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Molecular systematics of Psocomorpha (Psocoptera)

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Abstract. Previous classification of the insect order Psocoptera has relied on morphological characters. Psocoptera are generally divided into three suborders: Trogiomorpha, Troctomorpha, and Psocomorpha. Traditional classification divides the Psocomorpha into four infraorders (Homilopsocidea, Caeciliusetae, Psocetae and Epipsocetae), but a recent morphological cladistic study removed Archipsocidae from Homilopsocidea and Hemipsocidae from Psocetae. We investigated the phylogenetic relationships within the suborder Psocomorpha using DNA sequences from the nuclear 18S and mitochondrial 16S, 12S and cytochrome oxidase I genes. Phylogenetic analyses of these gene sequences supported monophyly for Psocomorpha. In addition, monophyly of the traditional subgroups Caeciliusetae and Psocetae was generally supported. Monophyly of Homilopsocidea was not supported, and *Archipsocus* is removed from this group. Although the molecular phylogeny is generally consistent with recent cladistic studies of morphological characters, we found no evidence that Hemipsocidae should be removed from Psocetae.

Introduction

The insect order Psocoptera (booklice and barklice) consists of over 5000 species with a world-wide distribution. Psocoptera are generally divided into three suborders: Trogiomorpha, Troctomorpha and Psocomorpha (Roesler, 1944; Badonnel, 1951; Mockford, 1993; Smithers, 1996; Lienhard & Smithers, 2002). There has been extensive consideration of the classification of Psocoptera from a morphological perspective. Smithers (1972) posited phylogenetic relationships for Psocoptera based on morphological characters, but the classification derived from this work has been largely abandoned (Mockford, 1993; Smithers, 1996; Lienhard, 1998; Lienhard & Smithers, 2002).

The suborder Psocomorpha is the largest within Psocoptera, containing twenty-five of the thirty-nine extant families (Lienhard & Smithers, 2002). Most current classification within Psocomorpha follows the general scheme of Badonnel (1951). Psocomorpha are divided into four infraorders: Epipsocetae, Caeciliusetae, Homilopsocidea and Psocetae (Lienhard & Smithers, 2002), based on general impressions of morphology. A recent formal phylogenetic analysis of morphological characters (Yoshizawa, 2002) did not recover monophyly of traditional Homilopsocidea or Psocetae (as defined by Lienhard & Smithers, 2002). Archipsocidae was removed from Homilopsocidea and Hemipsocidae was removed from Psocetae (Yoshizawa, 2002; see Table 1).

The goal of the present study was to test these previous classifications using data from DNA sequences for members of Psocomorpha and outgroup taxa (Trogiomorpha and Troctomorpha). Using partial sequences of four genes, we tested the monophyly of three of the four infraorders recognized by Lienhard & Smithers (2002) and compared our phylogenetic results with those of Yoshizawa (2002). Our study represents the first molecular systematic study of the higher classification of Psocoptera.

Methods

Sequences

We obtained fresh specimens of seventeen species of Psocomorpha and eight outgroup taxa in suborders Trogiomorpha and Troctomorpha (Table 2) and stored these in 95% ethanol in a freezer. These samples included representatives of each of the four infraorders of Psocomorpha in a diversity of families, as well as representatives of the enigmatic families Archipsocidae and Hemipsocidae (Yoshizawa, 2002). Genomic DNA was extracted from whole specimens using the Qiagen DNAeasy Tissue Kit with the manufacturer's protocols (using a 36 h initial incubation). Because this procedure did not destroy the specimen, we retained the specimens in ethanol as extraction

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Table 1. Previous classification schemes of the families of Psocomorpha. Families are listed below infraorder. Families in quotation marks are those considered to be tentative by Yoshizawa (2002). We follow the classification of Lienhard & Smithers (2002) throughout.

Lienhard & Smithers (2002)	Yoshizawa (2002)
Infraorder: Epipsocetae	Infraorder: Archipsocetae
Epipsocidae	Archipsocidae
Neurostigmatidae	Infraorder: Hemipsocetae
Dolabellopsocidae	Hemipsocidae
Cladiopsocidae	Infraorder: Psocetae
Ptiloneuridae	Myopsocidae
Infraorder: Caeciliusetae	Psilopsocidae
Asiopsocidae	Psocidae
Caeciliusidae	Infraorder: Homilopsocidea
Stenopsocidae	Elipsocidae
Amphipsocidae	Ectopsocidae
Dasydemellidae	'Lachesillidae'
Infraorder: Homilopsocidea	Trichopsocidae
Lachesillidae	'Pseudocaeciliidae'
Ectopsocidae	Calopsocidae
Peripsocidae	Bryopsocidae
Calopsocidae	Peripsocidae
Trichopsocidae	Philotarsidae
Archipsocidae	Mesopsocidae
Pseudocaeciliidae	Infraorder: Epipsocetae
Bryopsocidae	'Cladiopsocidae'
Philotarsidae	Ptiloneuridae
Elipsocidae	Dolabellopsocidae
Mesopsocidae	Epipsocidae
Infraorder: Psocetae	Infraorder: Caeciliusetae
Hemipsocidae	Asiopsocidae
Psocidae	Stenopsocidae
Psilopsocidae	Amphipsocidae
Myopsocidae	'Caeciliusidae'

vouchers (deposited at the Illinois Natural History Survey insect collection).

We used the polymerase chain reaction to amplify various gene regions from the DNA extracts. The polymerase chain reaction protocols followed Johnson & Clayton (2000). We amplified a portion of the nuclear 18S ribosomal RNA gene using the primers 18Sai and 18Sbi (Whiting *et al*., 1997). Portions of the mitochondrial 12S ribosomal RNA, 16S ribosomal RNA and cytochrome oxidase I (COI) genes were amplified. We used the primers 12Sai and 12Sbi (Simon *et al*., 1994) for 12S, 16Sar and 16Sbr (Simon *et al*., 1994) for 16S, and L6625 and H7005 (Hafner *et al*., 1994) for COI.

The polymerase chain reaction products were purified and sequenced as described by Johnson & Clayton (2000). We used the polymerase chain reaction primers in the respective sequencing reactions, sequencing both forward and reverse complementary strands (GenBank accession numbers AY275275–AY275374). Complementary sequences were reconciled using SEQUENCHER 3.0 (GeneCodes). Cross-species alignment of the protein coding COI gene was straightforward. We aligned 18S sequences by eye, because most regions of the 18S gene are highly conserved. One portion of the 18S gene (aligned bases 257–458) was highly variable, making alignment difficult. This section was excluded from all phylogenetic analyses. We aligned 12S and 16S sequences across species using the program CLUSTAL X (Thompson *et al*., 1994).

Phylogenetic analyses

All phylogenetic analyses were performed using the program PAUP* (Swofford, 2002). We used representatives from Troctomorpha and Trogiomorpha (Table 1) as a composite outgroup to root the tree for Psocomorpha. Data from all gene regions were combined and analysed using parsimony, neighbour joining and maximum likelihood. We used ten random addition replicates with tree bisection-reconnection (TBR) branch swapping in unordered, unweighted parsimony analyses. We bootstrapped (Felsenstein, 1985) the parsimony dataset using 1000 replicates. We also conducted parsimony and bootstrap analyses of each gene separately, to determine which nodes in the combined tree were supported by which genes in separate analyses. For neighbour joining analyses we used uncorrected *p*-distance, but the results did not change under distances that correct for multiple substitutions (e.g. Kimura 2-parameter, HKY85). For maximum likelihood analyses we used the parsimony tree and nested likelihood ratio tests (Huelsenbeck & Crandall, 1997) to determine the simplest likelihood model that could not be rejected in favour of a more complex model. A general time reversible model, with unequal base frequencies, invariant sites and rate heterogeneity according to a gamma distribution was favoured over simpler models. We used the resulting estimated parameters in likelihood searches (ten random addition, tree bisection-reconnection (TBR) replicates).

Results

The aligned dataset resulted in a total of 2181 base pairs included in the phylogenetic analysis. In total, 867 of these bases were potentially phylogenetically informative. Within Psocomorpha, genetic divergences varied among the four gene regions, with the aligned region of 18S being the most conserved (Table 3). Within the outgroup, the mitochondrial divergence between the two species of *Liposcelis* (28.8% for COI, 39.2% for 12S, and 36.8% for 16S) was higher than among all lineages of Psocomorpha (Table 3). However, the divergence between *Liposcelis bostrychophila* and *Liposcelis decolor* for the nuclear 18S gene (5.2%) was considerably less than the maximum divergence of that gene within Psocomorpha. Thus, it appears that the rate of molecular substitution in the mitochondrion of *Liposcelis* is elevated relative to other Psocoptera. The long branches leading to Liposcelididae in the phylogenetic trees (Figs 1–3) also provide evidence of a rate increase relative to other Psocoptera. This elevated rate, however, does not seem to affect dramatically the inferred topology of the ingroup

Table 2. Specimens used in the study (classification according to Lienhard & Smithers, 2002).

Species	Suborder	Infraorder	Family
Ingroup			
Ectopsocus meridionalis	Psocomorpha	Homilopsocidea	Ectopsocidae
Lachesilla anna	Psocomorpha	Homilopsocidea	Lachesillidae
Peripsocus madidus	Psocomorpha	Homilopsocidea	Peripsocidae
Peripsocus subfasciatus	Psocomorpha	Homilopsocidea	Peripsocidae
Archipsocus nomas	Psocomorpha	Homilopsocidea	Archipsocidae
Aaroniella badonneli	Psocomorpha	Homilopsocidea	Philotarsidae
Graphopsocus cruciatus	Psocomorpha	Caeciliusetae	Stenopsocidae
Xanthocaecilius sommermanae	Psocomorpha	Caeciliusetae	Caeciliusidae
Valenzuela flavidus	Psocomorpha	Caeciliusetae	Caeciliusidae
Polypsocus corruptus	Psocomorpha	Caeciliusetae	Amphipsocidae
Loensia moesta	Psocomorpha	Psocetae	Psocidae
Metylophorus novaescotiae	Psocomorpha	Psocetae	Psocidae
Trichadenotecnum 'alexanderae'[a]	Psocomorpha	Psocetae	Psocidae
Blastopsocus lithinus	Psocomorpha	Psocetae	Psocidae
Lichenomima sp.	Psocomorpha	Psocetae	Myopsocidae
Hemipsocus chloroticus	Psocomorpha	Psocetae	Hemipsocidae
Bertkauia crosbyana	Psocomorpha	Epipsocetae	Epipsocidae
Outgroup			
Embidopsocus needhami	Troctomorpha	Nanopsocetae	Liposcelididae
Liposcelis bostrychophila	Troctomorpha	Nanopsocetae	Liposcelididae
Liposcelis decolor	Troctomorpha	Nanopsocetae	Liposcelididae
Tapinella sp.	Troctomorpha	Nanopsocetae	Pachytroctidae
Compsocus elegans	Troctomorpha	Amphientometae	Compsocidae
Stimulopalpus japonicus	Troctomorpha	Amphientometae	Amphientomidae
Echmepteryx hageni	Trogiomorpha	Atropetae	Lepidopsocidae
Neolepolepis occidentalis	Trogiomorpha	Atropetae	Lepidopsocidae

[a]DNA extraction voucher could not be identified to species because these species are part of a difficult complex of mostly parthenogenetic forms (*alexanderae* species complex).

(Psocomorpha), because the differences between trees resulting from the different analytical methods were slight.

Parsimony analysis of the combined dataset produced a single completely resolved tree (Fig. 1). This tree recovered monophyly of Psocomorpha (89% bootstrap support) relative to the other Psocoptera included in the study. Monophyly of Caeciliusetae was also strongly supported (84%). Monophyly of Psocetae was recovered in this tree, but supported by less than 50% of bootstrap replicates. *Hemipsocus* was sister to Psocidae, within Psocetae. Parsimony analysis did not recover monophyly of Homilopsocidea, because the genera *Archipsocus* and *Aaroniella* were placed outside of this group. *Archipsocus* was sister to all other Psocomorpha with 54% bootstrap support. Within the outgroup, monophyly of Troctomorpha was not recovered, although this was weakly supported. Parsimony bootstrap analyses of each gene separately indicated that the nuclear 18S gene tended to support nodes deep in the tree, whereas the mitochondrial genes supported shallower nodes (Table 4). As expected, the longer sequence fragments (18S and 16S) provided more resolution when analysed alone than the shorter fragments (12S and COI).

Table 3. Uncorrected pairwise genetic divergences of aligned regions within Psocomorpha.

Gene	Minimum divergence (%)	Maximum divergence (%)
18S	0.1	8.9
COI	13.6	24.0
12S	8.1	29.2
16S	8.6	23.2

Neighbour joining analysis of the combined gene regions produced very similar results (Fig. 2). Monophyly of Psocomorpha received strong support (100%). Monophyly of Caeciliusetae was supported by 98% of bootstrap replicates. In contrast to parsimony, neighbour joining analysis did not recover monophyly of Psocetae, because *Aaroniella* (Homilopsocidea) was sister to *Lichenomima* (Psocetae). *Hemipsocus* was again sister to Psocidae, but with weak support. In the neighbour joining analysis, paraphyly of Homilopsocidea was strongly supported, with *Archipsocus* being sister to all other Psocomorpha with 91% bootstrap support. In addition, *Aaroniella* (Philotarsidae) was removed from other members of Homilopsocidea. Neighbour joining analysis recovered monophyly of Troctomorpha in the outgroup (bootstrap 69%).

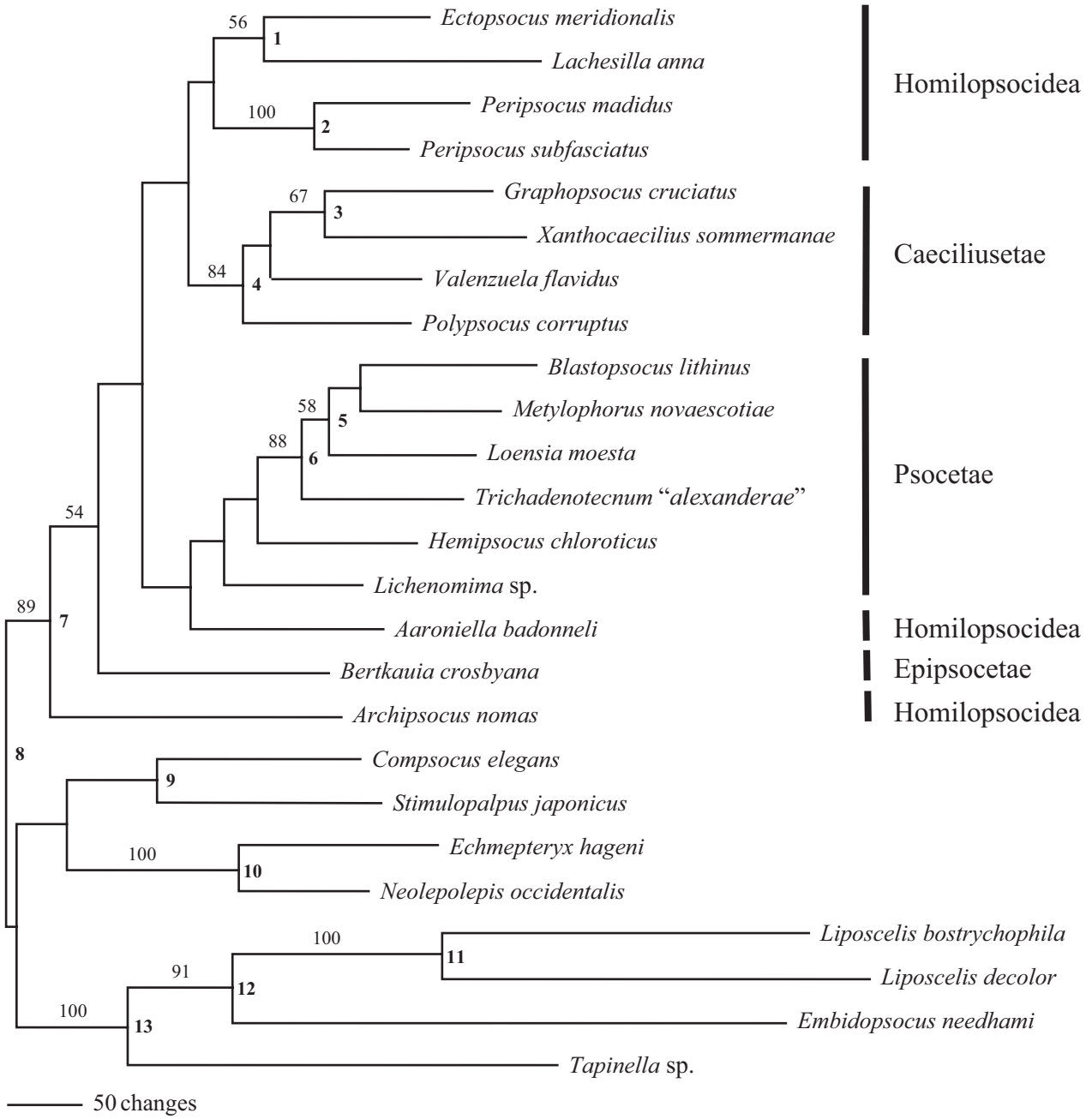

Fig. 1. Tree (length = 4631, consistency index = 0.442) derived from maximum parsimony analysis of 18S, 12S, 16S and cytochrome oxidase I DNA sequences for Psocomorpha and outgroup taxa (Troctomorpha and Trogiomorpha). All bases were treated as unweighted and unordered. Infraorders are classified according to Lienhard & Smithers (2002), and indicated. The numbers above the nodes are support from 1000 bootstrap replicates. Bold numbers indicate nodes referenced in Table 4. Branch lengths are proportional to reconstructed changes under parsimony.

Finally, maximum likelihood analysis of the combined gene regions produced a single most likely tree (Fig. 3). This tree was largely similar to the other two trees. Monophyly of Psocomorpha was recovered (bootstrap 98%), as was monophyly of Psocetae (78%) and Caeciliusetae (94%). As in the parsimony and neighbour joining analyses, Homilopsocidea was not shown to be monophyletic. *Archipsocus* appeared as the sister taxon of all other Psocomorpha, and this was supported in 78% of bootstrap replicates. *Aaroniella* was sister to *Bertkauia* in the likelihood tree. The remainder of Homilopsocidea formed a weakly supported grade leading to Caeciliusetae. In the outgroup, monophyly of Troctomorpha was not recovered.

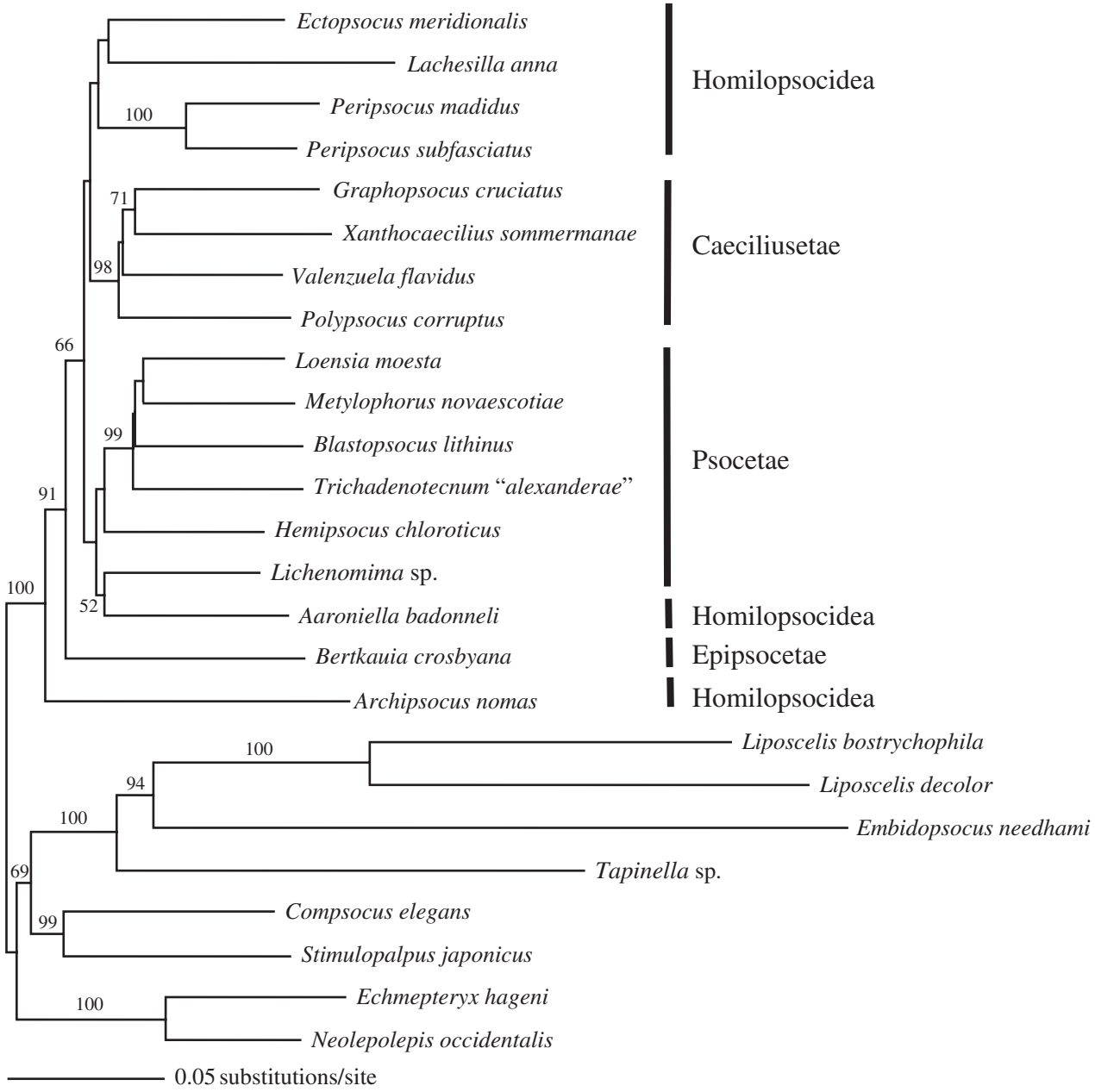

Fig. 2. Tree derived from neighbour joining analysis of uncorrected pairwise divergences of 18S, 12S, 16S and cytochrome oxidase I DNA sequences for Psocomorpha and outgroup taxa (Troctomorpha and Trogiomorpha). Infraorders are classified according to Lienhard & Smithers (2002), and indicated. The numbers associated with the nodes are support from 1000 bootstrap replicates. Branch lengths are proportional to uncorrected *p*-distances.

Discussion

Phylogenetic analyses of DNA sequences from one nuclear (18S) and three mitochondrial (COI, 12S, and 16S) genes produced generally well-resolved and well-supported trees for Psocomorpha (Insecta: Psocoptera). There appears to be considerable variation in rates of molecular evolution within Psocoptera. Mitochondrial divergences within the single genus *Liposcelis* are larger than those among all other Psocoptera. It is unlikely that the high divergences within *Liposcelis* represent great age for this genus, because fossil Psocoptera range back to the lower Jurassic, *c*. 190 mya (Badonnel & Lienhard, 1988), whereas the oldest fossil of *Liposcelis* is only Oligocene, *c*. 36 mya (Enderlein, 1911). In addition, genetic divergences within *Liposcelis* for the nuclear 18S are less than other divergences within

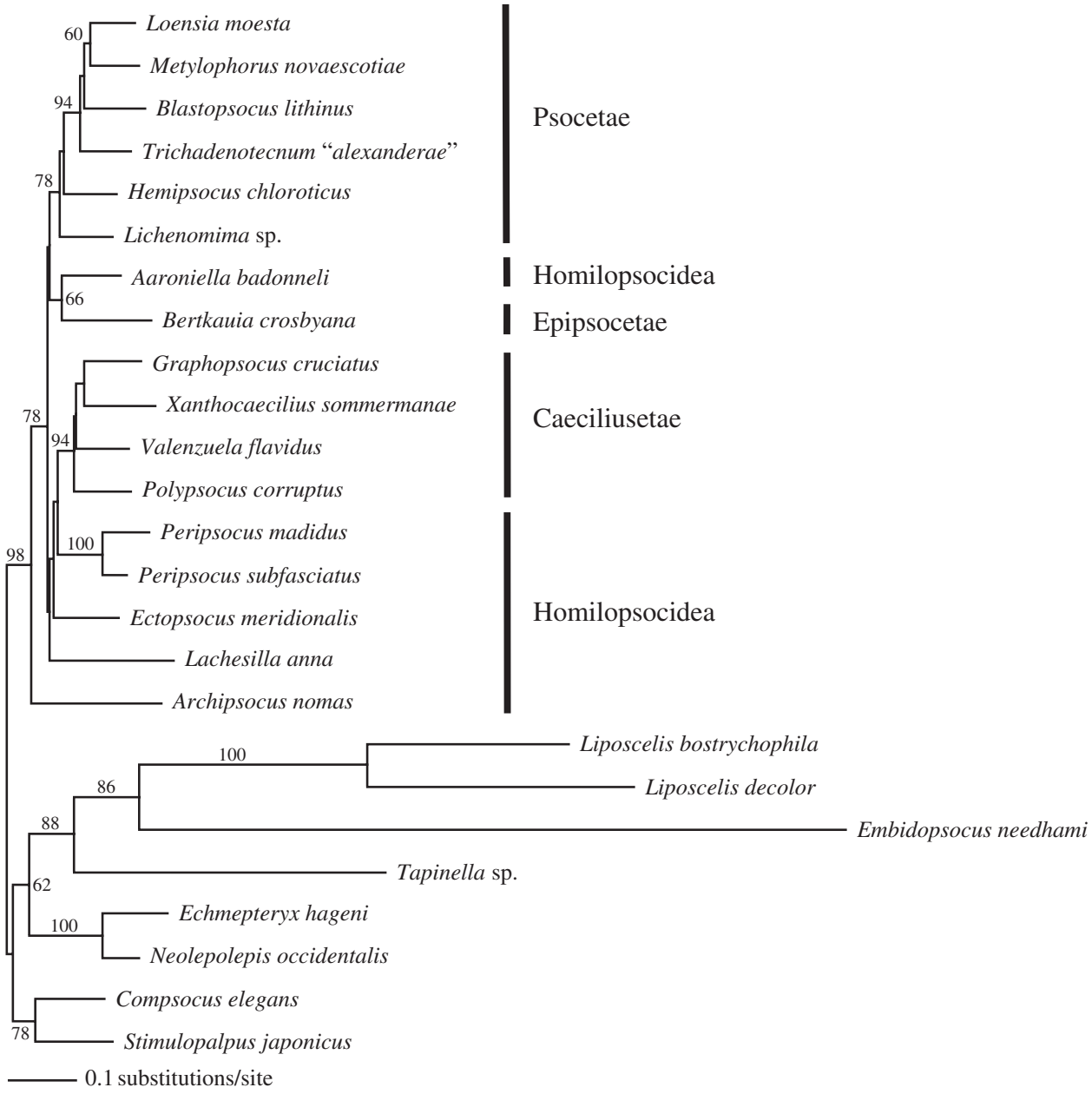

Fig. 3. Tree (likelihood = 21 517.98) derived from maximum likelihood analysis of 18S, 12S, 16S and cytochrome oxidase I DNA sequences for Psocomorpha and outgroup taxa (Troctomorpha and Trogiomorpha). The model incorporated general time reversible substitutions (A–C = 1.270, A–G = 4.270, A–T = 4.509, C–G = 1.00, C–T = 5.688, G–T = 1.0), unequal base frequencies (A = 0.312, C = 0.132, G = 0.188, T = 0.367), rate heterogeneity according to a gamma distribution (four rate categories, shape parameter = 0.452) and invariant sites ($P = 0.193$). Infraorders are classified according to Lienhard & Smithers (2002), and indicated. The numbers associated with the nodes are support from 100 bootstrap replicates. Branch lengths are proportional to the number of substitutions per site under the maximum likelihood model.

Psocoptera. Lyal (1985) suggested that Liposcelididae represents the closest living relatives of lice (Insecta: Phthiraptera). Lice also have a dramatically elevated rate of mitochondrial evolution (Page *et al*., 2002; Johnson *et al*., 2003) and a substantially rearranged mitochondrial genome (Shao *et al*., 2001a). Psocoptera are also known to possess some mitochondrial rearrangements (Shao *et al*., 2001b).

In all analyses, the monophyly of Psocomorpha, with respect to Troctomorpha and Trogiomorpha, was recovered with strong support. In addition, the monophyly of the infraorder Caeciliusetae was consistently recovered with relatively high bootstrap support. Both parsimony (Fig. 1) and likelihood analyses (Fig. 3) recovered monophyly of Psocetae, inclusive of *Hemipsocus*, and *Hemipsocus* was sister to

Table 4. Support for nodes in the combined parsimony tree by analyses of genes separately. Node refers to nodes labelled in the combined analysis tree (Fig. 1).

Node	18S	16S	12S	Cytochrome oxidase I
1	–	–	X	–
2	X	X	X	–
3	X	X	–	–
4	X	–	–	–
5	–	–	X	–
6	–	–	X	–
7	X	–	–	–
8	X	–	–	–
9	–	X	–	–
10	X	X	X	X
11	X	X	X	X
12	X	–	–	–
13	X	–	–	–

X, node is supported in ≥50% of bootstrap replicates in gene indicated analysed separately. –, node not supported in ≥50% of bootstrap replicates in separate analysis.

Psocidae in the neighbour joining analysis (Fig. 2). Monophyly of Homilopsocidea was not recovered in any analysis, with the genus *Archipsocus* consistently falling near the base of Psocomorpha, and *Aaroniella* removed from the remainder of Homilopsocidea. The position of our single representative of Epipsocetae (*Bertkauia*) was somewhat unstable, but generally fell just inside *Archipsocus*.

The phylogenetic arrangement among the infraorders of Psocomorpha was not well supported, but was relatively stable to method of analysis. Caeciliusetae and the majority of Homilopsocidea formed a clade in all analyses. *Aaroniella* (Philotarsidae) fell in a group with Psocetae in all analyses, and in one case maximum likelihood (ML) *Bertkauia* also fell within this group (Fig. 3). Additional data will be needed to recover the relationships among the major groups within Psocomorpha with confidence.

The classification of Psocomorpha into four infraorders (Epipsocetae, Caeciliusetae, Homilopsocidea and Psocetae) follows Lienhard & Smithers (2002). However, a recent analysis of morphological characters for Psocomorpha (Yoshizawa, 2002) did not find complete support for Lienhard & Smithers's (2002) classification. Rather, Archipsocidae was removed from other Homilopsocidea and placed into a monotypic infraorder Archipsocetae, and Hemipsocidae was removed from Psocetae and placed in the monotypic infraorder Hemipsocetae (Table 1). In other respects, the classification of Yoshizawa (2002), based on a morphological phylogeny, is quite similar to that of Lienhard & Smithers (2002). In general, we found that elements of both classifications were supported with DNA sequence data. Our molecular data indicate that Archipsocidae is removed from other Homilopsocidea, and sister to all other Psocomorpha. This finding is consistent with Yoshizawa's (2002) classification rather than that of Lienhard & Smithers (2002). We also do not have support for monophyly of the remainder of Homilopsocidea, because *Aaroniella* never appeared in a group with the remainder of Homilopsocidea. Monophyly of the traditional Psocetae was recovered in most analyses, and *Hemipsocus* was always recovered as the sister taxon of Psocidae. Therefore, there is no evidence from DNA sequences that Hemipsocidae should be removed from Psocetae, as suggested by Yoshizawa (2002). Rather, we support its traditional placement (Lienhard & Smithers, 2002) within Psocetae. We only included one species of Epipsocetae in the analyses, so we cannot comment on the monophyly of this group.

We also recovered other phylogenetic results of interest at the family level. Specifically, we never recovered the monophyly of Caeciliusidae. *Graphopsocus* (Stenopsocidae) was sister to *Xanthocaecilius* in all analyses. Yoshizawa's morphological analysis also did not recover monophyly of Caeciliusidae, but his taxon sampling was sufficiently different from ours that we cannot evaluate if this is a result of the rearrangement of similar taxa. We also sampled four members of Psocidae (Table 2), and the monophyly of this family was always highly supported (>80%).

In summary, there is a good correspondence between molecular and morphological phylogenies for Psocomorpha. Our results contain similarities to two recent classifications of the group, but are not completely consistent with either. More resolution is needed on the phylogenetic affinities of the members of Homilopsocidea, but the basal position of Archipsocidae within Psocomorpha now has support from both molecular and morphological data.

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