lienhard (1997) and Yoshizawa (2002) sampled *Idatenopsocus* and *Mesopsocus*, taxa analyzed in the present study, and identified several synapomorphies between them. In the present analyses, *Idatenopsocus* was placed sister to *Kilauella*, but this relationship received marginal support values only (91% pp and 72% bs). Monophyly of Mesopsocidae could not be rejected statistically using the AU test (P = 0.461), so that this family should be retained until more taxa and genes are analyzed.

Pseudocaeciliidae was shown to be paraphyletic for two reasons: Bryopsocidae was placed within the subfamily Zelandopsocinae; and Calopsocidae was placed within the subfamily Pseudocaeciliinae. Placement of Calopsocidae within Pseudocaeciliidae has already been strongly suggested using morphological data (Smithers 1967; Thornton & Smithers 1984; Yoshizawa 2002). Therefore, the present analyses corroborate this suggestion. Given the strong morphological and molecular support, Calopsocidae should be synonymized with Pseudocaeciliidae (see below). The placement of Bryopsocidae as close to Pseudocaeciliidae, concordant to the present result, has also been proposed based

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on morphological data (Mockford, 1984). Furthermore, *Bryopsocus townsendi*, the type species of the genus, was originally described under the genus *Austropsocus* (Smithers 1969; Thorngon, Wong & Smithers 1977), which closely matches to the present result. In contrast, the phylogeny based on morphological data places Bryopsocidae distant to Pseudocaeciliidae (Fig. 3) (Yoshizawa 2002). However, in the previous morphological analyses, no taxa were sampled from Zelandopsocinae, and morphological information of Bryopsocidae was only scored based on published literatures (Thornton, Wong & Smithers 1977; Mockford 1984). Support values for the placement of Bryopsocidae as sister to *Zelandopsocus* based on the molecular data are high (100% pp and bs for Bryopsocidae + *Zelandopsocus* and 97% pp and 67% bs for Bryopsocidae within Zelandopsocinae). Monophyly of Pseudocaeciliidae + Calopsocidae, excluding Bryopsocidae, was also rejected using the AU test (P = 0.006), providing strong support for the placement of Bryopsocidae within the Pseudocaeciliidae + Calopsocidae clade.

Non-monophyly of Epipsocidae and the placement of Neurostigmatidae within the family have already been suggested by Casasola González (2006) and accepted by Lienhard (2007). However, because the placement of *Neurostigma* (monotypic genus of Neurostigmatidae) was not stable based on morphological data, no official nomenclatural change was proposed to date (Casasola González 2006). This arrangement received strong support from the present molecular data, and *Neurostigma* is placed to the sister of *Mesepipsocus* with strong support values (100% pp and bs).

TAXONOMIC SUMMARY

In conclusion, based on the molecular phylogenetic results, we propose several novel taxonomic arrangements (Table 3). The validity of Psocomorpha receives strong support from both molecular and morphological data (Yoshizawa 2002). Six infraorders are proposed within Psocomorpha, of which five are proposed previously (Pearman 1936; Yoshizawa 2002), and one (Philotarsetae) is newly proposed here. The infraorder Hemipsocetae proposed by Yoshizawa (2002) is unjustified. Superfamilies proposed within Caeciliusetae (Mockford & García Aldrete 1976) and Homilopsocidea (Yoshizawa 2002) are all rejected (see also Yoshizawa, Mockford & Johnson 2014). At the family level, monophyly of Elipsocidae, Lachesillidae, and Mesopsocidae are questionable, but

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additional gene and taxon sampling is needed to draw more finalized conclusions about the status of these families. The family Bryopsocidae (Mockford 1984) is treated as a new junior synonym of Zelandopsocinae within Pseudocaeciliidae, and the family Calopsocidae is newly synonymized with Pseudocaeciliidae. The family Neurostigmatidae is treated as a junior synonym of Epipsocidae, as proposed by Casasola González (2006).

REEVALUATION OF MORPHOLOGICAL CHARACTERS

Results from the morphological phylogeny presented in Yoshizawa (2002) were largely congruent with the ML tree estimated from the molecular data in the current study. This clearly shows that the morphological data contains a considerable amount of phylogenetic signal congruent with the molecular information. However, some significant incongruence is also identified between the morphological and molecular phylogenies. Comparisons of consistency and retention indices of the morphological data reconstructed on the molecular and morphological trees enable us to identify the source of congruence and incongruence between two data sets and to reevaluate the importance of the morphological data for phylogenetic reconstruction of this group.

Comparisons of the consistency and retention indices of each morphological category on the molecular MP trees show that the thoracic and female genital characters are more congruent with these tree topologies; whereas those from the wings, legs, and male genitalia are less congruent with the MP molecular tree (Table 2). When morphological characters were reconstructed over the constrained ML tree, consistency and retention indices decreased for most morphological categories, but the degree of decrease is largest for female genital characters (0.35 for CI, whereas 0-0.07 for other categories; 0.24 for RI, in contrast to 0-0.10 for other categories). This clearly shows that the characters coded from the female genitalia are the main source of the conflict between the morphological and molecular trees. For example, monophyly of Homilopsocidea excluding Archipsocidae was supported by the morphological phylogeny, and the characters supporting this clade were both selected from female genitalia (Yoshizawa 2002: see above). Monophyly of Homilopsocidea was strongly rejected by the molecular data, which is one of the most substantial differences between the morphological and

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molecular phylogeny.

Characters from the thorax were also more congruent with molecular phylogeny, as was the case for female genital characters. However, in contrast to the female genital characters, no decrease of consistency and retention indices was detected when the characters were reconstructed on the constrained ML tree. As discussed above, the molecular and morphological phylogenies were almost completely concordant concerning the major clades of Psocomorpha, and thoracic characters contributed mostly to the resolution of the deep level phylogeny. Genital characters are known to evolve very rapidly, frequently utilized for delimitating closely related species (Song & Bucheli 2010, but they also argued that male genitalia are potentially useful in resolving a variety of levels in a phylogeny), whereas useful signal for deeper phylogenetic scales have been detected from more slowly evolving thoracic characters for many insect groups (e.g., Friedrich & Beutel 2010a b). The present results are also congruent with these previous suggestions. In contrast, the thoracic characters do not contain any signal in resolving shallower clades, and inclusion of both rapidly and slowly evolving characters are important in obtaining a fully resolved phylogeny. To avoid the negative effects from the rapidly evolving morphological characters, information as presented in Table 2 may be useful for establishing an empirical scheme of character weighting.

Except for the basal split of Archipsocetae and sister relationship between Epipsocetae + Psocetae, no unambiguous morphological apomorphies are identified for the relationships among infraorders in the constrained ML tree (Fig. 3). Further morphological investigation of Psocomorpha is required to test or verify the molecular phylogeny presented here and to provide new apomorphies for the major groups we identified.

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Figure captions

Figure 1. Maximum likelihood tree estimated from the data set with all taxa included. Branch lengths are proportional to ML estimated branch length. Numbers associated with the branches are Bayesian posterior probabilities (above) and ML bootstrap support values (below). See text for dotted circle.

Figure 2. Maximum likelihood tree estimated from the data set excluding *Lachesilla*. Branch lengths are proportional to ML estimated branch length. Numbers associated with the branches are Bayesian posterior probabilities (above) and ML bootstrap support values (below). See text for dotted circle.

Figure 3. Most parsimonious reconstruction of morphological characters on the MP tree (above: strict consensus of trees obtained by successive and implied weighting schemes) and ML topology (bottom). Black and gray bars on branches indicate non-homoplasious and homoplasious character states supporting the branch, respectively. Numbers associated with character bar indicate character number and its state (see Online Supplement). Characters supporting interfamilial relationships only are indicated, but lengths for intrafamilial branches are also proportional to the number of characters supporting the branch.

Table 1. Taxa examined in the study. Families and higher level taxon names of Psocomorpha and Troctomorpha followed Lienhard & Smithers (2002). Infraorders for Troctomorpha followed Yoshizawa, Lienhard and Johnson (2006).

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Table 2. Comparisons of homology indices calculated on MP trees and ML topology. Numbers of characters included in each morphological category are follow: head 11, thorax 6, wings 22, legs 4, male (M.) genitalia 8, and female (F.) genitalia 17.

	ML constrained	MP trees	ΔML–MP
Tree Length	212	175	37
Consistency Index			
Total	0.41	0.49	-0.08
Head	0.41	0.48	-0.07
Thorax	0.67	0.67	0.00
Wings	0.40	0.44	-0.04
Legs	0.18	0.20	-0.02
M. genitalia	0.36	0.43	-0.07
F. genitalia	0.45	0.80	-0.35
Retention Index			
Total	0.73	0.81	-0.08
Head	0.80	0.85	-0.05
Thorax	0.92	0.92	0.00
Wings	0.69	0.73	-0.04
Legs	0.62	0.66	-0.04
M. genitalia	0.60	0.70	-0.10
F. genitalia	0.70	0.94	-0.24

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Table 3. Higher level classification of Psocomorpha based on this study. Families marked with "" indicate their monophyly was not supported, but could also not be rejected statistically.

ARCHIPSOCETAE
- Archipsocidae

CAECILIUSETAE (see Yoshizawa, Mockford & Johnson 2014 for detail)
- Amphipsocidae
- Stenopsocidae
- Dasydemellidae
- Asiopsocidae
- Paracaeciliidae
- Caeciliusidae

HOMILOPSOCIDEA
- Peripsocidae
- Ectopsocidae
- "Elipsocidae"
- "Lachesillidae"
- "Mesopsocidae"

PHILOTARSETAE
- Philotarsidae
- Trichopsocidae
- Pseudocaeciliidae (including Calopsocidae and Bryopsocidae as new synonym of Pseudocaeciliidae and Zelandpsocinae, respectively)

EPIPSOCETAE
- Dolabellopsocidae
- Cladiopsocidae
- Ptiloneuridae
- Epipsocidae (including Neurostigmatidae as a new synonym)

PSOCETAE
- Psilopsocidae
- Hemipsocidae
- Myopsocidae
- Psocidae

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Suborder	Infraorder	Family	Genus	Species	Locality	Extract Code	18S	H3	16S	COI
Trogiomorpha	Prionoglaridetae	Prionoglaridae	*Prionoglaris*	*sp 1*	Greece	KY249	AY630456	DQ104773	DQ104745	-
Trogiomorpha	Prionoglaridetae	Prionoglaridae	*Siamoglaris*	*zebrina*	Thailand	KY255	DQ104798	-	DQ104746	AB918973
Trogiomorpha	Prionoglaridetae	Prionoglaridae	*Speleketor*	*irwini*	USA	KY308	DQ104799	DQ104774	DQ104747	-
Trogiomorpha	Psyllipsocetae	Psyllipsocidae	*Dorypteryx*	*domestica*	Czech Rep.	KY97, KY253	AY630454	DQ104777	DQ104749	-
Trogiomorpha	Psyllipsocetae	Psyllipsocidae	*Psyllipsocus*	*oculatus*	Mexico	Psocu.2.4.2002.12	AY630455	DQ104776	DQ104748	GU569242
Trogiomorpha	Atropetae	Psoquillidae	*Rhyopsocus*	*sp.*	USA	KY297	DQ104801	DQ104778	DQ104750	-
Trogiomorpha	Atropetae	Trogiidae	*Lepinotus*	*reticulatus*	UK	Leret.11.17.2003.5	AY630452	-	DQ104756	AB918974
Trogiomorpha	Atropetae	Trogiidae	*Lepinotus*	*sp.*	USA	Lesp.11.2.2001.6	AY630451	DQ104783/	DQ104755	-
Trogiomorpha	Atropetae	Trogiidae	*Trogium*	*pulsatorium*	UK	Tgpul.11.17.2003.4	AY630453	DQ104786	DQ104759	GU569243
Trogiomorpha	Atropetae	Lepidopsocidae	*Echmepteryx*	*hageni*	USA	Echag.1.16.2001.1	AY630448	DQ104782	DQ104754	GU569245
Trogiomorpha	Atropetae	Lepidopsocidae	*Echmepteryx*	*madagascarensis*	Japan	KY61, KY246	AY630447	DQ104781	DQ104753	AB918975
Trogiomorpha	Atropetae	Lepidopsocidae	*Lepium*	*sp.*	PNG	Lpsp.11.17.2003.11	AY630451	GU569312	GU569187	GU569244
Trogiomorpha	Atropetae	Lepidopsocidae	*Neolepolepis*	*occidentalis*	USA	Neocc.8.31.2001.13	AY630446	DQ104779	DQ104751	GU569246
Trogiomorpha	Atropetae	Lepidopsocidae	*Pteroxanium*	*kelloggi*	USA	Pxkel.12.4.2003.7	AY630449	DQ104784	DQ104757	-
Trogiomorpha	Atropetae	Lepidopsocidae	*Soa*	*sp.*	PNG	KY323	DQ104802	DQ104780	DQ104752	-
Troctomorpha	Amphientometae	Amphientomidae	*Stimulopalpus*	*japonicus*	USA	Stjap.8.31.2001.15	AY630459	GU569345	GU569220	GU569286
Troctomorpha	Amphientometae	Amphientomidae	*Cymatopsocus*	*sp.*	Malaysia	KY220	AY630460	AB919021	AB918935	AB918976
Troctomorpha	Amphientometae	Amphientomidae	*Genus*	*sp.*	Malaysia	KY197, KY256	AY630458	AB919022	AB918936	-
Troctomorpha	Amphientometae	Compsocidae	*Compsocus*	*elegans*	Costa Rica	Coele.3.24.2001.14	AY630462	DQ104790	DQ104763	GU569287
Trocotomorpha	Amphientometae	Electrentomidae	*Epitroctes*	*sp.*	Mexico	Eisp.11.17.2003.6	AY630463	AB919023	AB918937	-
Troctomorpha	Amphientometae	Musapsocidae	*Musapsocus*	*sp.*	Mexico	Musp.2.4.2002.13	AY630461	DQ104789	DQ104762	GU569285
Troctomorpha	Amphientometae	Protroctopsocidae	*Protroctopsocus*	*enigmaticus*	Mexico	Preni.3.2.2004.10	AB919004	AB919024	AB918938	-
Troctomorpha	Amphientometae	Troctopsocidae	*Selenopsocus*	*sp.*	Malaysia	KY198	AY630457	AB919025	AB918939	-
Troctomorpha	Amphientometae	Troctopsocidae	*Thaipsocus*	*sp.*	Malaysia	KY258	AB919005	AB919026	AB918940	AB918977
Troctomorpha	Nanopsocetae	Sphaeropsocidae	*Badonnelia*	*titei*	Switzerland	Batit.12.4.2003.12	AY630464	GU569346	GU569221	GU569288
Psocomorpha	Epipsocetae	Cladiopsocidae	*Spurostigma*	*sp.*	Mexico	Spsp.3.2.2004.16	AB919008	AB919028	AB918942	-
Psocomorpha	Epipsocetae	Cladiopsocidae	*Spurostigma*	*sp.*	Dominica	Spsp.3.2.2004.15	AB919007	AB919027	AB918941	-
Psocomorpha	Epipsocetae	Cladiopsocidae	*Cladiopsocus*	*sp.*	Mexico	Cloco.3.2.2004.14	AB919009	AB919029	AB918943	-
Psocomorpha	Epipsocetae	Dolabellopsocidae	*Dolabellopsocus*	*sp.*	Costa Rica	Dosp.3.2.2004.6	AB919010	AB919030	AB918944	AB918978
Psocomorpha	Epipsocetae	Epipsocidae	*Bertkauia*	*crosbyana*	USA	Becro.8.31.2001.14	AY630537	DQ104793	DQ104766	GU569250
Psocomorpha	Epipsocetae	Epipsocidae	*Goja*	*sp.*	Costa Rica	Gosp.12.4.2003.3	AY630538	GU569315	GU569191	GU569251
Psocomorpha	Epipsocetae	Epipsocidae	*Epipsocus*	*sp.*	Malaysia	KY205	AY630539	GU569314	GU569189	GU569249
Psocomorpha	Epipsocetae	Epipsocidae	*Mesepipsocus*	*sp.*	Dominica	Mpsp.3.2.2004.13	AB919011	AB919031	AB918945	AB918979
Psocomorpha	Epipsocetae	Neurostigmatidae	*Neurostigma*	*sp.*	Peru	KY471	AB919012	AB919032	AB918946	-
Psocomorpha	Caeciliusetae	Amphipsocidae	*Polypsocus*	*corruptus*	USA	Pocor.8.31.2001.6	AY630488	GU569334	GU569209	GU569273
Psocomorpha	Caeciliusetae	Amphipsocidae	*Kolbia*	*fusconervosa*	Japan	KY208	AY630487	GU569333	GU569208	GU569272
Psocomorpha	Caeciliusetae	Amphipsocidae	*Amphipsocus*	*japonicus*	Japan	KY211	AY630489	GU569331	AB918947	AB918980
Psocomorpha	Caeciliusetae	Amphipsocidae	*Taeniostigma*	*elongatum*	Malaysia	KY221	AY630486	GU569335	GU569210	GU569274
Psocomorpha	Caeciliusetae	Amphipsocidae	*Calocaecilius*	*decipiens*	Malaysia	KY201	AY630485	GU569332	GU569207	GU569271
Psocomorpha	Caeciliusetae	Amphipsocidae	*Tagalopsocus*	*sp.*	Malaysia	KY257	AB856949	AB856968	-	AB918981
Psocomorpha	Caeciliusetae	Asiopsocidae	*Asiopsocus*	*sonorensis*	USA	Assp.11.17.2003.3	AY630481	GU569330	GU569205	GU569269
Psocomorpha	Caeciliusetae	Caeciliusidae	*Valenzuela*	*flavidus*	USA	Vafla.8.31.2001.5	AY630499	GU569343	GU569218	GU569283
Psocomorpha	Caeciliusetae	Caeciliusidae	*Valenzuela*	*flavidus*	Japan	KY223	AY630498	AB919033	AB918948	AB918982
Psocomorpha	Caeciliusetae	Caeciliusidae	*Valenzuela*	*oyamai*	Japan	KY210	AY630497	AB856966	AB856930	-
Psocomorpha	Caeciliusetae	Caeciliusidae	*Xanthocaecilius*	*sommermanae*	USA	Xasom.8.31.2001.4	AY630500	GU569344	GU569219	GU569284
Psocomorpha	Caeciliusetae	Caeciliusidae	*Caecilius*	*fuscopterus*	Japan	KY227	AY630484	AB856969	AB856933	-
Psocomorpha	Caeciliusetae	Caeciliusidae	*Dypsocus*	*coleoptratus*	Japan	KY202	AY630482	GU569341	GU569216	GU569281
Psocomorpha	Caeciliusetae	Caeciliusidae	*Fuelleborniella*	*sp.*	Ghana	Fusp.11.24.2003.6	AY630496	GU569339	GU569214	GU569279
Psocomorpha	Caeciliusetae	Caeciliusidae	*Isophanes*	*sp.*	Japan	KY230	AY630483	GU569342	GU569217	GU569282
Psocomorpha	Caeciliusetae	Caeciliusidae	*Paracaecilius*	*japanus*	Japan	KY233	AY630501	AB856970	AB856934	-
Psocomorpha	Caeciliusetae	Caeciliusidae	*Pericaecilius*	*sp.*	Taiwan	KY239	AY630495	GU569340	GU569215	GU569280
Psocomorpha	Caeciliusetae	Dasydemellidae	*Matsumuraiella*	*radiopicta*	Japan	KY236	AY630493	DQ104797	DQ104770	GU569275
Psocomorpha	Caeciliusetae	Dasydemellidae	*Ptenopsila*	*sp.*	Chile	KY243	AY630494	-	AB856929	-
Psocomorpha	Caeciliusetae	Dasydemellidae	*Teliapsocus*	*conterminus*	USA	Tecon.3.2.2004.1	AB856951	AB856972	AB856936	AB918983
Psocomorpha	Caeciliusetae	Stenopsocidae	*Graphopsocus*	*cruciatus*	USA	Grcru.11.2.2001.5	AY630490	GU569336	GU569211	GU569276
Psocomorpha	Caeciliusetae	Stenopsocidae	*Stenopsocus*	*aphidiformis*	Japan	KY219	AY630491	GU569337	GU569212	GU569277
Psocomorpha	Caeciliusetae	Stenopsocidae	*Stenopsocus*	*nigricellus*	Japan	KY241	AY630492	GU569338	GU569213	GU569278
Psocomorpha	Homilopsocidea	Archipsocidae	*Archipsocus*	*nomas*	USA	Arnom.3.16.2001.2	AY900133	AB919034	AY275354	AY275279
Psocomorpha	Homilopsocidea	Archipsocidae	*Archipsocus*	*recens*	Taiwan	KY206	AY630480	AB919035	AB918949	-
Psocomorpha	Homilopsocidea	Archipsocidae	*Archipsocus*	*sp. 1*	Malaysia	KY209	GU569164	GU569313	GU569188	GU569247
Psocomorpha	Homilopsocidea	Archipsocidae	*Archipsocus*	*sp. 2*	Malaysia	KY226	AY630478	DQ104791	DQ104764	GU569248
Psocomorpha	Homilopsocidea	Archipsocidae	*Pararchipsocus*	*sp.*	Costa Rica	Pasp.3.2.2004.5	AB919006	AB919036	AB918950	AB918984
Psocomorpha	Homilopsocidea	Philotarsidae	*Aaroniella*	*badonneli*	USA	Aabad.8.31.2001.8	AY630532	GU569317	GU569192	GU569253
Psocomorpha	Homilopsocidea	Philotarsidae	*Aaroniella*	*sp.*	Japan	KY216	AY630533	AB919037	AB918951	AB918985
Psocomorpha	Homilopsocidea	Philotarsidae	*Haplophallus*	*wongae*	Australia	Hawon.12.4.2003.5	AY630528	-	AB918952	AB918986
Psocomorpha	Homilopsocidea	Philotarsidae	*Haplophallus*	*sp.*	Japan	KY204	AY630529	AB919038	AB918953	AB918987
Psocomorpha	Homilopsocidea	Philotarsidae	*Philotarsopsis*	*ornatus*	Australia	Prsp.12.4.2003.6	AY630531	-	AB918954	AB918988
Psocomorpha	Homilopsocidea	Philotarsidae	*Philotarsus*	*kwakiutl*	USA	Phkwa.11.17.2003.	AY630530	GU569318	GU569193	GU569254
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Allocaecilius*	*sinensis*	Japan	KY232	AY630526	DQ104796	DQ104769	GU569258
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Phallocaecilius*	*hirsutus*	Japan	KY217	AY630523	GU569320	GU569195	GU569256
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Mepleres*	*suzukii*	Japan	KY242	AY630525	AB919039	AB918955	AB918989
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Ophiodopelma*	*glyptocephalum*	Japan	KY234	AY630524	AB919040	AB918956	-
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Heterocaecilius*	*solocipennis*	Japan	Hcsol.12.4.2003.8	AY630521	AB919041	AB918957	AB918990
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Heterocaecilius*	*fuscus*	Japan	KY237	AY630520	DQ104795	DQ104768	GU569257
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Lobocaecilius*	*monicus*	Australia	Lomon.12.4.2003.1	AY630522	AB919042	AB918958	
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Pseudocaecilius*	*citricola*	Australia	Pccit.11.17.2003.12	AY630527	GU569321	GU569196	GU569259
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Australopsocus*	*sp.*	New Caledonia	Ausp.12.4.2003.9	AY630534	AB919043	AB918959	AB918991
Psocomorpha	Homilopsocidea	Pseudocaeciliidae	*Zelandopsocus*	*sp.*	New Caledonia	Zesp.11.24.2003.9	AY630535	AB919044	AB918960	-
Psocomorpha	Homilopsocidea	Bryopsocidae	*Bryopsocus*	*sp.*	New Zealand	KY470	AB919013	AB919045	AB918961	-
Psocomorpha	Homilopsocidea	Trichopsocidae	*Trichopsocus*	*dalii*	Switzerland	KY248	AY630536	AB919046	AB918962	-
Psocomorpha	Homilopsocidea	Trichopsocidae	*Trichopsocus*	*sp.*	USA	KY322	AB919014	AB919047	AB918963	AB918992
Psocomorpha	Homilopsocidea	Calopsocidae	*Calopsocus*	*marginalis*	PNG	Camar.12.4.2003.1	AB919015	AB919048	AB918964	AB918993
Psocomorpha	Homilopsocidea	Calopsocidae	*Calopsocus*	*furcata*	Malaysia	KY199	AY630519	GU569319	GU569194	GU569255
Psocomorpha	Homilopsocidea	Ectopsocidae	*Ectopsocopsis*	*cryptomeriae*	USA	Etcry.11.17.2003.2	AY630511	GU569323	GU569198	GU569261
Psocomorpha	Homilopsocidea	Ectopsocidae	*Ectopsocus*	*meridionalis*	USA	Epmer.2.3.2001.4	AY630512	GU569322	GU569197	GU569260
Psocomorpha	Homilopsocidea	Ectopsocidae	*Ectopsocus*	*sp.*	Japan	KY212	AY630510	AB919049	AB918965	AB918994
Psocomorpha	Homilopsocidea	Elipsocidae	*Kilauella*	*sp.*	Hawaii	Kisp.11.24.2003.10	AY630517	GU569329	GU569204	GU569267
Psocomorpha	Homilopsocidea	Elipsocidae	*Cuneopalpus*	*cyanops*	USA	KY318	AB919016	AB919050	AB918966	AB918995
Psocomorpha	Homilopsocidea	Elipsocidae	*Elipsocus*	*sp.*	USA	KY319	AB919017	AB919051	AB918967	AB918996
Psocomorpha	Homilopsocidea	Elipsocidae	*Propsocus*	*pulchripennis*	USA	KY320	AB919018	AB919052	AB918968	AB918997
Psocomorpha	Homilopsocidea	Elipsocidae	*Reuterella*	*helvimacula*	USA	Rehel.3.2.2004.7	AB919019	AB919053	AB918969	-
Psocomorpha	Homilopsocidea	Elipsocidae	*Nepiomorpha*	*sp.*	Malaysia	KY200	AY630518	-	AB856928	AB918998
Psocomorpha	Homilopsocidea	Mesopsocidae	*Mesopsocus*	*unipunctatus*	USA	Meuni.12.4.2003.4	AY630515	-	AB856927	AB918999
Psocomorpha	Homilopsocidea	Mesopsocidae	*Mesopsocus*	*hongkongensis*	Japan	KY224	AY630516	DQ104794	DQ104767	GU569268
Psocomorpha	Homilopsocidea	Mesopsocidae	*Idatenopsocus*	*orientalis*	Japan	KY203	AY630513	-	AB918970	-
Psocomorpha	Homilopsocidea	Peripsocidae	*Kaestneriella*	*sp.*	USA	Kasp.11.24.2003.5	AY630506	GU569324	GU569199	GU569262
Psocomorpha	Homilopsocidea	Peripsocidae	*Peripsocus*	*madidus*	USA	Pemad.8.31.2001.7	AY630508	AB919054	AB918971	AB919000

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

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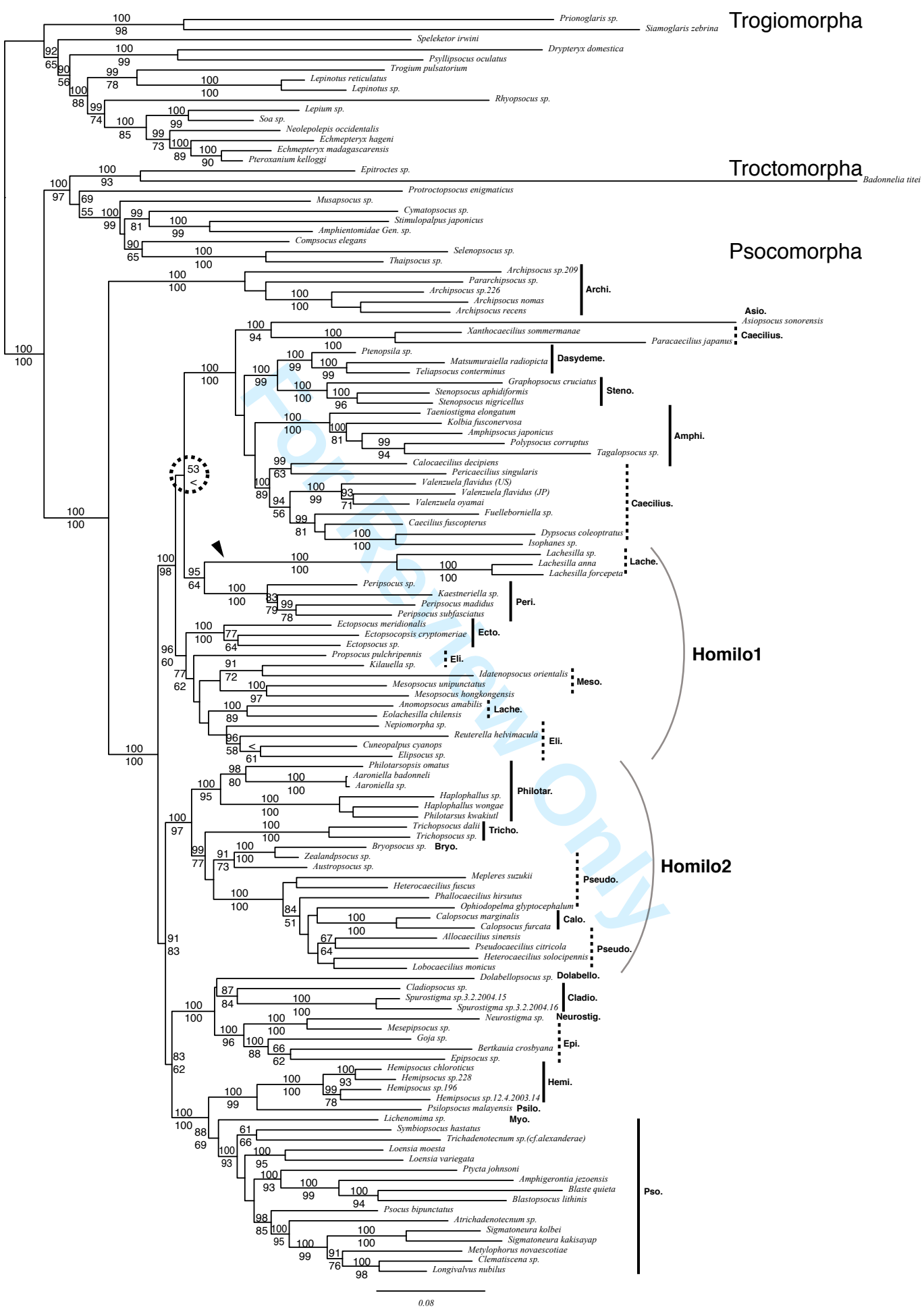

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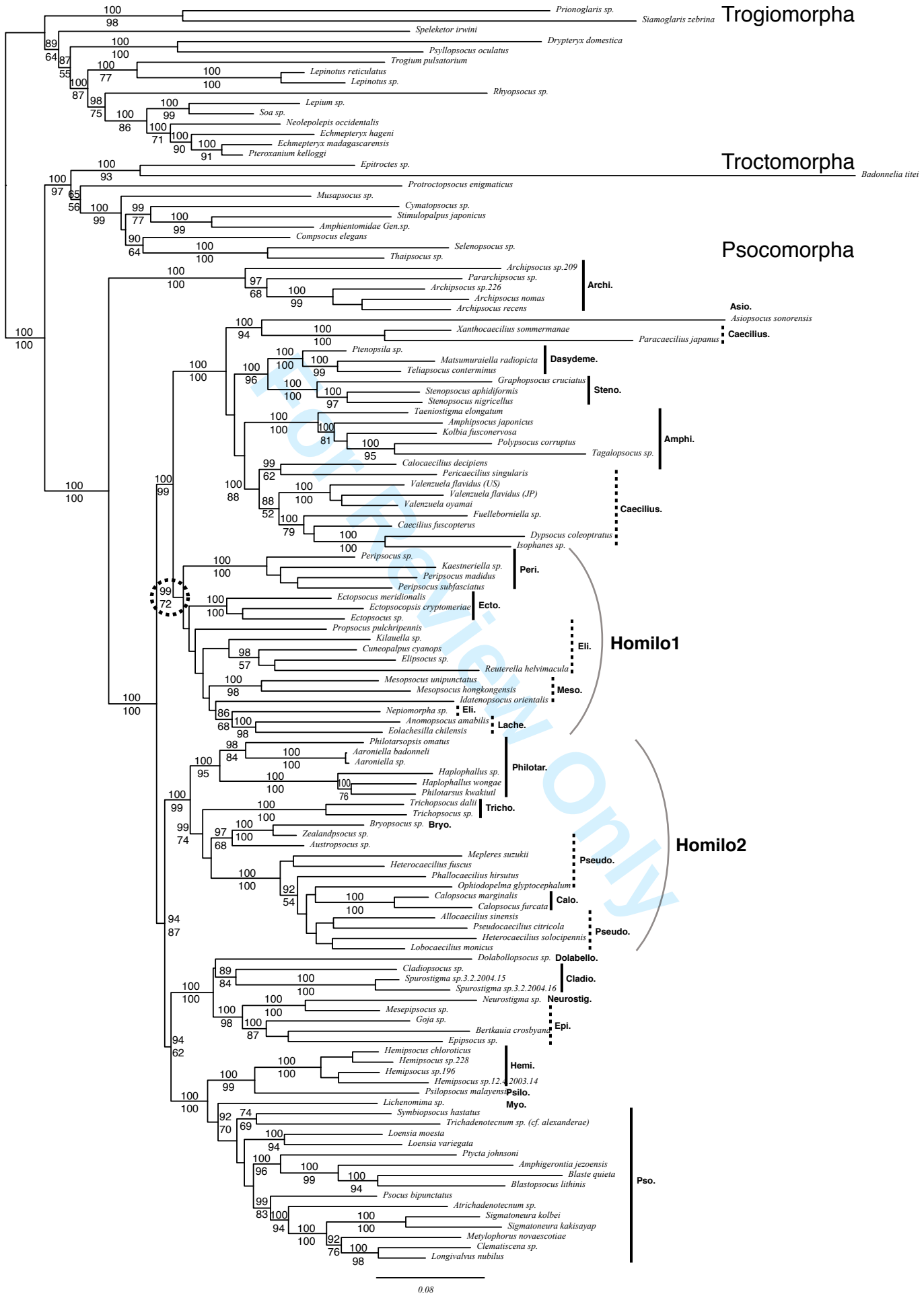

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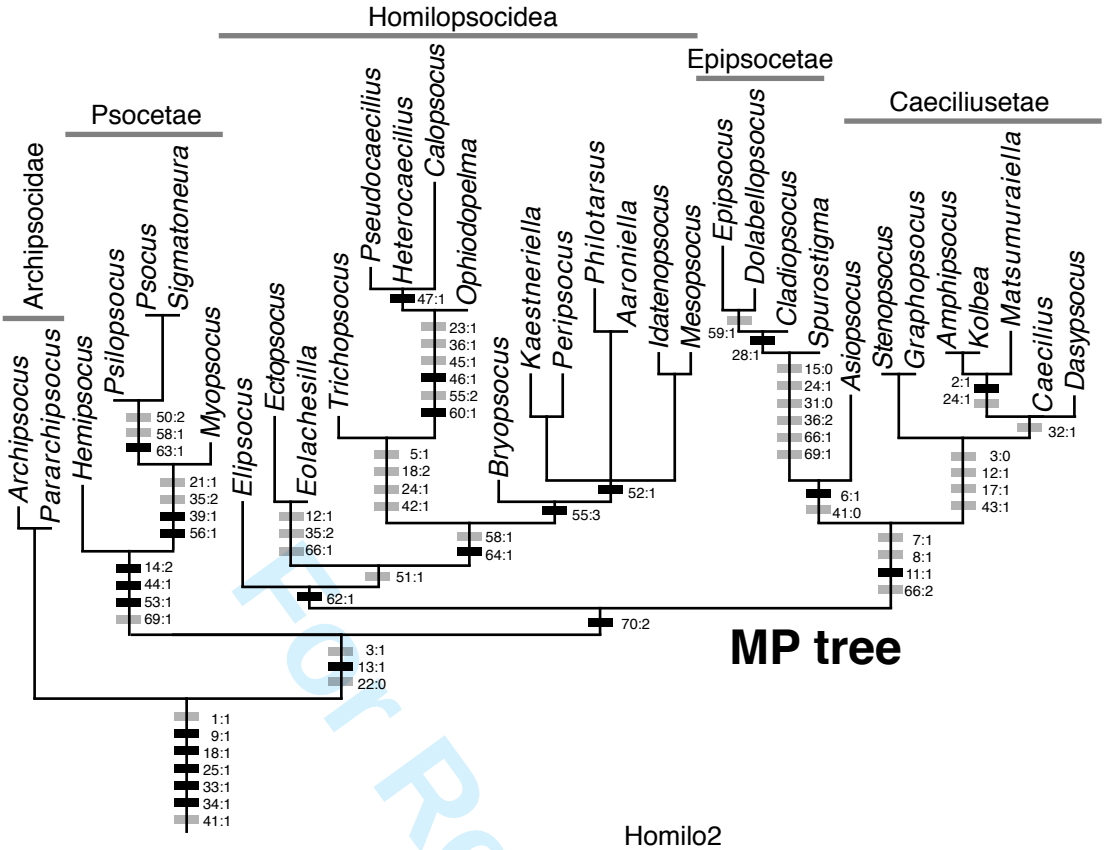

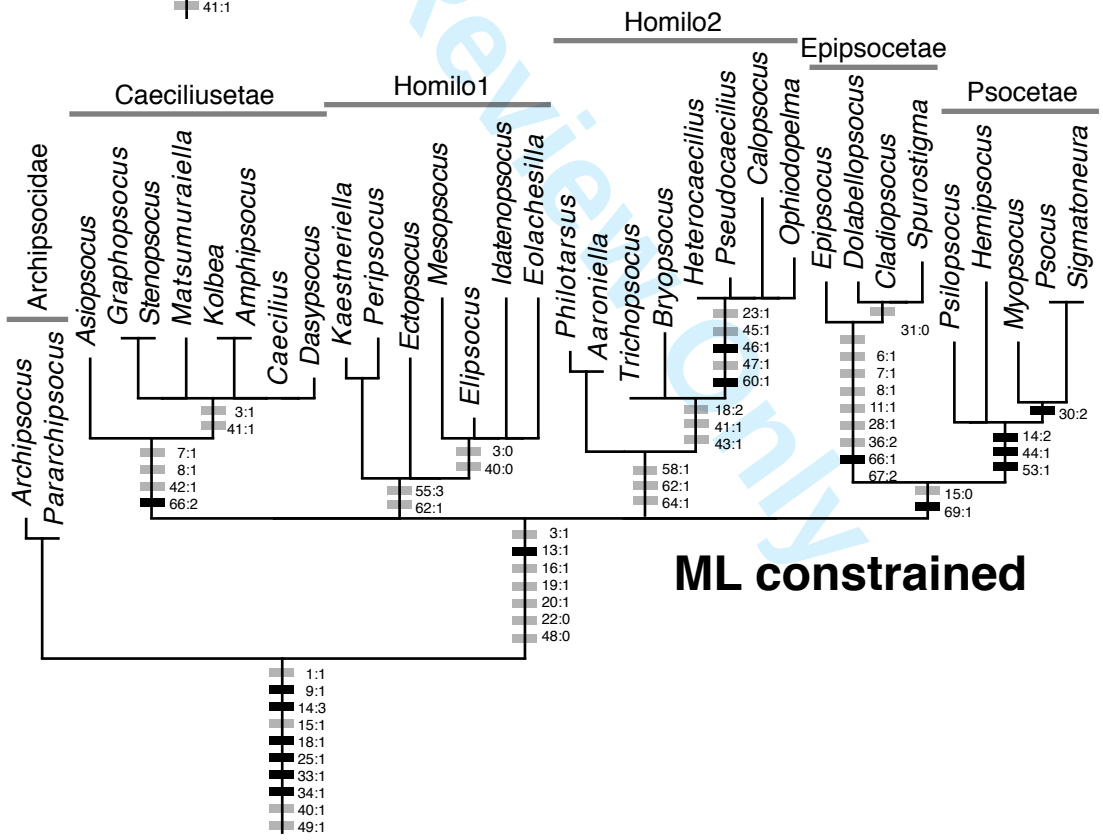

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