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Original Paper

Multiple origins of parasitism in lice: phylogenetic analysis of SSU rDNA indicates that the Phthiraptera and Psocoptera are not monophyletic

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Abstract The Paraneoptera (Hemipteroid Assemblage) comprises the orders Thysanoptera (thrips), Hemiptera (bugs), Phthiraptera (lice) and Psocoptera (booklice and barklice). The phylogenetic relationships among the Psocodea (Phthiraptera and Psocoptera), Thysanoptera and Hemiptera are unresolved, as are some relationships within the Psocodea. Here, we present phylogenetic hypotheses inferred from SSU rDNA sequences; the most controversial of which is the apparent paraphyly of the Phthiraptera, which are parasites of birds and mammals, with respect to one family of Psocoptera, the Liposcelididae. The order Psocoptera and the suborder that contains the Liposcelididae, the Troctomorpha, are also paraphyletic. The two remaining psocopteran suborders, the Psocomorpha and the Trogiomorpha, are apparently monophyletic. The Liposcelididae is most closely related to lice from the suborder Amblycera. These results suggest that the taxonomy of the Psocodea needs revision. In addition, there are implications for the evolution of parasitism in insects; parasitism may have evolved twice in lice or have evolved once and been subsequently lost in the Liposcelididae.

Keywords Phylogeny - Phthiraptera - Psocoptera - Parasitism - SSU rDNA

Introduction

The orders Phthiraptera (lice) and Psocoptera (book and bark lice) constitute the Psocodea. The Psocodea, and the orders Thysanoptera and Hemiptera, constitute the Paraneoptera (Hemipteroid Assemblage). The grouping of the Thysanoptera and Hemiptera to form the Condylgnatha is supported by some studies (Yoshizawa and Saigusa [2001](#) and references cited within; Yoshizawa and Saigusa [2003](#)) whereas other studies support the grouping of Thysanoptera

with Psocodea (Whiting et al. [1997](#); Wheeler et al. [2001](#)).

There are over 4,900 species of [lice \(Phthiraptera\)](#). [Lice](#) are [ectoparasites](#) of birds and mammals.

Phylogenetic relationships within the [Phthiraptera](#) have been studied extensively with molecular (Paterson et al. [2000](#); Cruickshank et al. [2001](#); Johnson et al. [2001a](#), [2001b](#), [2004](#); Johnson and Whiting [2002](#); Barker et al. [2003](#)) and morphological characters (Clay [1970](#); Kim and Ludwig [1978](#); Lyal [1985](#); Smith [2000](#), [2001](#); Marshall [2003](#)). A molecular study by Barker et al. ([2003](#)) indicated monophyly of each of the four suborders of [lice](#) and the following phylogeny: (Amblycera (Ischnocera ([Anoplura](#), Rhynchiphthirina))).

The Psocoptera are free-living; some phylogenetic relationships within the order have been studied. In particular, monophyly of the suborder Psocomorpha has been supported (Yoshizawa [2002](#); Johnson and Mockford [2003](#); Yoshizawa and Johnson [2003](#); Johnson et al. [2004](#)). Until recently, however, no study had sufficient taxonomic sampling to properly address the phylogenetic relationships of both the [Phthiraptera](#) and Psocoptera, and to test for reciprocal monophyly of each order. This is surprising considering that Lyal ([1985](#)) suggested that a family within Psocoptera, the Liposcelididae, is the sister-group to the [lice](#), and consequently that Psocoptera is paraphyletic. However, Yoshizawa and Johnson ([2003](#)) and Johnson et al. ([2004](#)) used nuclear and [mitochondrial DNA](#) to study the phylogenetic relationships of both the Psocoptera and [Phthiraptera](#) relative to each other and found support for a sister-group relationship between the Liposcelididae and the Amblycera. Johnson et al. ([2004](#)) also found that the Pachytroctidae was sister to this Amblycera-Liposcelididae assemblage and therefore that Psocoptera is paraphyletic.

Here we use a nuclear gene (SSU rDNA) to address phylogenetic relationships within the Psocodea. We demonstrate that not only is there support for paraphyly of the Psocoptera with respect to [Phthiraptera](#), but also for paraphyly of the [Phthiraptera](#) with respect to the Psocoptera. Indeed, one suborder of [lice](#), the Amblycera, is the sister-group to the Liposcelididae in our phylogenies. Other phylogenetic relationships within the Psocoptera are also addressed with this gene. Reciprocal paraphyly of the Psocoptera and [Phthiraptera](#) has fascinating implications for both systematics and the evolution of parasitism in the Insecta.

Materials and methods

Taxa studied

We studied 57 species of insects (Table [1](#)). One species from each of the following orders was included for out-group reference: [Siphonaptera](#), Raphidioptera, Megaloptera, Coleoptera, Trichoptera, Hymenoptera and Lepidoptera. The in-group contained species of Thysanoptera, [Hemiptera](#), Psocoptera and [Phthiraptera](#) (which together constitute the Paraneoptera or the Hemipteroid Assemblage). Seventeen of the 57 sequences used were generated for this study and have not been previously published. The remaining 40 sequences were from Genbank (see Table [1](#) for accession numbers).

Table 1 List of species studied

Species (Voucher number ^a)	Taxonomy	Genbank
<i>Liposcelis</i> sp. (B1093)	Psocoptera; Troctomorpha; Nanopsocetae; Liposcelididae	AY077779
<i>Liposcelididae</i> sp. (B1763)	Psocoptera; Troctomorpha; Nanopsocetae; Liposcelididae	AY900135 ^b

<i>Stimulopalpus japonicus</i> (B1557)	Psocoptera; Troctomorpha; Amphientometae; Amphientomidae	AY900127 ^b
Sphaeropsocidae sp. (B1642)	Psocoptera; Troctomorpha; Sphaeropsocidae	AY900134 ^b
<i>Echmepteryx hageni</i> (B1560)	Psocoptera; Trogiomorpha; Atropetae; Lepidopsocidae	AY900140 ^b
<i>Pteroxanium insularum</i> (B1509)	Psocoptera; Trogiomorpha; Atropetae; Lepidopsocidae	AY900139 ^b
<i>Lepinotus</i> prob. <i>patruelis</i> (B1549)	Psocoptera; Trogiomorpha; Trogiidae	AY900130 ^b
<i>Ectopsocus</i> prob. <i>australis</i> (B1548)	Psocoptera; Psocomorpha; Homilopsocidea; Ectopsocidae	AY900124 ^b
<i>Ectopsocus briggsi</i> (B1514)	Psocoptera; Psocomorpha; Homilopsocidea; Ectopsocidae	AY900136 ^b
<i>Lachesilla anna</i> (B1561)	Psocoptera; Psocomorpha; Homilopsocidea; Lachesillidae	AY900129 ^b
<i>Archipsocus nomas</i> (B1563)	Psocoptera; Psocomorpha; Homilopsocidea; Archipsocidae	AY900133 ^b
<i>Peripsocus</i> sp. (B2049)	Psocoptera; Psocomorpha; Homilopsocidea; Peripsocidae	AY900131 ^b
<i>Valenzuela</i> sp.	Psocoptera; Psocomorpha; Caeciliusetae; Caeciliusidae	AF423793
<i>Blastopsocus lithinus</i> (B1556)	Psocoptera; Psocomorpha; Psocetae; Psocidae	AY900132 ^b
Tubulifera thrips sp. (B1808)	Thysanoptera; Tubulifera	AY900137 ^b
<i>Taenothrips inconsequens</i>	Thysanoptera; Terrebrantia; Thripoidae; Thripidae	U65123
<i>Terrebrantia thrips</i> sp. (B1920)	Thysanoptera; Terrebrantia	AY900128 ^b
<i>Heterodoxus calabyi</i> (B796)	Phthiraptera ; Amblycera; Boopiidae	AY077759
<i>Latumcephalum</i> sp. (B955)	Phthiraptera ; Amblycera; Boopiidae	AY077760
<i>Boopia</i> sp. cf. <i>uncinata</i> (B560)	Phthiraptera ; Amblycera; Boopiidae	AY077761
<i>Gliricola porcelli</i> (B836)	Phthiraptera ; Amblycera; Gyropidae	AY077762
Menoponidae sp. (B1279)	Phthiraptera ; Amblycera; Menoponidae	AY900138 ^b
<i>Neophilopterus incompletus</i> (B1110)	Phthiraptera ; Ischnocera; Philopteridae	AY077763
<i>Degeeriella fulva</i> (B1105)	Phthiraptera ; Ischnocera; Philopteridae	AY077766
<i>Pectinopygus sulae</i> (B769)	Phthiraptera ; Ischnocera; Philopteridae	AY077768
<i>Naubates fuliginosus</i> (B1539)	Phthiraptera ; Ischnocera; Philopteridae	AY900126 ^b
<i>Nesiotinus demersus</i> (B1540)	Phthiraptera ; Ischnocera; Philopteridae	AY900125 ^b
<i>Goniodes dissimilis/giga</i> (B927)	Phthiraptera ; Ischnocera; Gonioididae	AY077767
<i>Bovicola ovis</i> (B801)	Phthiraptera ; Ischnocera; Trichodectidae	AY077769
<i>Felicola subrostratus</i> (B888)	Phthiraptera ; Ischnocera; Trichodectidae	AY077770
<i>Hoplopleura pacifica</i> (B1182)	Phthiraptera ; Anoplura ; Hoplopleuridae	AY077773
<i>Linognathus vituli</i> (B802)	Phthiraptera ; Anoplura ; Linognathidae	AY077774
<i>Pediculus capitis</i> (B761)	Phthiraptera ; Anoplura ; Pediculidae	AY077775
<i>Pthirus pubis</i> (B931)	Phthiraptera ; Anoplura ; Pthiridae	AY077776
<i>Pedicinus</i> sp. (B1371)	Phthiraptera ; Anoplura ; Pedicinidae	AY077777
<i>Lepidophthirus macrorhini</i> (B933)	Phthiraptera ; Anoplura ; Echinophthiridae	AY077771(2)
<i>Haematomyzus elephantus</i> (B1191)	Phthiraptera ; Rhynchophthirina; Haematomyzidae	AY077778
<i>Acyrtosiphon pisum</i>	Hemiptera ; Sternorrhyncha; Aphidiformes; Aphidoidea; Aphididae	X62623
<i>Mindarus kinseyi</i>	Hemiptera ; Sternorrhyncha; Aphidiformes; Aphidoidea; Mindaridae	AH003127

<i>Aonidiella auranti</i>	Hemiptera ; Sternorrhyncha; Aphidiformes; Coccoidea; Diaspididae	U06475
<i>Pealius kelloggii</i>	Hemiptera ; Sternorrhyncha; Aleyrodiformes; Aleyrodidae	U06479
<i>Trioza eugeniae</i>	Hemiptera ; Sternorrhyncha; Psylliformes; Triozidae	U06482
<i>Philaenus spumarius</i>	Hemiptera ; Euhemiptera; Clypeorrhyncha; Cercopoidea; Aphrophoridae	U06480
<i>Okanaga utahensis</i>	Hemiptera ; Cicadomorpha; Cicadidae	U06478
<i>Spissistilus festinus</i>	Hemiptera ; Euhemiptera; Clypeorrhyncha; Membracoidea; Membacidae	U06477
<i>Lygus hesperus</i>	Hemiptera ; Cimicomorpha; Miridae	U06476
<i>Triatoma picturata</i>	Hemiptera ; Cimicomorpha; Reduviidae	AJ243332
<i>Graphosoma lineatum</i>	Hemiptera ; Euhemiptera; Prosorrhyncha; Pentatomorpha; Pentatomidae	U88339
<i>Hackeriella veitchi</i>	Hemiptera ; Euhemiptera; Prosorrhyncha; Peloridiomorpha; Peloridiidae	AF004766
<i>Prokelisia marginata</i>	Hemiptera ; Euhemiptera; Archaeorrhyncha; Fulguroidea; Delphacidae	U09207
<i>Tunga monositus</i>	Siphonaptera	AF286279
<i>Nehga inflata</i>	Raphidioptera	AF286272
<i>Sialis</i> sp.	Megaloptera	X89497
<i>Loricera pilicornis</i>	Coleoptera	AF201396
<i>Oecetus avara</i>	Trichoptera	AF286300
<i>Polistes dominulus</i>	Hymenoptera	X77785
<i>Papilio troilus</i>	Lepidoptera	AF286299

^a Numbers in *parentheses* are voucher specimen numbers for sequences generated in this laboratory

^b Sequences generated for this study and not previously published

DNA methods

The DNA was extracted from whole arthropods after Crampton et al. ([1996](#)). In most cases the entire SSU rDNA was amplified in three pieces with the published primers Ns1 (5'GTA GTC ATA TGC TTG TCT C 3'), Ns2a (5'CGC GGC TGC TGG CAC CAG ACT TGC 3'), Ns5a (5'TGA AAC TTA AAG GAA TTG ACG GAA G 3') and Ns8 (5'TCC GCA GGT TCA CCT ACG GA 3') (Black et al. [1997](#)) and Ns10 (5'AGG CTC TGC AAT CGG AAT G 3') and Ns11 (5'GTC AAA TTA AGC CGC AAG C 3') (Barker et al. [2003](#)). These primers and the primers, 13 + a (5'TTT CAA ATG TCT GAC TTA TCA ACT 3'), 13 - a (5'AGT TGA TAA GTC AGA CAT TTG A 3'), 35 + a (5'ATA GGG ACA GGC GGG GCA TTA GT 3') and 35 - a (5'CGA CGA TCC AAG AAT TTC ACC TCT 3') designed by Barker et al. ([2003](#)) and 58 - 2a (5'ATC GGT AGT AGC GAC GGG CGG TGT G 3') and 58 + 2a (5'AAT TCC GAT AAC GAA CGA GAC TC 3'), designed by Black et al. ([1997](#)), were used for sequencing. The PCR protocol was 95°C for 3 min, (95°C for 30 s, 40°C for 1 min and 72°C for 1 min) for ten cycles, (95°C for 30 s, 50°C for 1 min and 72°C for 1 min) for 25 cycles, then 72°C for 5 min and the 25 µl recipe had 25 ng DNA, 2.25 mM MgCl₂, 0.1 µM each primer, 0.2 mM each dNTP, 2.5 µl ten times buffer and 0.5 U Redhot TAQ polymerase (Advanced Biotechnologies). Negative controls (no DNA template) were always run simultaneously with our PCR experiments; all reaction mixtures were discarded when any DNA appeared in the negative control. The QIAGEN Purification columns were used to purify 50-150 µl of PCR product according to the manufacturers instructions. Nucleotide sequences were obtained by direct sequencing of PCR products with the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit; ~50 ng of purified PCR product was used for each reaction and extension products were purified by ethanol precipitation prior to electrophoresis in an ABI 377 sequencer.

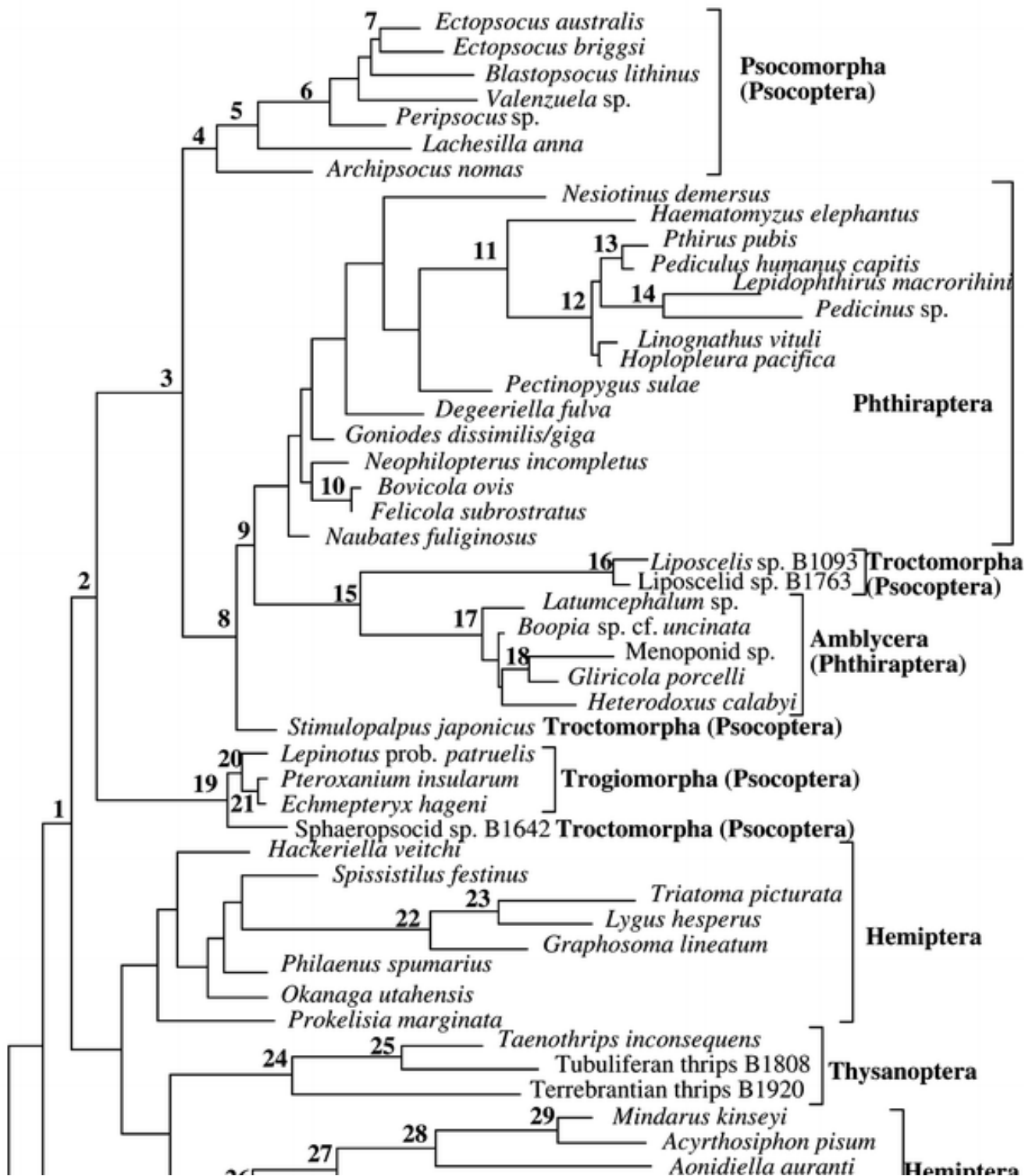
Phylogenetic analyses

Consensus sequences were compiled from both forward and reverse sequences. Sequences were aligned with ClustalX 1.83, using the default parameters (Thompson et al. [1997](#)). The resulting multiple sequence alignment was 3,300 bp long; Gblocks 0.91 b (Castresana [2000](#)) was used to exclude poorly aligned or divergent regions from the alignment and the reduced alignment was 1,401 bp (parameters: minimum number of sequences for a conserved position = 30, minimum number of sequences for a flanking position = 50, maximum number of contiguous nonconserved positions = 8, minimum length of a block = 10, allowed gap positions = with half, use similarity matrices = Yes). Phylogenetic analyses with PAUP 4.0b10 (Swofford [2002](#)) were with maximum parsimony (MP), genetic distance neighbour joining (NJ; Saitou and Nei [1987](#)) of maximum likelihood distances and with maximum likelihood (ML). The MP and ML searches were with the heuristic algorithm; gaps were treated as a “fifth base” in MP analyses. One thousand random taxon addition replicates were used to find the shortest MP trees. Consistency indices, retention indices and tree lengths were calculated after parsimony-uninformative characters were excluded. Five hundred cycles of bootstrap resampling (Felsenstein [1985](#)) were used to test support for branches in phylogenetic trees inferred by MP (Heuristic search) and genetic distance (NJ). The model used for ML analyses and for calculating ML distances for neighbour-joining was SYM + I + G (equal base frequencies, number of substitution types = 6, Rmat = (1.4775 3.4148 1.3246 0.7221 4.4672), rates = gamma, shape = 0.6717 Pinvar = 0.2732), which best fit the data, as determined with a likelihood ratio test in Modeltest 3.06 (Posada and Crandall [1998](#)). Markov Chain Monte Carlo (MCMC) analysis of ML was executed with MrBayes 3.0b4 (Huelsenbeck and Ronquist [2001](#)). The number of substitution types was set at six and the substitution rate was according to a gamma distribution (shape parameter = 0.6717). These values were based on the ML model that best fit the data, as calculated above in Modeltest 3.06 (Posada and Crandall [1998](#)). Two replicates of 500,000 MCMC generations or 5000 trees were executed with MrBayes 3.0b4; the first 400 trees were excluded from the consensus tree, (these are the “burn-in”, as the ln likelihood sum converges on a stable value-see Huelsenbeck and Ronquist [2001](#)). The percentage representation of each branch was then calculated; this is called the posterior probability. Bremer support values for branches (Bremer [1988](#), [1994](#)) were calculated with TreeRot v2c (Sorensen [1999](#)) and PAUP 4.0b10. Bremer support is the number of extra steps required to lose a branch from an MP tree. Nucleotide substitution rates were evaluated with RRTree (Robinson-Rechavi and Huchon [2000](#)).

Results

The mean nucleotide content of the SSU rDNA sequences was as follows: 26.8% A (range 24.9-27.8%), 22.3% C (21-25.3%), 27.3% G (26.3-29.2%) and 23.6% T (20.7-24.5%). A chi-square test of homogeneity of nucleotide content among taxa did not show any significant non-homogeneity ($P = 1$). Nucleotide substitution rates were compared among lineages; these rates were significantly higher in the Liposcelididae than in other lineages: Liposcelididae versus Psocomorpha ($P = 0.001$), Liposcelididae versus Trogiomorpha ($P = 10^{-7}$), Liposcelididae versus *Phthiraptera* excluding Amblycera ($P = 4.13 \times 10^{-5}$), Liposcelididae versus Amblycera ($P = 0.018$). Nucleotide substitution rates were also significantly higher in the Psocomorpha than in the Trogiomorpha ($P = 0.0007$). Within the Troctomorpha substitution rates in the Liposcelididae and *Sphaeropsocidae* sp. were not significantly different to each other but both were higher than of *Stimulopalpus japonicus* ($P = 0.003$ versus Liposcelididae; $P = 0.01$ versus *Sphaeropsocidae* sp.). Trees from MP, ML, genetic distance neighbour joining (NJ) and Bayesian (MCMC) methods were mostly congruent. The ML tree ($-\ln L = 13363.902$; not shown) and MCMC consensus of 1496 trees (Fig. [1](#)) were identical. MP analysis yielded 160 shortest trees (length = 2263 steps, CI = 0.377, RI = 0.569, RCI = 0.215); most relationships in the strict consensus and majority rule consensus trees (not shown) were the same as those in the ML and MCMC trees and the NJ tree (not shown). Although there were some differences in the trees produced by different methods they were minor, being branches that had little support from bootstrap resampling or posterior probability. Only relationships, which were found by all methods and which were also supported with bootstrap support (ML bootstrap support values were not calculated due to the size of the

dataset) or MCMC values of >70% are considered here (Fig. 1, Table 2). The following relationships met these criteria: (i) Psocodea (Psocoptera + **Phthiraptera**) is monophyletic (90-100% bootstrap support/posterior probability, ten steps Bremer support), however, the Liposcelididae (order Psocoptera) and the **Phthiraptera** form a **clade** to the exclusion of the remaining Psocoptera (70-77%, three steps); (ii) within this **clade** the Liposcelididae is the sister-group to the suborder Amblycera (76-100%, seven steps) so the **Phthiraptera** is also paraphyletic; (iii) within the **Phthiraptera** the suborders Amblycera (100%, 24 steps) and **Anoplura** (100%, 19 steps) are monophyletic but the status of the suborder Ischnocera (monophyly or paraphyly) could not be resolved; (iv) the Psocomorpha (88-100%, five steps) and Trogiomorpha are monophyletic (72-100%, zero steps); (v) the Troctomorpha is not monophyletic due to the inclusion of **Phthiraptera** (see above; 76-100%, four steps), Psocomorpha, and Trogiomorpha (96-100%, six steps), and (vi) Thysanoptera is monophyletic (97-100%, ten steps) but its relationship with **Hemiptera** and Psocodea is not resolved.



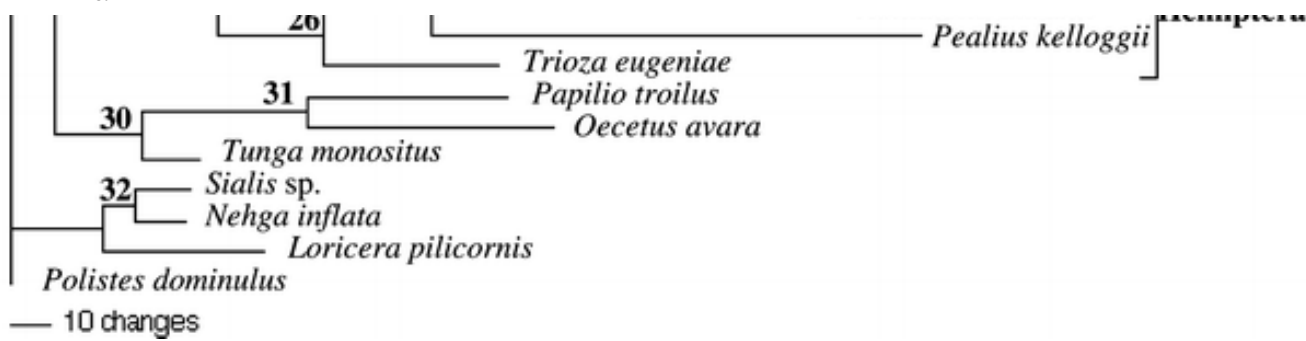


Fig. 1 Markov Chain Monte Carlo (MCMC) tree (consensus of 1496 trees). Support values for each numbered node for Bootstrap Resampling, Bremer Support and MCMC posterior probability are listed in Table 2

Table 2 Support values for nodes in Fig. 1

Node	MCMC posterior probability (%)	MP bootstrap resampling (%)	NJ bootstrap resampling (%)	Bremer support (no. of steps)
1	100	70	85	3
2	100	90	100	10
3	100	54	-	2
4	100	88	93	5
5	100	95	100	15
6	94	-	76	0
7	100	<50	86	0
8	100	76	-	4
9	77	73	70	3
10	100	100	100	7
11	100	98	99	11
12	100	100	100	19
13	100	74	73	2
14	70	65	99	1
15	100	89	76	7
16	100	100	100	59
17	100	100	100	24
18	93	98	-	2
19	100	96	100	6
20	100	72	74	0
21	100	99	91	4
22	100	100	100	26
23	99	70	57	1

24	100	97	99	10
25	100	66	55	2
26	100	86	99	6
27	66	68	68	4
28	100	95	100	8
29	100	93	69	10
30	100	56	80	2
31	100	87	100	20
32	100	83	94	2

Note:-indicates that a node was not found in the tree(s) produced by that method

Discussion

Phylogenetic relationships

Paraphyly of Psocoptera and [Phthiraptera](#)

Based on a number of loss characters, Lyal ([1985](#)) suggested that Psocoptera was paraphyletic because the family Liposcelididae was the sister-group to the [lice \(Phthiraptera\)](#). In this study, we not only found evidence for paraphyly of the Psocoptera, but also for paraphyly of the [Phthiraptera](#). This is due to the Liposcelididae being the sister-group to the Amblycera rather than to the entire order [Phthiraptera](#). Another molecular study of the Psocodea, which used 12 S and 16 S rDNA sequences, indicated a sister-group relationship between the Liposcelididae and the [Phthiraptera](#) (Yoshizawa and Johnson [2003](#)), although with some of the methods they used there was low support for paraphyly of [Phthiraptera](#) with respect to the Liposcelididae. A study that also used SSU rDNA found support for polyphyly of [Phthiraptera](#), however taxon sampling between that study and ours differed (Johnson et al. [2004](#)).

Paraphyly of Troctomorpha

There are three lineages of Troctomorpha in our phylogenies: (i) the Liposcelididae, which is the sister-group to the Amblycera; (ii) *S. japonicus* (infraorder Amphientometae), which is the sister-group to the [clade](#) containing the [Phthiraptera](#) + Liposcelididae; and, (iii) the *Sphaeropsocidae* sp., which is the sister-group to the Trogiomorpha. Yoshizawa and Johnson ([2003](#)) found only two lineages of Troctomorpha but this is to be expected, considering they did not have a representative of the Sphaeropsocidae.

Monophyly of Trogiomorpha and Psocomorpha

Both the Trogiomorpha and Psocomorpha were supported as monophyletic in all of our analyses. This is consistent with a previous molecular study (Yoshizawa and Johnson [2003](#)) and with morphology (Yoshizawa [2002](#)).

Phylogenetic relationships within [Phthiraptera](#)

The relationships found within the [Phthiraptera](#) by Barker et al. (2003) using SSU rDNA are the same as found in this study, with the exception of the relationship of the Liposcelididae to Amblycera (above). Barker et al. (2003) used a *Liposcelis* species for out-group reference; this may not have been appropriate based on the results of the present study. However, incorrectly rooting the tree with a *Liposcelis* sp., (which may actually be an in-group) would not affect the phylogenetic relationships among [lice](#) that Barker et al. (2003) inferred and discussed (if *Liposcelis* had in fact been closely related to any suborder other than Amblycera then this would not have been so). The Amblycera is apparently the earliest diverging suborder so whether the genus *Liposcelis* is the sister-group to the [Phthiraptera](#) or to the entire [Phthiraptera](#) has no bearing on the relationships of the other suborders, which was the subject of that paper.

Phylogenetic utility and rates of nucleotide substitution of SSU rDNA

The SSU rDNA resolved and provided support for many phylogenetic relationships in our trees, from all methods. Some relationships were poorly resolved, however. These included the phylogenetic position of the thrips (Thysanoptera) and whether the louse suborder Ischnocera was monophyletic or paraphyletic. A previous study of the [Phthiraptera](#) with the same gene found support for monophyly of the Ischnocera (Barker et al. 2003). The lack of support in the present study might be due to the inclusion of taxa from the Psocoptera and additional taxa within the [Phthiraptera](#) because species sampling can affect support values (Lecointre et al. 1993). Rates of nucleotide substitution did not vary greatly among the taxa sampled. The exception was the family Liposcelididae that had a consistently faster rate of nucleotide substitution relative to all other taxa tested. The fast rate of evolution of the Liposcelididae and the controversial phylogenetic position of that family in this study may make long branch attraction a possibility; however, nucleotide substitution rates in the Amblycera were not significantly higher than other taxa; so this seems unlikely.

Systematics of Psocodea














Our analyses indicate that the current, long-standing classification of the Psocodea should be revised. To retain a monophyletic [Phthiraptera](#) the family Liposcelidae would have to be added to that order as either a fifth suborder or as part of the suborder Amblycera. In addition, revision of the remaining Psocoptera might also be necessary since in our study they do not form a monophyletic group. One possibility is to elevate the Psocomorpha and Trogiomorpha to the rank of order and relegate some species of Troctomorpha to other groups, but future study is necessary.

The evolution of parasitism

The implication of a sister-group relationship between Liposcelididae and Amblycera is that either that parasitism has evolved twice in the Psocodea, once in the ancestor of Amblycera and once in the ancestor of Ischnocera + [Anoplura](#) + Rhynchophthirina, or that it has evolved once but has been secondarily lost in the Liposcelididae. Both scenarios are equally parsimonious. Two origins of parasitism in the [Phthiraptera](#) was proposed by Kim and Ludwig (1982), namely that the ectoparasitic habit was adopted separately in [Anoplura](#) (sucking [lice](#)) and [Mallophaga](#) (biting/chewing [lice](#); Ischnocera, Amblycera and Rhynchophthirina) but that scenario is not consistent with this study since the monophyly of [Mallophaga](#) is not supported (see also Barker et al. 2003).

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