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Citation	Systematic Entomology, 39(2), 279-285 https://doi.org/10.1111/syen.12054
Issue Date	2014-04
Doc URL	https://hdl.handle.net/2115/58545
Rights	The definitive version is available at www.blackwell-synergy.com
Type	journal article
File Information	2014Cae.pdf

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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/Caeciliusetaae/.

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 remainingtrees 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.

Whiletaxon 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 (*Amphiposcus* Smithers and *Taeniostigma* 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 notableexceptions.

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 R_5 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 beattempted 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**

Acknowledgements

This work was supported by NSF grants DEB-0612938 to KPJ and JSPS grant 18770058 and 1877058 to KY. KY's field work to Malaysia and Nepal were supported by JSPS grants 14255016 and 17255001 (project leader: O. Yata at Kyushu University). KY thanks A.B. Idris, H. Kojima, S. Nomura, I. Ohshima, M. Shrestha and N. Takahashi for help in the field. We thank T. Muroi, G. Svenson, and M. Whiting for assistance in obtaining samples.

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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	AY630481	GU569330	GU569205	AB856916
Dasydemellidae						
Dasydemelliinae						
Dasydemella sp.	Malaysia	KY380	AB856955	AB856976	AB856940	AB856920
Teliapsocus conterminus	USA	Tecon.3.2.2004.1	AB856951	AB856972	AB856936	missing
Matsumuraiella radiopicta	Japan	KY236	AY630493	DQ104797	DQ104770	AB856912
Ptenopsilinae						
Ptenopsilla sp.	Chile	KY243	AY630494	missing	AB856929	AB856899
Stenopsocidae						
Graphopsocus cruciatus	USA	Grcru11.2.2001.5	AY630490	GU569336	GU569211	AY275306
Malostenopsocus sp.	Malaysia	KY349	AB856950	AB856971	AB856935	AB856915
Stenopsocus aphidiformis	Japan	KY219	AY630491	GU569337	GU569212	AB856910
Stenopsocus nigricellus	Japan	KY241	AY630492	GU569338	GU569213	AB856911
Amphipsocidae						
Amphipsocinae						
Amphipsocini						
Amphipsocus japonicus	Japan	KY211	AF630489	GU569331	GU569206	AB856909
Taeniostigma elongatum	Malaysia	KY221	AY630486	GU569335	GU569210	AB856907
Tagalopsocus sp.	Malaysia	KY257	AB856949	AB856968	AB856932	AB856902
Kolbiini						
Kolbia fusconervosa	Japan	KY208	AY630487	GU569333	GU569208	AB856908
Polypsocini						
Polypsocus corruptus	USA	Pocor. 8.31.2001.6	AY630488	GU569334	GU569209	AY275309
Calocaeciliinae						
Calocaecilius decipiens	Malaysia	KY201	AY630485	GU569332	GU569207	AB856906
Caeciliusidae						

Caeciliusinae						
Caeciliusini						
Caecilius fuscopterus	Japan	KY227	AY630484	AB856969	AB856933	AB856905
Caecilius sp.	Nepal	KY403	AB856960	AB856981	missing	missing
Caecilius sp.	Malaysia	KY389	AB856989	AB856980	AB856944	AB856924
Dypsocus coleoptratus	Japan	KY209	AY630482	GU569341	GU569216	AB856903
Isophanessp.	Japan	KY230	AY630483	GU569342	GU569217	AB856904
Coryphacini						
Coryphosmila dolobrata	Japan	KY385	AB856956	AB856977	AB856941	AB856921
Valenzuela badiostigma	Japan	KY387	AB856954	AB856975	AB856939	AB856919
Valenzuela flavidus	USA	Vafla.8.31.2001.5	AY630499	GU569343	GU569218	AY275308
Valenzuela kamakurensis	Japan	KY223	AB856948	AB856967	AB856931	AB856901
Valenzuela oyamai	Japan	KY210	AY630497	AB856966	AB856930	AB856900
Valenzuela sp.	Taiwan	KY392	AB856957	AB856978	AB856942	AB856922
Kodamaiini						
Genus (nr. Austrocaecilius) sp.	Nepal	KY390	AB856958	AB856979	AB856943	AB856923
Genus (nr. Asiocaecilius or *Isophanopsis*) sp.	Malaysia	KY382	AB856953	AB856974	AB856938	AB856918
Kodamaius sp.	Taiwan	KY393	AB856952	AB856973	AB856937	AB856917
Pericaecilius singularis	Taiwan	KY239	AY630495	GU569340	GU569215	AB856914
Fuellebornielinae						
Fuelleborniella sp.	Ghana	Fusp. 11.24.2003.6	AY630496	GU569339	GU569214	missing
Paracaeciliinae						
Enderleinella sp.	Malaysia	KY473	AB856961	AB856982	AB856945	missing
Enderleinella sp.	Peru	KY472	AB856962	missing	AB856946	missing
Paracaecilius japanus	Japan	KY233	AY630501	AB856970	AB856934	AB856913

Xanthocaecilius sommermanae	USA	Xasom. 8.31.2001.4	AY630500	GU569344	GU569219	AY139903

Outgroup

Ectopsocidae

Ectopsocus meridionalis	USA	Epmer.2.3.2001.4	AY630512	GU569322	GU569197	AY275300
Ectopsocus sp.	Japan	KY212	AY630510	AB856965	AB856926	missing
Ectopsocopsis cryptomeriae	USA	Etcry. 11.17.2003.2	AY630511	GU569323	GU569198	missing

Lachesillidae

Anomopsocus amabilis	USA	Anama. 11.17.2003.9	AY630509	GU569326	GU569201	missing
Eolachesilla chilensis	Chile	KY214	AY630514	GU569328	GU569203	missing
Lachesilla anna	USA	Laann.1.16.2001.2	AY630504	missing	AY275351	AY275301
Lachesilla forcepeta	USA	Lafor.8.31.2001.10	AY630503	GU569327	GU569202	AB856898
Lachesilla sp.	Malaysia	KY229	AB856947	AB856994	AB856925	missing

Mesopsocidae

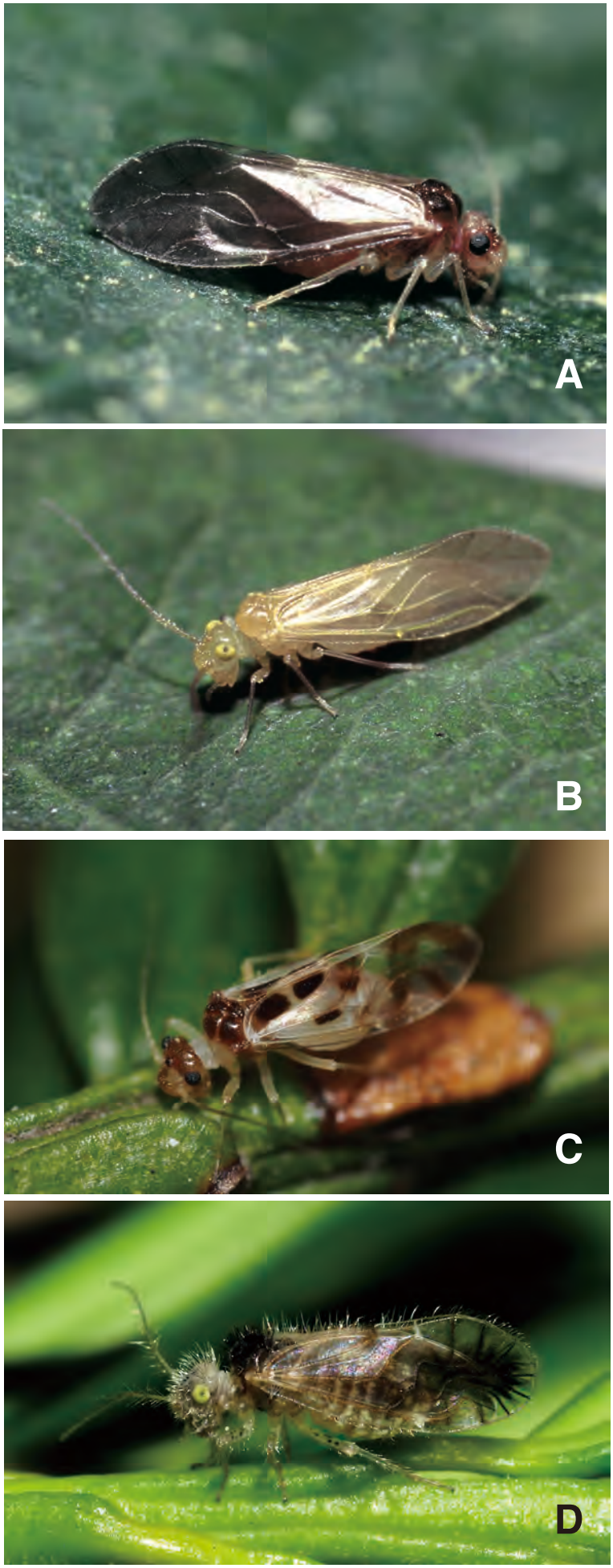
Idatenopsocus orientalis	Japan	KY203	AY630513	missing	AY139956	AY139909
Mesopsocus hongkongensis	Japan	KY224	AY630516	DQ104794	DQ104767	missing
Mesopsocus unipunctatus	USA	Meuni. 12.4.2003.4	AY630515	missing	AB856927	missing

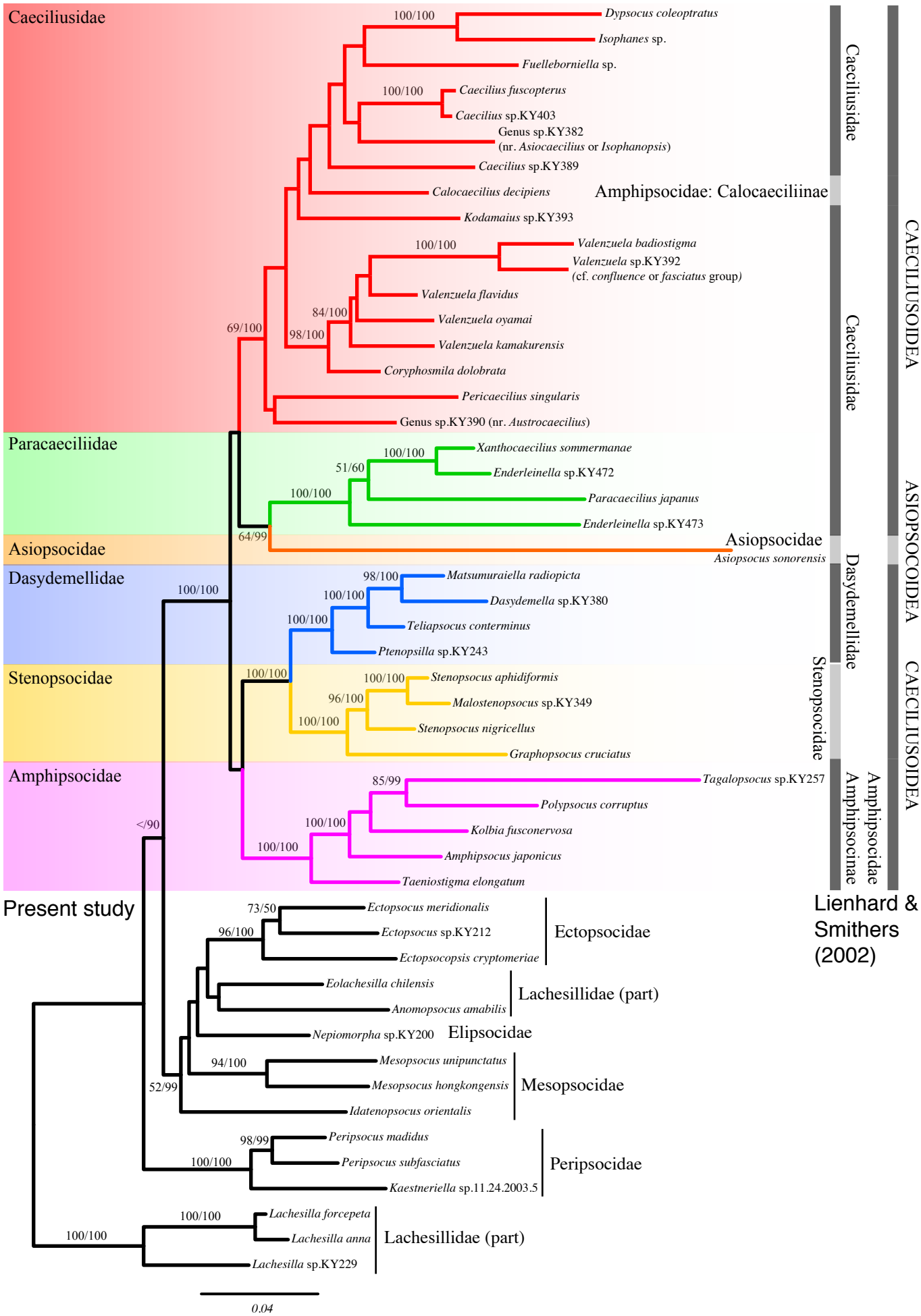
Peripsocidae

Kaestneriella sp.	USA	Kasp.11.24.2003.5	AY630506	GU569324	GU569199	missing
Peripsocus madidus	USA	Pemad. 8.31.2001.7	AY630508	missing	AY275352	AY275302
Peripsocus subfasciatus	USA	Pesub.2.3.2001.2	AY630507	GU569325	GU569200	AY275303

Elipsocidae

Nepiomorpha sp.	Malaysia	KY200	AY630518	missing	AB856928	missing


A
B
C
D


Caeciliusidae
Paracaeciliidae
Asiopsocidae
Dasydemellidae
Stenopsocidae
Amphipsocidae
Dypsocus coleoptratus
Isophanes sp.
Fuelleborniella sp.
Caecilius fuscopterus
Caecilius sp.KY403
Genus sp.KY382
(nr. Asiocaecilius or Isophanopsis)
Caecilius sp.KY389
Calocaecilius decipiens
Kodamaius sp.KY393
Valenzuela badiostigma
Valenzuela sp.KY392
(cf. confluence or fasciatus group)
Valenzuela flavidus
Valenzuela oyamai
Valenzuela kamakurensis
Coryphosmila dolobrata
Pericaecilius singularis
Genus sp.KY390 (nr. Austrocaecilius)
Xanthocaecilius sommermanae
Enderleinella sp.KY472
Paracaecilius japanus
Enderleinella sp.KY473
Asiopsocidae
Asiopsocus sonorensis
Matsumuraiella radiopicta
Dasydemella sp.KY380
Teliapsocus conterminus
Ptenopsilla sp.KY243
Stenopsocus aphidiformis
Malostenopsocus sp.KY349
Stenopsocus nigricellus
Graphopsocus cruciatus
Tagalopsocus sp.KY257
Polypsocus corruptus
Kolbia fusconervosa
Amphipsocus japonicus
Taeniostigma elongatum
Amphipsocidae: Calocaeciliinae
Caeciliusidae
Caeciliusidae
Dasydemellidae
Stenopsocidae
Amphipsocidae
Amphipsocinae
CAECILIUSOIDEA
ASIOPSOCOIDEA
CAECILIUSOIDEA
Present study
Lienhard & Smithers (2002)
Ectopsocus meridionalis
Ectopsocus sp.KY212
Ectopsocopsis cryptomeriae
Ectopsocidae
Eolachesilla chilensis
Anomopsocus amabilis
Lachesillidae (part)
Nepiomorpha sp.KY200
Elipsocidae
Mesopsocus unipunctatus
Mesopsocus hongkongensis
Idatenopsocus orientalis
Mesopsocidae
Peripsocus madidus
Peripsocus subfasciatus
Kaestneriella sp.11.24.2003.5
Peripsocidae
Lachesilla forcepeta
Lachesilla anna
Lachesilla sp.KY229
Lachesillidae (part)
0.04