

Molecular Systematics of the bark lice infraorder Caeciliusetae (Insecta: Psocodea)

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Abstract

The phylogenetic relationships of bark lice and parasitic lice (Insecta: Psocodea) have been studied in a number of recent molecular phylogenetic analyses based on DNA sequences. Many of these studies have focused on the position of parasitic lice within the free-living bark lice. However, fewer such studies have examined the relationships among major groups of free-living bark lice and their implications for classification. In this study we focus on the infraorder Caeciliusetae, a large group of bark lice (~1000 species) within the suborder Psocomorpha.

Using sequences of two mitochondrial and two nuclear genes, we estimated the phylogeny for relationships among the five recognized families within the infraorder Caeciliusetae. Based on the results, the monophyly of two families is strongly supported, Stenopsocidae and Dasydemellidae, as well as a sister relationship between these two families. Monophyly of the larger families Amphipsocidae and Caeciliusidae was not supported, though the causes of this were the positions of two distinct subfamilies (Paracaeciliinae and Calocaeciliinae). The monophyly of the final family Asiopsocidae could not be tested because it was only sampled by one species.

Based on these results and consideration of morphological characters, we propose a new classification for the Caeciliusetae, recognizing six families: Amphipsocidae, Stenopsocidae, Dasydemellidae, Asiopsocidae, Paracaeciliidae, and Caeciliusidae. We expect this new classification will stabilize the higher level taxonomy of this group and help to identify groups in need of further work among these insects.

Introduction

A number of previous phylogenetic studies have focused on Psocodea, an insect order containing over 10,000 species of bark lice and parasitic lice. Prior work has shown that parasitic lice are phylogenetically derived from free-living bark lice (Lyal, 1985; Yoshizawa & Johnson, 2003, 2010; Johnson *et al.*, 2004). Within bark lice, formerly classified as the order Psocoptera, three suborders are traditionally recognized: Trogiomorpha, Troctomorpha, and Psocomorpha (Lienhard & Smithers, 2002). The phylogenetic relationships among the first of these, Trogiomorpha, have been examined in detail (Yoshizawa *et al.*, 2006) and a new classification proposed. The second, Troctomorpha, is likely to be paraphyletic with respect to parasitic lice (Phthiraptera) (Johnson *et al.*, 2004), yet remains to be investigated in detail. The phylogeny of the third and largest suborder, Psocomorpha (>4000 species), has received some attention using molecular data (Johnson & Mockford, 2003; Johnson *et al.*, 2004; Yoshizawa & Johnson, 2010); however, considerable work is needed before an exhaustive new classification system can be proposed.

The goal of the present study is to understand the phylogenetic relationships within a major clade of the Psocomorpha, the infraorder Caeciliusetae, which contains around 1000 species. First recognized formally as a taxon by Pearman (1936), the group underwent important changes with removal of what is currently the family Calopsocidae by Roesler (1944), which was followed by Smithers (1967), and the addition of the family Asiopsocidae by Mockford and Gracia Aldrete (1976). Monophyly of the infraorder Caeciliusetae has been supported on the basis of both morphological (Badonnel, 1951; Mockford & Garcia Aldrete, 1976; Mockford, 1993; Lienhard, 1998; Yoshizawa, 2002) and molecular (Johnson & Mockford, 2003; Johnson *et al.*, 2004; Yoshizawa & Johnson, 2010) characters. The majority of species are yellowish in color and found on dead or dying leaves, although there is considerable variation in the group in morphology and habits (Figure 1). No formal morphological analysis has been performed for the entire infraorder. Current classification (Lienhard & Smithers, 2002; see also Table 1) includes five families: Asiopsocidae, Caeciliusidae, Stenopsocidae, Amphipsocidae, and Dasydemellidae. Mockford (2000) provided an extensive revision of Caeciliusidae, the largest family in the infraorder. This family was divided into four subfamilies and the largest, Caeciliusinae, is further divided into five tribes (Table 1).

Here we evaluate the current classification scheme (Lienhard & Smithers, 2002) for the bark louse infraorder Caeciliusetae using molecular phylogenetic data from two mitochondrial and two nuclear genes. Taxon sampling was aimed at testing the monophyly and phylogenetic relationships among families. We are able to assess finer scale classification to a lesser extent. Based on our results, we propose a new classification scheme for this infraorder and evaluate this classification with respect to morphological characters.

Materials and Methods

Samples were obtained from all extant families of Caeciliusetae and a variety of outgroup taxa throughout the suborder Psocomorpha, focusing on taxa previously identified to be among the closer relatives of Caeciliusetae (Table 2). Methods of DNA extraction PCR amplification, and sequencing followed Johnson & Mockford (2003) and Johnson *et al.* (2004). We sequenced portions of the mitochondrial 16S and 12S rDNA genes and the nuclear 18S rDNA and histone 3 genes (GenBank Accession pending). Primers included 16Sar-16Sbr for 16S (Simon *et al.*, 1994), 12Sai-12Sbi for 12S (Simon *et al.*, 1994), Ns1-Ns2a, 18Sai-18Sbi, and Ns5a-Ns8P for 18S (Johnson *et al.*, 2004), and H3AF-H3AR for histone 3 (Colgan *et al.*, 1998). Alignment of the protein-coding histone 3 gene was straightforward and done manually. Ribosomal DNA was aligned according to secondary structure models as described in detail by Yoshizawa & Johnson (2003) for 12S

and 16S and Johnson et al. (2004) for 18S. Ambiguously aligned regions were selected manually and excluded from the analyses. Aligned data in nexus format is available as Supplementary data or at <http://psocodea.org/kazu/data/Caeciliusetae/>.

Using these aligned sequences, we conducted combined maximum likelihood and partitioned Bayesian analyses. For ML analyses, we used PAUP* (Swofford, 2002) with TBR branch swapping and a NJ starting tree. The best fit substitution model was estimated using hierarchical likelihood ratio tests (hLRT) as implemented in Modeltest 3.7 (Posada & Crandall, 1998) and the GTR+I+G model was selected. We also performed 100 ML bootstrap pseudoreplicates in PAUP* using the same search conditions. For Bayesian analysis, we separated characters into 6 partitions (18S, 12S, 16S, and the three codon positions of the histone 3 gene). The best fit model was estimated independently for each partition using hLRTs as implemented in MrModeltest (Nylander 2004), resulting in 18S and 16S (GTR+I+G), 12S (GTR+G), histone 3 first position (SYM+G), histone 3 second position (JC), and histone 3 third position (GTR+G). Detailed parameters and commands for ML and Bayesian analyses are described in the Supplementary data matrix. Bayesian analysis was conducted in MrBayes (Ronquist & Huelsenbeck, 2003) with two runs of four chains each for 2,000,000 generations and trees sampled every 1000 generations. The first 50% of trees were discarded as a burnin, and a 50% majority consensus tree of the remaining trees was used to calculate posterior probabilities.

Results

The phylogenetic trees resulting from maximum likelihood and Bayesian analyses of the four gene regions were well resolved and some key branches received strong support (Figure 2). These trees were nearly identical except for minor rearrangements of weakly supported branches. Both maximum likelihood and Bayesian analysis supported monophyly of Caeciliusetae (100% bootstrap and Bayesian posterior probability). Monophyly of the families Dasydemellidae and Stenopsocidae were strongly supported (100%) in all analyses. The family Asiopsocidae was only represented by a single species, so monophyly of this family could not be tested.

Monophyly of Amphipsocidae is not recovered, with the representative of the monogeneric subfamily Calocaeciliinae (*Calocaecilius* Mockford) being embedded within the Caeciliusidae. However, the five representatives of the other subfamily Amphipsocinae formed a monophyletic group (100% support). Similarly, monophyly of the family Caeciliusidae was also not supported, both because of the placement of *Calocaecilius* and because Asiopsocidae was recovered as the sister taxon to a clade of four species of the subfamily Paracaeciliinae. Monophyly of the remainder of Caeciliusidae (inclusive of *Calocaecilius*) was generally supported (69% bootstrap, 100% Bayesian posterior).

The families Dasydemellidae and Stenopsocidae were recovered as sister taxa with strong support (100%). However, other than the sister relationship between Asiopsocidae and the Paracaeciliinae, the relationships among the remainder of the families and major clades were less clear and generally weakly supported. The family Asiopsocidae does not appear to be sister to the remainder of Caeciliusetae and thus does not merit recognition as a distinct superfamily.

While taxon sampling does not permit an exhaustive evaluation of subfamilial classification schemes, some conclusions can be drawn from the phylogenetic results. First, within the Amphipsocinae, monophyly of the largest tribe, Amphipsocini is not supported because of a sister relationship between *Polypsocus* Hagen (Polypsocini) and *Tagalopsocus* (Amphipsocini), exclusive of the other sampled members of Amphipsocini (*Amphipsocus* Smithers and *Taeniosigma* Enderlein). Within the Stenopsocidae, the genus *Stenopsocus* Hagen

appears to be paraphyletic. The subfamily Paracaeciliinae appears to form a clade well separated from other groups, and within this clade, the genus *Enderleinella* Badonnel is not monophyletic.

Within the remainder of Caeciliusidae there is generally insufficient taxon sampling to assess the detailed tribal classification of Mockford (2000) and Lienhard & Smithers (2002). However, the genus *Valenzuela*, with five species sampled is strongly supported to be monophyletic and the sister relationship with this genus and *Coryphosmila* Enderlein provides support for the tribe Coryphacini, as well as the separation of *Valenzuela* Navas from *Caecilius* Curtis (Mockford, 2000). The genus *Fuelleborniella* Enderlein has previously been placed in a separate subfamily Fuelleborniellinae, together with *Smithersiella* Badonnel and *Ypsiloneura* Pearman. While its position in the tree is somewhat unclear, *Fuelleborniella* does not appear to be particularly distinct and the best estimates place it inside the Caeciliusinae, suggesting the subfamily Fuelleborniellinae may not merit recognition.

Discussion

A molecular phylogenetic analysis of two mitochondrial and two nuclear genes provides new insights into the phylogenetic relationships and classification of the bark louse infraorder Caeciliusetae. Monophyly of Caeciliusetae continues to receive strong support on the basis of molecular analysis. This infraorder also has strong support based on morphological characters (Yoshizawa, 2002) and we expect that this group will continue to be robust to additional taxon sampling. In general, many of the previously recognized groups within Caeciliusetae are supported. However, there are also several notable exceptions.

The monophyly of Dasydemellidae is noteworthy, because it has not consistently been recognized as a distinct family (e.g. Yoshizawa, 2001, 2002). Dasydemellidae was first recognized as a taxon by Mockford (1978), who regarded it as a subfamily of Amphipsocidae with the most important defining characters being 1) a broad and relatively flat lacinial tip, 2) setae of hindwings greatly reduced or absent, 3) sheath of the spermathecal duct short and broad, 4) the third ventral abdominal vesicle (v3) well sclerotized, and 5) the nymphal duplex spine and associated setae of the paraproct retained in adults of both sexes. In addition, a prior analysis of morphological characters (Yoshizawa, 2002) did not recover a sister relationship between Dasydemellidae and Stenopsocidae, while this is one of the most strongly supported results of our molecular analysis. Dasydemellidae and Stenopsocidae possess several morphological characters in common. These include 1) the reduction to near absence of hindwing setae, 2) relatively large body size, 3) a notable common stem of ventral abdominal vesicles v2 and v3, 4) v3 well sclerotized, and 5) a short and broad sheath of the spermathecal duct.

Even though it has been the subject of an extensive study and classification system (Mockford, 2000; Lienhard & Smithers, 2002), the large family Caeciliusidae still appears to be in need of additional evaluation from a morphological perspective and some reclassification. In particular, there is strong support from the molecular data for the separation of the subfamily Paracaeciliinae and even elevation to a separate family. There is also substantial support from morphological characters for the monophyly of Paracaeciliidae, including 1) distal inner labral sensilla consisting of three placoids alternating with four trichoids (type 3 of Mockford, 2000); 2) cell R₅ of forewing scarcely, if at all, constricted beyond its base; 3) usually with three ventral abdominal vesicles (*Mockfordiella* Badonnel, with two is the only exception); 4) endophallus bilobed (undivided in *Mockfordiella*); and 5) neck of spermathecal sac either wide throughout or widened at its junction with sheath (spermatheca absent in *Mockfordiella*).

The placement of the amphipsocid genus *Calocaecilius* within Caeciliusidae suggests that Caeciliusidae should be redefined to include Calocaeciliinae. *Calocaecilius*, partly because of its presumed beetle mimicry (Mockford, 1974), stands apart morphologically from the rest of Caeciliusidae. Its position within Caeciliusidae is not well resolved and it could possibly be sister to the remainder of the family. In fact, the relationships among the redefined Caeciliusidae are not well supported, so it is difficult to assess the subfamilial classification scheme of Mockford (2000) and Lienhard & Smithers (2002). Certainly the sister relationship between *Valenzuela* and *Coryphosmila*, both in the tribe Coryphacini, support elements of this classification. However, both further phylogenetic support and additional taxon sampling are needed before an exhaustive reclassification of Caeciliusidae can be attempted on the basis of molecular data.

In conclusion, we propose a new family level classification scheme for the Caeciliusetae based on our analysis of molecular data and reevaluation of morphological characters. This scheme abandons superfamilies and classifies the infraorder into six families: Amphipsocidae, Stenopsocidae, Dasydemellidae, Asiopsocidae, Paracaeciliidae, and Caeciliusidae. We do not revise the existing classification below family (Lienhard & Smithers, 2002) until further work on the group is performed, though it is likely that some rearrangement will be needed.

Key to the Families of Caeciliusetae

1. With 5 – 7 distal labral sensilla. Cell R5 in forewing lacking a median constriction or inward curvature of vein Rs.....**2**
 - With not more than 5 distal labral sensilla. Cell R5 in forewing with a median constriction or at least a median inward curvature of vein Rs.....**3**
2. Generally 3 ventral abdominal vesicles present (see Mockford, 1993, Fig. 113); v3 clearly enclosed in widened base of v2+3.....**Family Paracaeciliidae**
 - Ventral abdominal vesicles absent; v3, when present, a distinct lateral lobe on base of v2.....**Family Asiopsocidae**
3. In hindwing, marginal setae restricted to cell R3 or none.....**4**
 - In hindwing, marginal setae around most of wing except basal half of fore margin.....**5**
4. Forewing with pterostigma-rs crossvein and m-cu1a crossvein. Nymphal paraproctal duplex spine and associated setae not retained in adults.....**Family Stenopsocidae**
 - Forewing lacking pterostigma-rs crossvein and m-cu1a crossvein. Nymphal paraproctal duplex spine and associated setae retained in adults (see Mockford, 1978, Fig. 23).....**Family Dasydemellidae**
5. Basal R and M-Cu veins of forewing and often more distal veins with more than one rank of setae; In hindwing, Rs and distal M veins bearing setae; v3 a small lobe on base of v2 lacking a seta.....**Family Amphipsocidae**
 - Basal R and M-Cu veins of forewing, as well as other veins, with only one rank of setae; in hindwing all veins lacking setae; v3 generally a major lobe on base of v2 with one or more setae.....**Family Caeciliusidae**

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Figure Legends

Figure 1. Photographs of representative species of Caeciliusetae included in the study. A) *Valenzuela badiostigma*, B) *Paracaecilius japanus*, C) *Graphopsocus cruciatus*, D) *Matsumuraiella radiopicta*.

Figure 2. Phylogenetic tree resulting from maximum likelihood analyses of the 18S rDNA, histone 3, 16S rDNA, and 12S rDNA genes. Numbers associated with each branch indicate ML bootstrap / Bayesian posterior probabilities. Sidebars on right are classification according to Lienhard and Smithers (2002), while those on left reflect the revised classification proposed in the current study.

Table 1 Classification of Caeciliusetae Following Lienhard and Smithers (2002)

Superfamily: Asiopsocoidea

Family: Asiopsocidae

Superfamily: Caeciliusoidea

Family: Caeciliusidae

Subfamily: Caeciliusinae

Tribe: Caeciliusini

Tribe: Kodamaiini

Tribe: Maoripsocini

Tribe: Coryphacini

Tribe: Epicaeciliini

Subfamily: Aphyopsocinae

Subfamily: Paracaeciliinae

Subfamily: Fuelleborniellinae

Family: Stenopsocidae

Family: Amphipsocidae

Subfamily: Amphipsocinae

Tribe: Kolbiini

Tribe: Schizopechini

Tribe: Capillopsocini

Tribe: Dasypsocini

Tribe: Polypsocini

Tribe: Amphipsocini

Subfamily: Calocaeciliinae

Family: Dasydemellidae

Subfamily: Dasydemellinae

Subfamily: Ptenopsilinae

Table 2. Samples Included in Study

Species	Locality	Voucher	18S	Histone 3	16S	12S
Ingroup						
Asiopsocidae						
Asiopsocus sonorensis	USA	Assp. 11.17.2003.3	AY63048 1	GU56933 0	GU56920 5	AB85691 6
Dasydemellidae						
Dasydemelliinae						
Dasydemella sp.	Malaysia	KY380	AB85695 5	AB85697 6	AB85694 0	AB85692 0
Teliapsocus conterminus	USA	Tecon.3.2.2004.1	AB85695 1	AB85697 2	AB85693 6	missing
Matsumuraiella radiopicta	Japan	KY236	AY63049 3	DQ10479 7	DQ10477 0	AB85691 2
Ptenopsilinae						
Ptenopsilla sp.	Chile	KY243	AY63049 4	missing	AB85692 9	AB85689 9
Stenopsocidae						
Graphopsocus cruciatus	USA	Grcru11.2.2001.5	AY63049 0	GU56933 6	GU56921 1	AY27530 6
Malostenopsocus sp.	Malaysia	KY349	AB85695 0	AB85697 1	AB85693 5	AB85691 5
Stenopsocus aphidiformis	Japan	KY219	AY63049 1	GU56933 7	GU56921 2	AB85691 0
Stenopsocus nigricellus	Japan	KY241	AY63049 2	GU56933 8	GU56921 3	AB85691 1
Amphisocidae						
Amphisocinae						
Amphisocini						
Amphisocus japonicus	Japan	KY211	AF63048 9	GU56933 1	GU56920 6	AB85690 9
Taeniostigma elongatum	Malaysia	KY221	AY63048 6	GU56933 5	GU56921 0	AB85690 7
Tagalopsocus sp.	Malaysia	KY257	AB85694 9	AB85696 8	AB85693 2	AB85690 2
Kolbiini						
Kolbia fusconervosa	Japan	KY208	AY63048 7	GU56933 3	GU56920 8	AB85690 8
Polypsocini						
Polypsocus corruptus	USA	Pocor. 8.31.2001.6	AY63048 8	GU56933 4	GU56920 9	AY27530 9
Calocaeciliinae						
Calocaecilius decipiens	Malaysia	KY201	AY63048 5	GU56933 2	GU56920 7	AB85690 6
Caeciliusidae						

Caeciliusinae**Caeciliusini**

Caecilius fuscopterus	Japan	KY227	AY63048 4	AB85696 9	AB85693 3	AB85690 5
Caecilius sp.	Nepal	KY403	AB85696 0	AB85698 1	missing	missing
Caecilius sp.	Malaysia	KY389	AB85698 9	AB85698 0	AB85694 4	AB85692 4
Dypsocus coleopratus	Japan	KY209	AY63048 2	GU56934 1	GU56921 6	AB85690 3
Isophanessp.	Japan	KY230	AY63048 3	GU56934 2	GU56921 7	AB85690 4

Coryphacini

Coryphosmila dolobrata	Japan	KY385	AB85695 6	AB85697 7	AB85694 1	AB85692 1
Valenzuela badiostigma	Japan	KY387	AB85695 4	AB85697 5	AB85693 9	AB85691 9
Valenzuela flavidus	USA	Vafla.8.31.2001.5	AY63049 9	GU56934 3	GU56921 8	AY27530 8
Valenzuela kamakurensis	Japan	KY223	AB85694 8	AB85696 7	AB85693 1	AB85690 1
Valenzuela oyamai	Japan	KY210	AY63049 7	AB85696 6	AB85693 0	AB85690 0
Valenzuela sp.	Taiwan	KY392	AB85695 7	AB85697 8	AB85694 2	AB85692 2

Kodamaiini

Genus (nr. Austrocaecilius) sp.	Nepal	KY390	AB85695 8	AB85697 9	AB85694 3	AB85692 3
Genus (nr. Asiocaecilius or Isophanopsis) sp.	Malaysia	KY382	AB85695 3	AB85697 4	AB85693 8	AB85691 8
Kodamaius sp.	Taiwan	KY393	AB85695 2	AB85697 3	AB85693 7	AB85691 7
Pericaecilius singularis	Taiwan	KY239	AY63049 5	GU56934 0	GU56921 5	AB85691 4

Fuellebornielinae

Fuelleborniella sp.	Ghana	Fusp. 11.24.2003.6	AY63049 6	GU56933 9	GU56921 4	missing
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Paracaeciliinae

Enderleinella sp.	Malaysia	KY473	AB85696 1	AB85698 2	AB85694 5	missing
Enderleinella sp.	Peru	KY472	AB85696 2	missing	AB85694 6	missing
Paracaecilius japanus	Japan	KY233	AY63050 1	AB85697 0	AB85693 4	AB85691 3

Xanthocaecilius sommermanae	USA	Xasom. 8.31.2001.4	AY63050 0	GU56934 4	GU56921 9	AY13990 3
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Outgroup

Ectopsocidae

Ectopsocus meridionalis	USA	Epmer.2.3.2001.4	AY63051 2	GU56932 2	GU56919 7	AY27530 0
Ectopsocus sp.	Japan	KY212	AY63051 0	AB85696 5	AB85692 6	missing
Ectopsocopsis cryptomeriae	USA	Etry. 11.17.2003.2	AY63051 1	GU56932 3	GU56919 8	missing

Lachesillidae

Anomopsocus amabilis	USA	Anama. 11.17.2003.9	AY63050 9	GU56932 6	GU56920 1	missing
Eolachesilla chilensis	Chile	KY214	AY63051 4	GU56932 8	GU56920 3	missing
Lachesilla anna	USA	Laann.1.16.2001.2	AY63050 4	missing	AY27535 1	AY27530 1
Lachesilla forcepeta	USA	Lafor.8.31.2001.10	AY63050 3	GU56932 7	GU56920 2	AB85689 8
Lachesilla sp.	Malays ia	KY229	AB85694 7	AB85699 4	AB85692 5	missing

Mesopsocidae

Idatenopsocus orientalis	Japan	KY203	AY63051 3	missing	AY13995 6	AY13990 9
Mesopsocus hongkongensis	Japan	KY224	AY63051 6	DQ10479 4	DQ10476 7	missing
Mesopsocus unipunctatus	USA	Meuni. 12.4.2003.4	AY63051 5	missing	AB85692 7	missing

Peripsocidae

Kaestneriella sp.	USA	Kasp.11.24.2003.5	AY63050 6	GU56932 4	GU56919 9	missing
Peripsocus madidus	USA	Pemad. 8.31.2001.7	AY63050 8	missing	AY27535 2	AY27530 2
Peripsocus subfasciatus	USA	Pesub.2.3.2001.2	AY63050 7	GU56932 5	GU56920 0	AY27530 3

Elipsocidae

Nepiomorpha sp.	Malays ia	KY200	AY63051 8	missing	AB85692 8	missing
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