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Systematic revision and molecular phylogenetics refine the generic classification of the bark louse family Stenopsocidae (Insecta: Psocodea: Psocomorpha)

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Abstract

Psocomorpha, as one of the suborders of the order Psocodea, represents a large group of free-living bark lice. The phylogenetic relationships among/within the major groups, such as families, subfamilies, tribes, etc., of the bark lice need extensive investigation. The family Stenopsocidae belongs to the infraorder Caeciliusetae, which is a large group of Psocomorpha and is one of the common groups in Asia. Here we infer the intergeneric relationships of Stenopsocidae based on the mitochondrial genes and the nuclear 18S rRNA. The result supports the monophyly of Stenopsocidae and suggests the paraphyly of the genus *Stenopsocus*. Combining the morphological evidence, we propose a new genus, namely *Neostenopsocus* **gen. n.**, which includes a number of species previously placed in *Stenopsocus*. The checklist of this new genus is provided. This new genus can be distinguished from *Stenopsocus* by the glabrous forewing CuP. In the revised classification system, Stenopsocidae includes four genera: *Graphopsocus*, *Malostenopsocus*, *Neostenopsocus* **gen. n.**, and *Stenopsocus*. A key to the genera of Stenopsocidae is provided. We also present the diagnostic characters for each of these genera.

Keywords

mitochondrial genome, taxonomy, new genus, *Neostenopsocus* **gen. n.**

1. Introduction

The paraneopteran insect order Psocodea is an inconspicuous group, containing more than 10000 valid species, and is divided into three suborders: Trogiomorpha, Troctomorpha, and Psocomorpha (Lienhard & Smithers, 2002; de Moya et al., 2021; Zhang, 2011). Recent progress based on molecular data resolved the phylogenetic position of parasitic lice as the sister group of the family Liposcelididae in Psocodea (de Moya et al., 2021). Besides, many molecular phylogenetic studies recovered the relationships among the families or higher taxa of Psocodea (Johnson et al., 2004; Yoshizawa et al., 2006; Yoshizawa et al., 2014; Yoshizawa et al., 2018; de Moya et al., 2021). However,

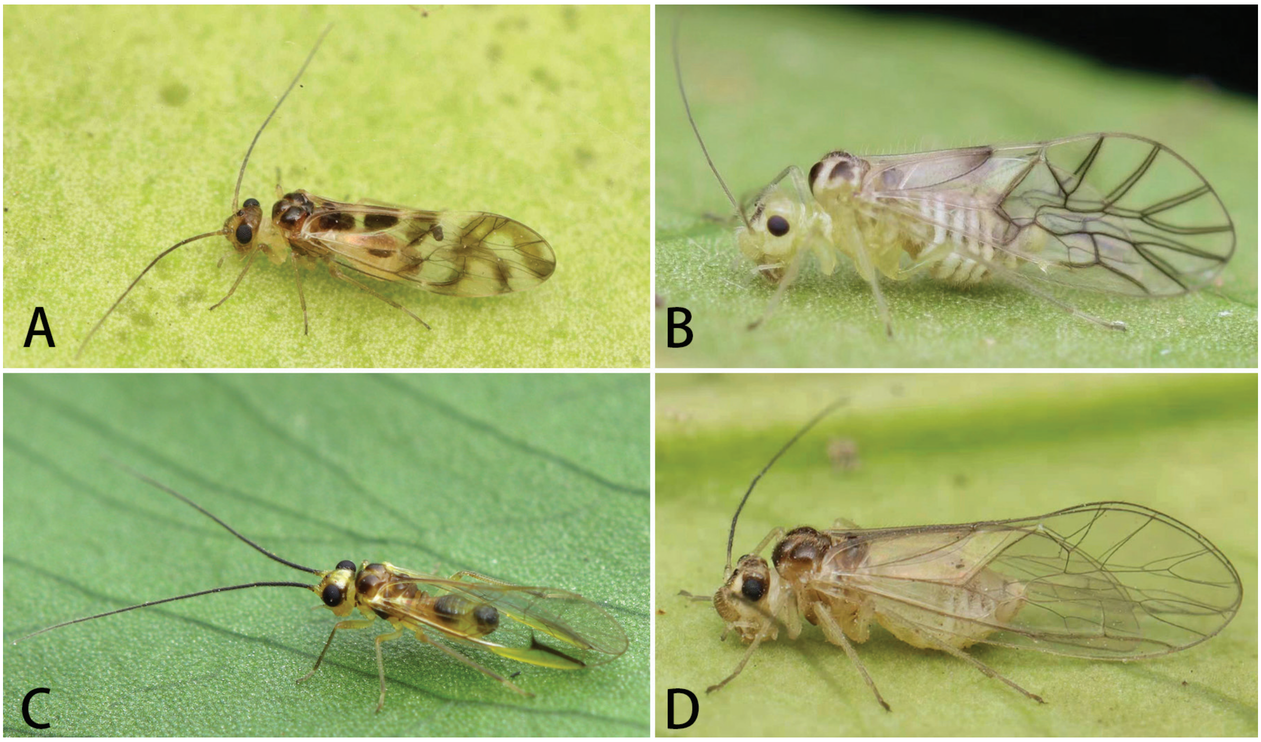

Figure 1. Photographs of representative species of Stenopsocidae. **A** *Graphopsocus cruciatus* (photo by Ruiyang Wang); **B** *Malostenopsocus* sp. (photo by Fan Gao); **C** *Neostenopsocus externus* (photo by Qianle Lu); **D** *Stenopsocus* sp. (photo by Ruiyang Wang).

among the 37 families of 'Psocoptera' (Mockford, 2018), the intergeneric or interspecific phylogenies within a family have been poorly studied. The only case refers to Saenz Manchola et al. (2022), in which the phylogenetic relationships within the family Lachesillidae were reconstructed based on a dataset of 2060 orthologous genes. Yoshizawa and Johnson (2008) evaluated the higher level (subfamilies and tribes) classification within the family Psocidae based on a multi-loci phylogenetic study.

The bark louse family Stenopsocidae is a large group of the suborder Psocomorpha, currently comprising over 190 valid species in the world (Hopkins et al., 2023). It is noticeable that the fauna of Stenopsocidae is extremely rich in Asia, especially in China, from which 168 species have been described (Lienhard & Smithers, 2002; Li, 2002, 2005; Liang et al., 2013, 2014, 2017). The adults of Stenopsocidae generally inhabit living trees, bamboos, etc., and are characterized by the abdomen with 2-3 ventral vesicles, and the forewing with pterostigma connecting to Rs by a crossvein and M connecting to areola postica cell by a crossvein (Fig. 1).

The genus *Stenopsocus* Hagen, 1866 was proposed by Hagen (1866) in his system of 'Psocina'. Kolbe (1880) established the tribe Stenopsocini which was placed in the family Psocidae, including the genera *Stenopsocus* and *Graphopsocus* Kolbe, 1880. In the early classification system of 'Psocoptera' proposed by Pearman (1936), Stenopsocidae was first considered as a family and was placed into the group Caecilietae along with four families Amphipsocidae, Caeciliidae, Polypsocidae and Calopsocidae. Roesler (1944) treated Stenopsocidae as a subfamily of Polypsocidae. Badonnel (1951) and Smithers (1972) recognized that Stenopsocidae has familial status and belongs to Caecilietae. In recent studies, the familial status and monophyly of Stenopsocidae were supported based on the morphological and molecular data (Yoshizawa, 2002; Yoshizawa et al., 2014).

Pearman (1936) considered *Stenopsocus* to have close affinities with *Caecilius*, and designated *Graphopsocus* to be the typical genus of the family Stenopsocidae. Roesler (1944) placed the genus *Stenopsocus* Hagen, 1866 into Stenopsocidae and treated *Graphopsocus* as a subgenus of *Stenopsocus*. *Stenopsocus* was considered the typical genus of Stenopsocidae by Roesler (1944) and the subsequent studies. Based on the revision made by Badonnel (1951) and Lienhard (1998), Stenopsocidae consists of two genera *Graphopsocus* and *Stenopsocus*, while six genera (*Graphopsocus*, *Stenopsocus*, *Kodamaius* Okamoto, 1907, *Epikodamaius* Kuwayama, 1961, *Teaniostigma* Enderlein, 1901, and *Matsumuraiella* Enderlein, 1906) were mentioned to be included in this family (Smithers 1972). Li (1992, 1993, 2002) described two more genera of Stenopsocidae: *Malostenopsocus* Li, 1992 and *Cubipilis* Li, 1993. Lienhard & Smithers (2002) stated that Stenopsocidae includes four valid genera (*Graphopsocus*, *Stenopsocus*, *Malostenopsocus* and *Cubipilis*), and they excluded *Kodamaius* and *Epikodamaius* currently placed in Caeciliusidae, *Teaniostigma* currently placed in Amphipsocidae, and *Matsumuraiella* currently placed in Dasypsocidae from this family. Li (1993) indicated that *Cubipilis* can be distinguished from *Stenopsocus* by the setose CuP in the forewing. However, Mockford (2003) considered *Cubipilis* as a synonym for *Stenopsocus* because this character is also present in *Stenopsocus immaculatus* (Stephens, 1836) which is the type species of *Stenopsocus*. Thus, Stenopsocidae includes three genera: *Graphopso-*

Table 1. Taxa included in this study with their number of Genbank accession number.

Family	Species	Mitogenome	18S	Reference
Stenopsocidae	*Graphopsocus cruciatus*	OR608384	AY630490	This study
	Malostenopsocus sp._HN	OR608385	OR544596	This study
	Malostenopsocus yunnanicus	OR608386	OR544597	This study
	Neostenopsocus brevicapitus	OR608387	OR544598	This study
	Neostenopsocus capacimacularus	OR608388	OR544599	This study
	Neostenopsocus dactylinus	OR608389	OR544600	This study
	Neostenopsocus externus	OR608390	OR544601	This study
	Neostenopsocus genostictus	OR608391	OR544602	This study
	Neostenopsocus longitudinalis	OR608392	OR544603	This study
	Neostenopsocus maximalis	OR608393	OR544604	This study
	Neostenopsocus metastictus	OR608394	OR544605	This study
	Neostenopsocus nepalensis	OR608395	OR544606	This study
	Neostenopsocus obscurus	OR608396	OR544607	This study
	Neostenopsocus periostictus	OR608397	OR544608	This study
	Neostenopsocus pygmaeus	OR608398	OR544609	This study
	Neostenopsocus tripartibilis	OR608403	OR544610	This study
	Neostenopsocus wangi	OR608399	OR544611	This study
	Stenopsocus aphidiformis	OR608400	OR544612	This study
	Stenopsocus lachali	OR608401	OR544613	This study
	Stenopsocus niger	OR608402	OR544614	This study
	Stenopsocus immaculatus	KX187004	—	Liu et al., 2017
Dasydemellidae	*Teliapsocus conterminus*	MZ274210	AB856951	Saenz Manchola et al., 2021; Yoshziawa et al., 2014
Amphipsocidae	*Polypsocus corruptus*	MZ274208	AY630488	
Paracaeciliidae	*Paracaecilius japanus*	MZ274207	AY630501	
	Xanthocaecilius sommermanae	MZ274212	AY630500	
Caeciliusidae	*Dypsocus coleoptratus*	MZ274186	AB856955	
	Fuelleborniella sp.	MZ274189	AY630496	
Asiopsocidae	*Asiopsocus sonorensis*	MZ274183	AY630481	
Lachesillidae	*Graphocaecilius interpretatus*	MZ274193	—	
Ectopsocidae	*Ectopsocopsis cryptomeriae*	MZ274187	AY630511	
Peripsocidae	*Kaestneriella* sp.	MZ274196	AY630506	
Archipsocidae	*Archipsocus nomas*	MG255135	—	

cus, *Malostenopsocus*, and *Stenopsocus*. Yoshizawa et al. (2014) confirmed the monophyly of the family Stenopsocidae, but indicated the genus *Stenopsocus* appears to be paraphyletic.

In the present study, we investigate the phylogenetic relationships within the family Stenopsocidae using DNA sequences from the mitochondrial genes and nuclear 18s rRNA gene. Combining the molecular phylogeny and morphological characters, we propose a new genus *Neostenopsocus* **gen. n.**, and present a revised generic classification of Stenopsocidae.

2. Material and Methods

2.1. DNA extraction, mitogenome sequencing and assembly

The genomic DNA was extracted from the thoracic muscle tissues of a single specimen using TIANamp Micro DNA Kit (TIANGEN, Beijing, China). For the sequencing library for each specimen and used the Illumina NovaSeq platform to obtain 4 GB sequence data. Raw reads were trimmed of adapters using BWA (Burrows-Wheeler Aligner) software (Li & Durbin, 2010). All sequences were assembled mapping to the mitogenome as the reference sequence using Geneious Prime 2023 (Kearse et al. 2012), with the parameters sets as follows: 95% minimum overlap identity, 4 maximum ambiguity and a minimum overlap of 25 bp. Each mitochondrial contig was inputted into MITOS web service (Bern et al., 2013) for initial mitogenome annotation. The resultant gene boundaries were checked by alignment with homologous genes of the published mitogenomes (Genbank accession number: KX187004, MZ274186, MZ274207, MZ274208) and 18S rRNA (Genbank accession number: AY63049, AB856950, AY630491, AY630492) of psocids. The mitogenomes and 18S rRNA herein sequenced are deposited in Genbank (Table 1).

2.2. Phylogenetic analysis

In this study, we used mitochondrial genes (exclude the control region, intergenic spacers and tRNA genes,

Table 2. Nucleotide composition of the mitogenomes in Stenopsocidae

Dataset		***Graphopsocus* (1 species)**	***Malostenopsocus* (2 species)**	***Neostenopsocus* (14 species)**	***Stenopsocus* (4 species)**	**Stenopsocidae (21 species)**
PCGs	A+T%	72.74	75.19	72.55	75.77	73.43
	AT-skew	–0.13	–0.15	–0.16	–0.15	–0.15
	GC-skew	0.017	0.027	0.021	0.055	0.026
	Size	11070	11106	11102	11108	11102
tRNAs	A+T%	77.75	79.57	78.26	79.67	78.63
	AT-skew	0.017	0.0036	0.0051	–0.0027	0.0041
	GC-skew	0.13	0.15	0.14	0.17	0.15
	Size	1411	1410	1413	1414	1413
rRNAs	A+T%	80.55	81.44	80.39	82.11	80.83
	AT-skew	–0.033	–0.044	–0.061	–0.047	–0.056
	GC-skew	0.25	0.22	0.23	0.23	0.23
	Size	1959	1937	1970	1961	1965
PCGs+RNAs	A+T%	74.29	76.50	74.18	77.01	74.94
	AT-skew	–0.10	–0.12	–0.13	–0.12	–0.12
	GC-skew	0.023	0.058	0.053	0.083	0.058
	Size	1440	14453	14485	14483	14480
Full	A+T%	75.30	77.09	74.76	78.07	75.63
	AT-skew	0.026	-0.017	-0.014	-0.016	-0.013
	GC-skew	-0.18	-0.087	-0.10	-0.095	-0.10
	Size	16215	15369	16602	16164	16367

including the protein-coding genes and rRNA genes) and partial nuclear18S rRNA. The alignment of 13 protein-coding genes was based on amino acid sequences translated with the invertebrate mitochondrial genetic codon table using MUSCLE (Edgar, 2004) complied in MEGA 7.0 (Kumar et al., 2016). The rRNA genes were aligned using MAFFT 7.0 (Katoh & Standley, 2013) under iterative refinement method incorporating the most accurate local (E-INS-i) pairwise alignment information. We used trimAl v1.2 (Capella-Gutiérrez et al., 2009) to remove poorly aligned regions from the alignments. All alignments were concatenated using PhyloSuite v1.2.3 (Zhang et al., 2020; Xiang et al., 2023). Phylogenetic relationships were inferred using Maximum-likehood (ML) and Bayesian inference (BI) methods. ML analysis was conducted in IQ-TREE v2.2.0 (Nguyen et al., 2015) under the model automatically selected by IQ-TREE for 5000 ultrafast (Minh et al. 2013) bootstraps. For Bayesian analysis, we use MrBayes 3.2.6 (Ronquist et al., 2012). The BI analysis contained four simultaneous Markov chain Monte Carlo (MCMC) runs of 5 million generations for the average standard deviation of split frequency was below 0.01, and tree samples were outputted every 1000 generations with a burn-in of 25%. We estimated the best partitioning scheme and model for our dataset with PartitionFinder 2 (Lanfear et al., 2017). The concatenated dataset was partitioned into six subsets and the GTR + I + G model was selected (File S1).

2.3. Illustration and morphological study

Genitalic preparations were made by clearing the apex of the abdomen in a cold, saturated NaOH solution for 6 h. After rinsing the NaOH with water, the apex of the abdomen was transferred to glycerin for further dissection and examination. Observations were made using an Olympus CX-33 (Olympus Imaging Corporation, Tokyo) light microscope. Photographs and drawings were taken using a Sony Alpha 7II (Sony Corporation, Tokyo) digital camera attached to the Olympus CX-33. The figures were prepared with Adobe Photoshop 24.0.0 (Adobe, San Jose, CA, USA). The terminology follows Yoshizawa (2005).

3. Results

3.1. Mitochondrial genome gene composition and general features

A total of 20 nearly complete mitochondrial genomes of Stenopsocidae were assembled. The mt genome of Stenopsocidae was determined to be a double-strand circular DNA molecule, including 37 typical genes: 13 PCGs, 22 tRNAs, and two rRNAs. In the 13 PCGs, *ND2*, *COX1*, *COX2*, *ATP8*, *ATP6*, *COX3*, *ND3*, *ND6* and *CytB* are encoded on the major strand (J-strand), and *ND5*, *ND4*, *ND4L* and *ND1* are encoded on the minor strand (Fig. 1). The PCGs show the typical ATN start codons. The majority of PCGs also show the typical TAR (TAA/TAG) stop

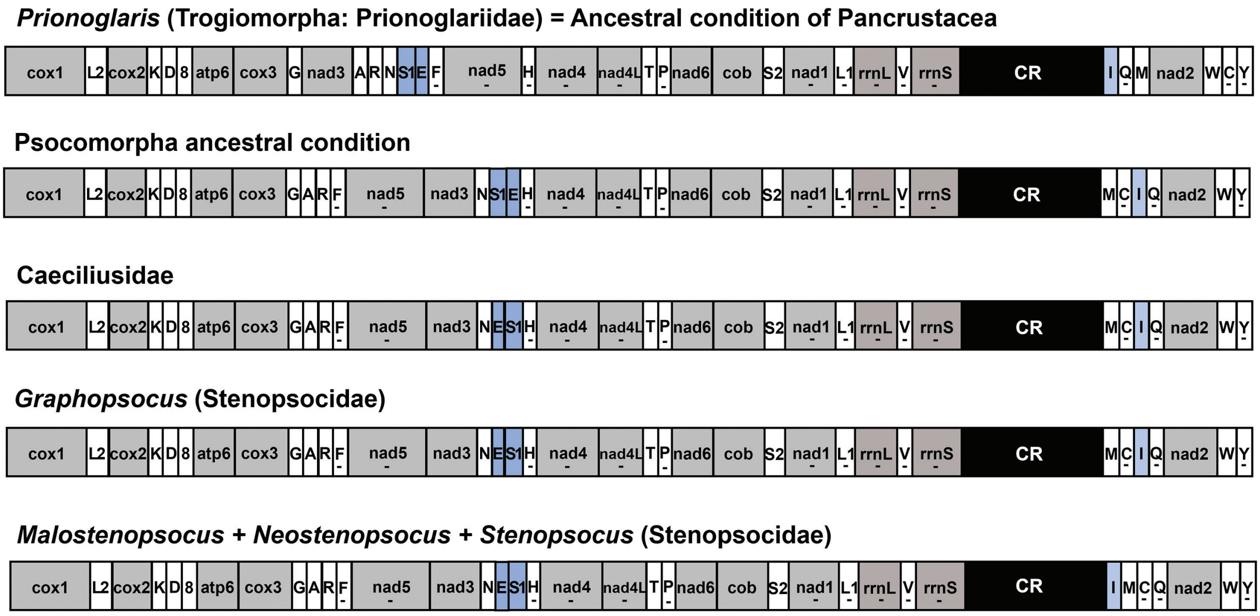

Figure 2. Mitochondrial genetic arrangement.

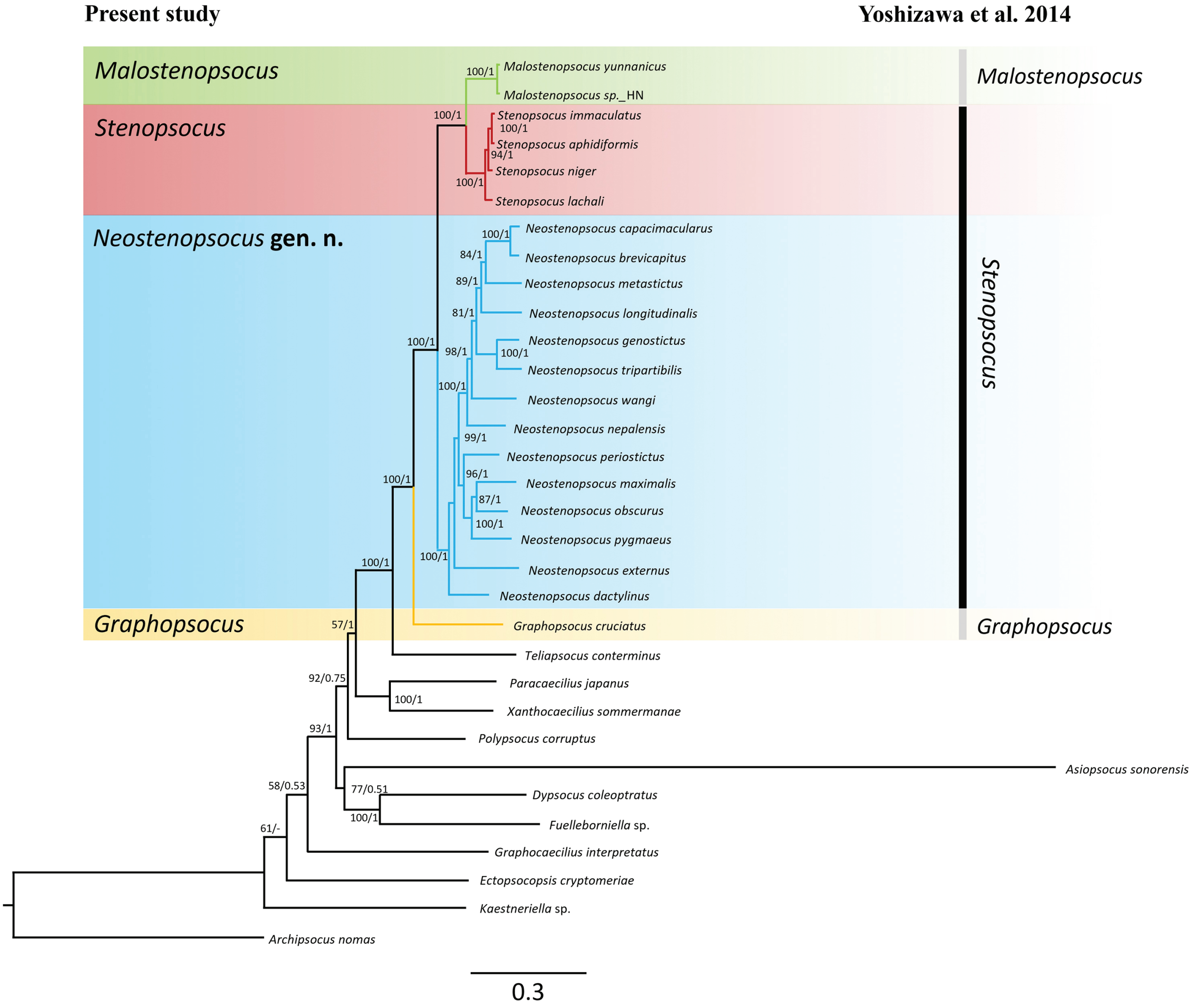

Figure 3. Phylogenetic tree inferred from maximum likelihood analyses of the mitochondrial genes (the protein-coding sequences and rRNA genes) and the 18S rRNA gene. Numbers associated with each branch indicate ML bootstrap/Bayesian posterior probabilities. Side bars on the right are classification according to Yoshizawa et al. (2014), whereas those on the left reflect the revised classification proposed in the current study.

codons, while the partial stop codon T for *COX1*, *ND5* in all species.

The mitogenome of Stenopsocidae shows highly biased AT composition (75.63%) (Table 2), similar to most insects. The AT content in the genera *Malostenopsocus* (77.09%) and *Stenopsocus* (78.07%) are higher than in the genera *Graphopsocus* (75.30%) and *Neostenopsocus* **gen. n.** (74.76%). Gene composition showed high AT% values for tRNAs (78.63%) and rRNAs (80.83%), while PCGs showed smaller AT content (73.43%). For PCGs, rRNAs, and PCGs+RNAs, all genera showed slightly negative AT-skews and slightly positive GC-skews. The whole mitogenome of *Graphopsocus* showed a slightly positive AT-skew (0.026) and a slightly negative GC-skew (–0.18). However, other genera showed slightly negative AT-skew and GC-skew.

3.2. Mitochondrial genetic arrangement

All species of Stenopsocidae share a similar mitochondrial genetic arrangement with the infraorder Caeciliusetae, and show the *trnE-trnS1* rearrangement which was considered to be an autapomorphy for Caeciliusetae by Saenz Manchola et al. (2021). Additionally, the family Stenopsocidae has two mitochondrial genetic arrangement types that were reported by Saenz Manchola et al. (2021) and Liu et al. (2017). *Graphopsocus* shares the *trnM-trnI-trnC-trnQ* gene block with the family Caeciliusidae (Fig. 2). *Neostenopsocus* **gen. n.**, *Malostenopsocus* and *Stenopsocus* show the same mitochondrial genetic arrangement that was reported by Liu et al. (2017). In these three genera, *trnM* was located next to *trnI*. The *trnI-trnM-trnC-trnQ* gene block has not been found in the other taxa of the suborder Psocomorpha.

3.3. Phylogenetic relationship of Stenopsocidae

In the present study, we use the mitogenomes and 18S rRNA of 21 species of Stenopsocidae with additional 11 mitogenomes of other bark lice as outgroup to infer the phylogeny of the family Stenopsocidae. The aligned and cleaned full data matrix was 14738 bp (mitogenomic data: 13006 bp, 18S rRNA data: 1732 bp) in length (File S1). Phylogenetic analyses under ML and BI analyses showed the same topology and overall high nodal supports (Fig. 3). The monophyly of the family Stenopsocidae was recovered. *Stenopsocus* is divided into two monophyletic clades which both received strong supports, i.e., the "*immaculatus-lachlani*" clade and the clade comprising the other *Stenopsocus* species. The former clade is assigned to be the sister group of the genus *Malostenopsocus*, suggesting the paraphyly of *Stenopsocus*. As the "*immaculatus-lachlani*" clade includes *S. immaculatus*, the type species of *Stenopsocus*, this clade is considered to represent the true *Stenopsocus*. Thus, the latter clade represents a different genus from *Stenopsocus*, and here we propose a new genus *Neostenopsocus* **gen. n.** based on the above inferred relationship. *Neostenopsocus* **gen. n.** was assigned to be the sister group of *Stenopsocus* + *Malostenopsocus*.

4. Taxonomy

Order Psocodea Hennig, 1966

Suborder Psocomorpha Badonnel, 1951

Infraorder Caeciliusetae Pearman, 1936

Family Stenopsocidae Koble, 1880

4.1. Genus *Graphopsocus* Kolbe, 1880

Graphopsocus Kolbe, 1880:185. Type species: *Hemerobius cruciatus* Linnaeus, 1768: 225, original designation.

Diagnosis. Body length 2–3 mm, from postclypeus to wing tip length 3–5 mm. Antenna slightly longer than body length, not longer than wing length. Labrum with distal styli. Head with brown vertex. Forewing with several dark markings, proximal half with one or two brown marking between CuP and A, and distal half with brown markings at middle and also long distal margin, forming a large and a small V-shaped patterns, pterostigma general with brown markings on basal region. Forewing anterior margin rather sparsely setose, costal vein without seta from base to pterostigma; CuP glabrous, all other veins with single-row setae; pterostigma broad, with a distinct posterior angle. Abdomen with two ventral vesicles. Male genitalia: tip of aedeagal arch not exceeding parameres (aedeagal arch exceeding parameres in *G. vietnamensis*); endophallus with one pair of weakly sclerotized lobes. Female genital: spermathecal sac with a small pouch.

Distribution. The genus is widely distributed in all main zoogeographical regions of the world.

4.2. Genus *Malostenopsocus* Li, 1992

Malostenopsocus Li, 1992: 250. Type species: *Malostenopsocus yunnanicus* Li, 1992: 250, original designation.

Diagnosis. Male body shorter than 3 mm, female body longer than 3 mm, from postclypeus to wing tip length 5–7 mm. Antenna slightly longer than body length, not longer than wing length. Labrum without distal styli. Head with several dark brown markings. Wings transparent, without distinct markings (*M. plurifasciatus* with markings on wings), veins darker than wing margin.

Forewing costal vein with setae from base of anterior margin to pterostigma, all veins with single-row setae at least, but R, Rs+M, CuA+M, and CuA with two rows of setae, and basal membranous part of forewing with setae. Pterostigma broad, with a distinct posterior angle. Abdomen with three ventral vesicles. Abdomen with segments 8–9 indistinctly sclerotized. Male phallosome strongly sclerotized, endophallus with three lobes. Female spermathecal sac with a lateral pouch connecting to spermathecal duct.

Distribution. Oriental region.

4.3. Genus *Neostenopsocus* gen. n.

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Type species. *Stenopsocus externus* Banks, 1937: 259.

Diagnosis. Body length from postclypeus to wing tip 4–7 mm. Antenna distinctly longer than body and forewing in length. Labrum with distal styli. Forewing with setose anterior margin and single-row setae on all veins except for CuP, CuP glabrous; pterostigma elongate, with a distinct posterior angle; Rsm slightly curved. Forewing pterostigma with variable brown markings, other regions transparent or yellowish. Genitalia from yellowish to dark brown. Male genitalia: tip of aedeagal arch not exceeding parameres. Female subgenital plate posteriorly convex; dorsal valve and ventral valve sclerotized, narrow; external valve reduced; spermathecal sac generally pear-shaped without pouch.

Distribution. Oriental, Palaearctic and Australian regions.

Etymology. The generic name is a combination of Greek "neo-" (meaning "new") and "*Stenopsocus*", meaning the new genus of Stenopsocidae. Gender masculine.

Remarks. Based on morphological characters, we transferred 115 species previously placed in Stenopsocus to ***Neostenopsocus* gen. n.**. The checklist is provided..

4.4. Genus *Stenopsocus* Hagen

Stenopsocus Hagen, 1866: 203. Type species: *Psocus immaculatus* Stephens, 1836: 125, original designation.

Cubipilis Li, 1993: 350. Type species: *Cubipilis hamaocaulis* Li, 1993.

Diagnosis. Body length from postclypeus to wing tip 4–7 mm. Antenna longer than body and forewing. Head with variable brown markings. Labrum without distal styli. Pterostigma transparent, partly brown or wholly brown. Forewing with setose anterior margin, all veins with single-row setae; pterostigma narrowly elongate, with indistinct or distinct posterior angle; Rsm slightly curved. Genitalia generally yellowish white, weakly sclerotized. Male genitalia: tip of aedeagal arch generally exceeding parameres; endophallus with complex sclerotized papillae regions. Female subgenital plate posteriorly convex; dorsal valve and ventral valve sclerotized; proximal portion of dorsal valve broad; external valve reduced; spermathecal sac generally pear-shaped.

Distribution. Oriental and Palaearctic regions.

4.5. Key to the genera of Stenopsocidae

1 Forewing with glabrous CuP; labrum with distal styli **2**
1' Forewing with setose CuP; labrum without distal styli **3**
2 Forewing: one or two markings between CuP and A; abdomen with two ventral vesicles .... ***Graphopsocus* Kolbe**
2' Forewing: no marking between CuP and A; abdomen with three ventral vesicles............ ***Neostenopsocus* gen. n.**
3 Forewing: base membrane with setae, Rsm obviously curved .... ***Malostenopsocus* Li**
3' Forewing: membrane without seta, Rsm slightly curved, nearly straight................................ ***Stenopsocus* Hagen**

4.5. Checklist of *Neostenopsocus*

Neostenopsocus abnormis (Liang, Li & Liu, 2017) **comb. n.**
Neostenopsocus adisoemartoi (Cole, New & Thornton, 1989) **comb. n.**
Neostenopsocus albipileus (Smithers, 1974) **comb. n.**
Neostenopsocus albus (Li, 1992) **comb. n.**
Neostenopsocus angustifurcus (Li, 2002) **comb. n.**
Neostenopsocus angustistriatus (Li, 2002) **comb. n.**
Neostenopsocus anthracinus (Li, 1989) **comb. n.**
Neostenopsocus aureus (Li, 2002) **comb. n.**
Neostenopsocus bellatulus (Li, 1989) **comb. n.**
Neostenopsocus betulus (Li, 2002) **comb. n.**
Neostenopsocus biconicus (Li, 2002) **comb. n.**
Neostenopsocus biconvexus (Li, 1997) **comb. n.**
Neostenopsocus bimaculatus (Li, 2002) **comb. n.**
Neostenopsocus bipunctatus (Li, 2002) **comb. n.**
Neostenopsocus bombusus (Li, 2002) **comb. n.**
Neostenopsocus brachychelus (Li & Yang, 1988) **comb. n.**
Neostenopsocus brachycladus (Li, 1989) **comb. n.**
Neostenopsocus brachyodicrus (Li, 2002) **comb. n.**
Neostenopsocus brevicapitus (Li, 1997) **comb. n.**
Neostenopsocus brevivalvaris (Li, 2002) **comb. n.**
Neostenopsocus capacimacularus (Li, 1993) **comb. n.**
Neostenopsocus cassideus (Li, 1992) **comb. n.**
Neostenopsocus ceuthozibrinus (Li, 2002) **comb. n.**
Neostenopsocus changbaishanicus (Li, 2002) **comb. n.**
Neostenopsocus concisus (Li, 2002) **comb. n.**
Neostenopsocus daozheniensis (Li, 2005) **comb. n.**

Neostenopsocus dichospilus (Li, 2002) **comb. n.**
Neostenopsocus dictyodromus (Li, 1993) **comb. n.**
Neostenopsocus disphaeroides (Li, 2002) **comb. n.**
Neostenopsocus emeishanicus (Li, 2002) **comb. n.**
Neostenopsocus eucallus (Li & Yang, 1988) **comb. n.**
Neostenopsocus externus (Banks, 1937) **comb. n.**
Neostenopsocus fanjingshanicus (Li & Yang, 1988) **comb. n.**
Neostenopsocus faungi (Li, 1999) **comb. n.**
Neostenopsocus flavicaudatus (Li, 2002) **comb. n.**
Neostenopsocus flavifrons (Li, 1989) **comb. n.**
Neostenopsocus flavinigrus (Li, 2002) **comb. n.**
Neostenopsocus floralis (Li, 2002) **comb. n.**
Neostenopsocus foliaceus (Li, 1997) **comb. n.**
Neostenopsocus formosanus (Banks, 1937) **comb. n.**
Neostenopsocus frontalis (Li, 1989) **comb. n.**
Neostenopsocus frontimaculatus (Li, 1992) **comb. n.**
Neostenopsocus fulivertex (Li, 2002) **comb. n.**
Neostenopsocus gannanensis (Li, 2002) **comb. n.**
Neostenopsocus gansuensis (Li, 2002) **comb. n.**
Neostenopsocus genostictus (Li, 2002) **comb. n.**
Neostenopsocus gibbulosus (Li, 1995) **comb. n.**
Neostenopsocus gracilimaculatus (Li, 2002) **comb. n.**
Neostenopsocus gracillimus (Li & Yang, 1988) **comb. n.**
Neostenopsocus guizhouiensis (Li, 2002) **comb. n.**
Neostenopsocus hemiostictus (Li, 2002) **comb. n.**
Neostenopsocus hexagonus (Li, 2002) **comb. n.**
Neostenopsocus huangshanicus (Li, 2002) **comb. n.**
Neostenopsocus isotomus (Li, 2002) **comb. n.**
Neostenopsocus jocosus (Banks, 1939) **comb. n.**
Neostenopsocus lacteus (Li, 1997) **comb. n.**
Neostenopsocus laterimaculatus (Li, 2002) **comb. n.**
Neostenopsocus lemniscsingulaeis (Li, 2005) **comb. n.**
Neostenopsocus lifashengi (Mockford, 2003) **comb. n.**
Neostenopsocus liuae (Li, 2002) **comb. n.**
Neostenopsocus liupanshanensis (Li, 2002) **comb. n.**
Neostenopsocus longicuspis (Li, 1997) **comb. n.**
Neostenopsocus longitudinalis (Li, 2002) **comb. n.**
Neostenopsocus macrocheirus (Li, 2002) **comb. n.**
Neostenopsocus maculosus (Li & Yang, 1988) **comb. n.**
Neostenopsocus makii (Takahashi, 1938) **comb. n.**
Neostenopsocus maximalis (Li, 1997) **comb. n.**
Neostenopsocus melanocephalus (Li, 1997) **comb. n.**
Neostenopsocus metastictus (Li, 2002) **comb. n.**
Neostenopsocus naevicapitatus (Li, 2002) **comb. n.**
Neostenopsocus nepalensis (New, 1971) **comb. n.**
Neostenopsocus nigricellus (Okamoto, 1907) **comb. n.**
Neostenopsocus obscurus (Li, 1997) **comb. n.**
Neostenopsocus oculimaculatus (Li, 1992) **comb. n.**
Neostenopsocus pallidus (Thornton & Wong, 1966) **comb. n.**
Neostenopsocus parviforficatus (Li, 2002) **comb. n.**
Neostenopsocus pavonicus (Li, 2002) **comb. n.**
Neostenopsocus paxillivalvaris (Li, 2002) **comb. n.**
Neostenopsocus percussus (Li, 1995) **comb. n.**
Neostenopsocus periostictus (Li, 2002) **comb. n.**
Neostenopsocus perspicuus (Li, 1997) **comb. n.**
Neostenopsocus phaeostigmus (Li, 1992) **comb. n.**
Neostenopsocus phaneostriatus (Li, 2002) **comb. n.**
Neostenopsocus platynotus (Li, 1995) **comb. n.**
Neostenopsocus platyocephalus (Li, 2002) **comb. n.**
Neostenopsocus podorphus (Li, 1997) **comb. n.**
Neostenopsocus polyceratus (Li, 2002) **comb. n.**
Neostenopsocus pygmaeus (Enderlein, 1906) **comb. n.**
Neostenopsocus qianipullus (Li, 2005) **comb. n.**
Neostenopsocus radimaculatus (Li, 1989) **comb. n.**
Neostenopsocus revolutus (Li, 1993) **comb. n.**
Neostenopsocus rubellus (Thornton, 1984) **comb. n.**
Neostenopsocus shennongjiaensis (Li, 2002) **comb. n.**
Neostenopsocus sichuanicus (Li, 2002) **comb. n.**
Neostenopsocus signatipennis (New, 1978) **comb. n.**
Neostenopsocus silvaticus (Li, 2002) **comb. n.**
Neostenopsocus spongiosus (Li, 2002) **comb. n.**
Neostenopsocus stigmaticus (Imhoff & Labram, 1842) **comb. n.**
Neostenopsocus striolatus (Li, 1992) **comb. n.**
Neostenopsocus symipsarous (Li, 2002) **comb. n.**
Neostenopsocus thermophilus (Li, 2002) **comb. n.**
Neostenopsocus tibialis (Banks, 1937) **comb. n.**
Neostenopsocus tribulbus (Li, 1993) **comb. n.**
Neostenopsocus tripartibilis (Li, 2002) **comb. n.**
Neostenopsocus trisetus (Li, 2002) **comb. n.**
Neostenopsocus turgidus (Li, 1997) **comb. n.**
Neostenopsocus uniformis (Hagen, 1859) **comb. n.**
Neostenopsocus valvilacteus (Li, 2005) **comb. n.**
Neostenopsocus wangi (Liang, Li & Liu, 2017) **comb. n.**
Neostenopsocus wuxiaensis (Li, 1997) **comb. n.**
Neostenopsocus xanthophaeus (Li, 2002) **comb. n.**
Neostenopsocus xanthostigmus (Li, 2002) **comb. n.**
Neostenopsocus xiangxiensis (Li, 1992) **comb. n.**
Neostenopsocus xilingxianicus (Li, 1997) **comb. n.**
Neostenopsocus zonatus (Li, 1989) **comb. n.**

5. Discussion

5.1. Comparative morphology among genera of Stenopsocidae

Lienhard (1998) redescribed the four species of Stenopsocidae from Europe, and indicated several important diagnostic characteristics, i.e., the presence or absence of labral styli, the number of ventral vesicles, the ciliation of the forewing. Moreover, Stenopsocidae shows rich biodiversity in the Oriental region. All genera and most species of Stenopsocidae are living in this region. After examining many materials of Stenopsocidae from Asia, we consider the above characteristics to be the diagnostic features among the genera of Stenopsocidae. Several characteristics are reviewed in the following.

Shape of the vertex (Fig. 4). The vertex in male is in a similar shape because of the presence of the large compound eyes. In females, with small compound eyes, the shape of vertex is different among the genera. In the genera *Graphopsocus* and *Neostenopsocus* **gen. n.**, the vertex is rounded. In the genera *Malostenopsocus* and *Stenopsocus*, the vertex is extended and bulbed. The phylogenetic result implies that the round vertex is plesiomorphic for Stenopsocidae.

Presence or absence of labral styli (Fig. 5). The labral styli are present in *Graphopsocus* and *Neostenopsocus*

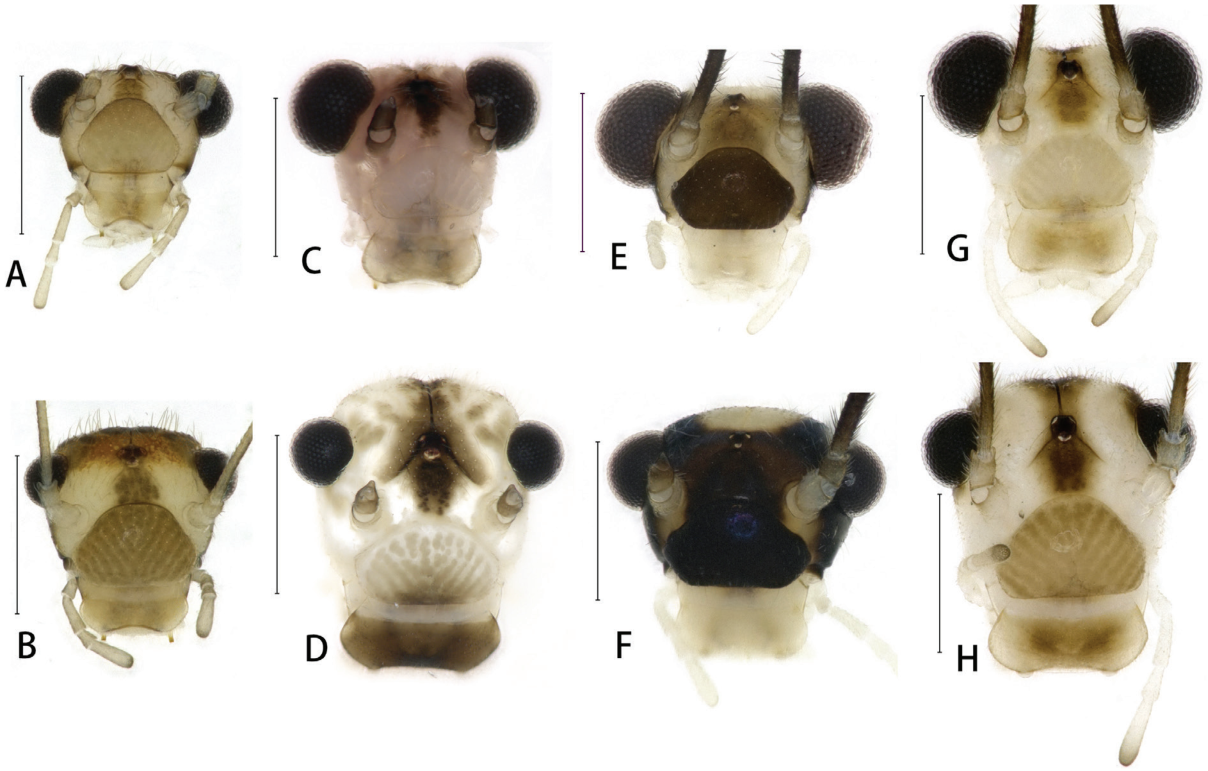

Figure 4. Head of stenopsocid species in frontal view. **A** *Graphopsocus cruciatus*, male; **B** *Graphopsocus cruciatus*, female; **C** *Malostenopsocus yunnanicus*, male; **D** *Malostenopsocus yunnanicus*, Female; **E** *Neostenopsocus externus*, male; **F** *Neostenopsocus externus*, female; **G** *Stenopsocus immaculatus*, male; **H** *Stenopsocus immaculatus*, female. Scar bars = 0.5 mm.

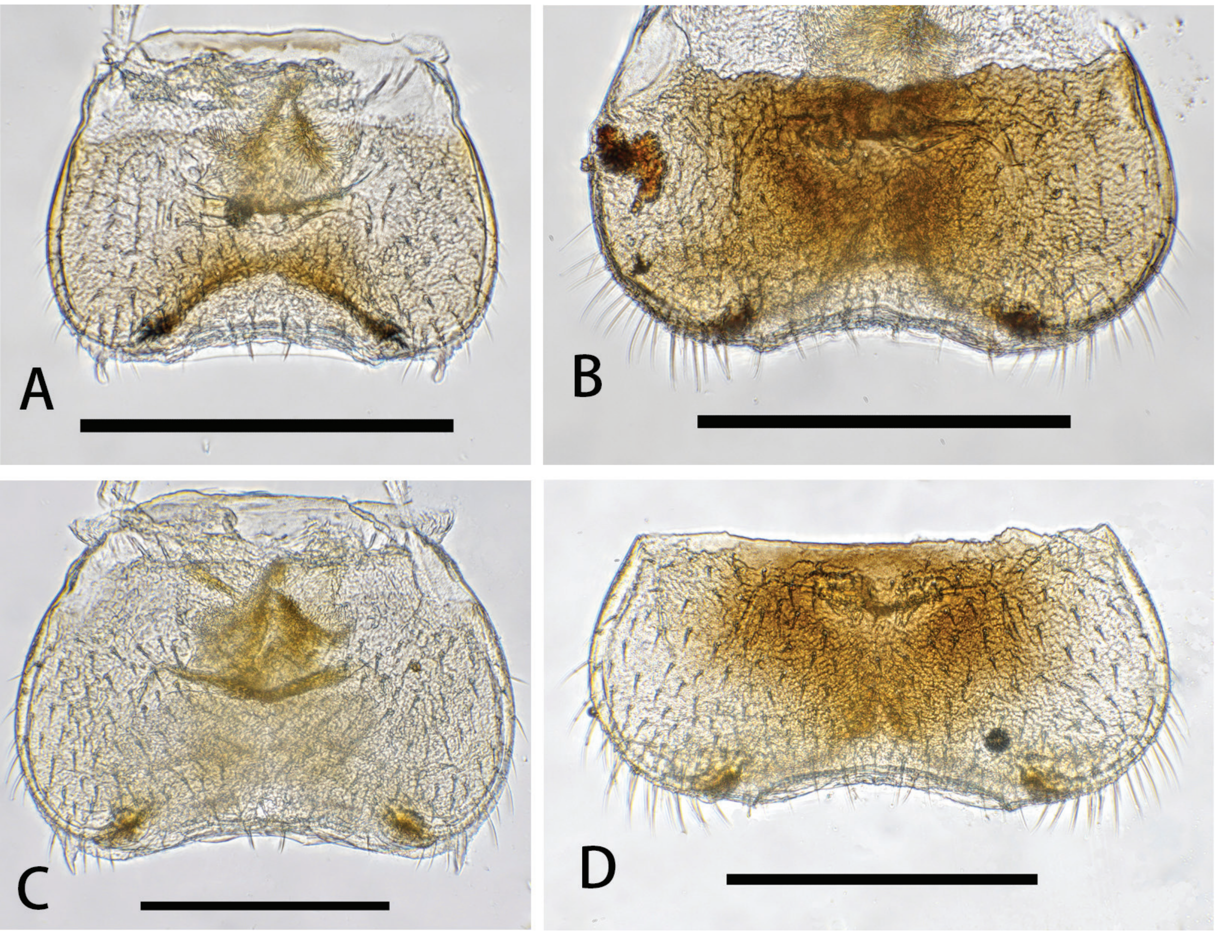

Figure 5. Labrum of of stenopsocid species in frontal view. **A** *Graphopsocus cruciatus*; **B** *Malostenopsocus yunnanicus*; **C** *Neostenopsocus externus*; **D** *Stenopsocus immaculatus*. Scar bars = 0.25 mm.

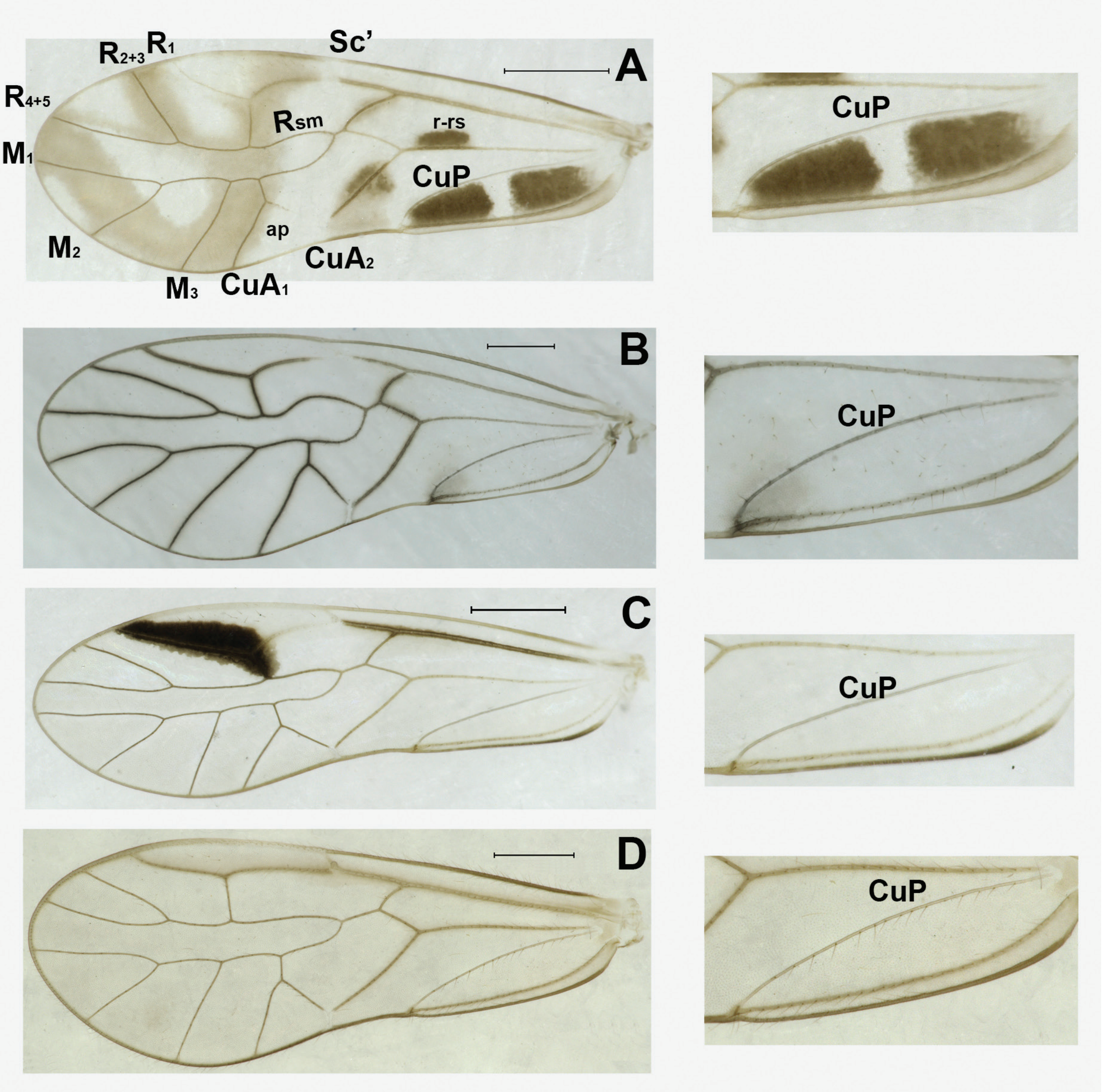

Figure 6. Forewing of stenopsocid species. **A** *Graphopsocus cruciatus*; **B** *Malostenopsocus yunnanicus*; **C** *Neostenopsocus externus*; **D** *Stenopsocus immaculatus*. Scar bars = 0.5 mm. ap: areola postica.

gen. n., but are absent in *Stenopsocus* and *Malostenopsocus*. In addition, the labral stylus has a round apex in the genus *Graphopsocus*, while has a sharp apex in *Neostenopsocus*. The presence of labral styli is considered to be plesiomorphic for Stenopsocids. Mockford (2000) interpreted that the presence of labral styli is plesiomorphic in caeciliusids. Considering the labral styli are present in some amphipsocids (Amphipsocidae) and absent in all members of Dasydemellidae, this character should be plesiomorphic in the infraorder Caeciliusetae.

The markings on forewing (Fig. 6). In *Graphopsocus*, several brown markings are generally present on forewing. In *Malostenopsocus*, the marking is often absent on forewing. In *Neostenopsocus*, the markings are often present near Rs or pterostigma. In *Stenopsocus*, the marking is often absent on forewing except for the pterostigma region. *Graphopsocus* can be easily distinguished from the other genera based on the markings covering most of forewing. However, some taxa of other families also share the similar distribution pattern of markings on forewing, i.e., *Caecilius caligonoides* (Ceaciliusidae) (see Mockford, 1969, fig. 153), *Mesocaecilius elegans* (Pseudocaeciliidae) (see Li, 2002, fig. 924). This condition is regarded to be highly homoplasious.

Forewing venation (Fig. 6). (i) shape of the pterostigma. In *Graphopsocus*, *Malostenopsocus* and *Neostenopsocus*, the pterostigma is broad with a distinct posterior angle. In *Stenopsocus*, the pterostigma is generally narrow, and the posterior angle of pterostigma is not obvious. (ii) shape of cell r5. Differences in shape are conferred on this cell by the curved Rsm. An essentially parallel-side cell r5 occurs in the genera *Graphopsocus*, *Neostenopsocus* **gen. n.** and *Stenopsocus*. The genus *Malostenopsocus* shows curved Rsm and broad base of

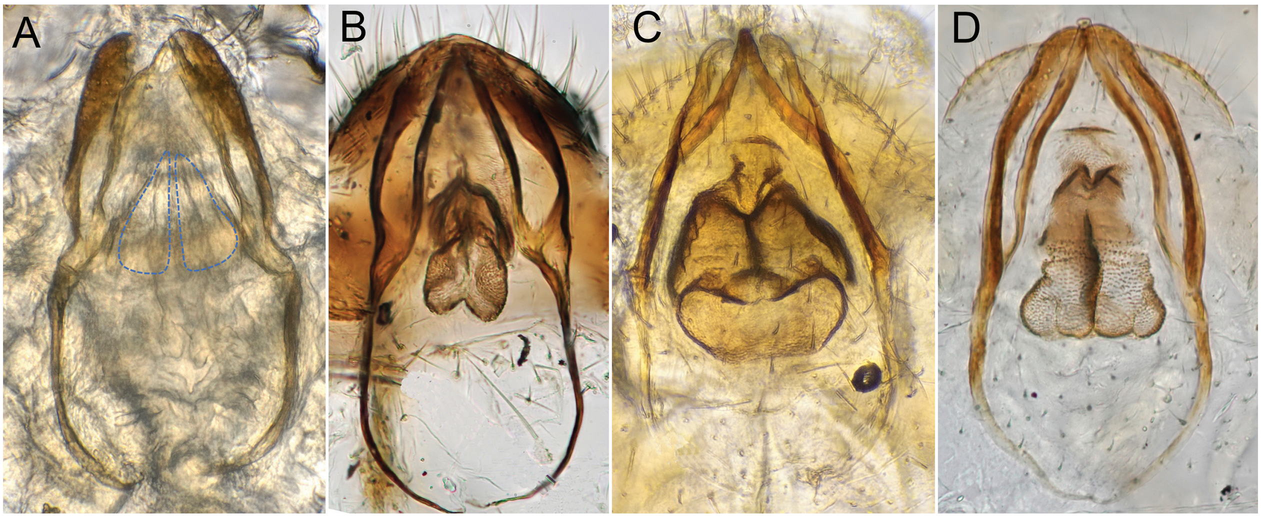

Figure 7. Phallosome of stenopsocid species in non-active position. **A** *Graphopsocus cruciatus*, the blue dotted lines circle the endophallus; **B** *Neostenopsocus externus*; **C** *Malostenopsocus yunnanicus*; **D** *Stenopsocus immaculatus*.

cell r5. The broad pterostigma with a distinct posterior angle and the straight Rsm are plesiomorphic for Stenopsocidae based on the phylogenetic result in the present study. The narrow pterostigma with an indistinct posterior angle is considered to be an autapomorphy for the genus *Stenopsocus*. The curved Rsm is regarded as a derived condition but homoplastic, it is also found in the family Dasydemellidae.

Ciliation of forewing (Fig. 6). Veins of forewing except CuP are setose, with one-row setae. In *Graphopsocus* and *Neostenopsocus*, the basal half of forewing anterior margin and CuP are glabrous. In *Malostenopsocus* and *Stenopsocus*, the basal half of forewing anterior margin and CuP is pilosity. The glabrous anterior margin and CuP of forewing are considered to be plesiomorphic for Stenopsocidae. In addition, sparse setae are present in the basal membrane of forewing in *Malostenopsocus*. This condition is also present in the family Dasydemellidae.

Number of ventral abdominal vesicles. In *Graphopsocus*, two ventral vesicles are present. In *Neostenopsocus* **gen. n.**, *Malostenopsocus* and *Stenopsocus*, three ventral vesicles are present. There can be no question that the condition of two ventral abdominal vesicles is plesiomorphic for Stenopsocidae. Turner (1974) and New (1987) considered the presence of abdominal vesicles to be associated with living open-live leaf surfaces.

Phallosome (Fig. 7). The phallosome consists of the parameres, the aedeagus, the phallobase and the endophallus (Yoshizawa, 2005). Mockford (2002) indicated only the endophallus shows promise of phylogenetic interpretation. The endophallus of Stenopsocidae consists of several lobes with or without minute sclerotized papillae. In *Graphopsocus*, the endophallus is simple, with weakly sclerotized portion. This condition is probably plesiomorphic for Stenopsocidae. In the other three genera, the endophallus is more complex than the bilobed endophallus in *Graphopsocus*. The sclerotized portion is present in the endophallus, which is divided into two parts: the upper part and the base part. In *Malostenopsocus*, the upper part is divided into two lobes, and the base part is undivided. In *Stenopsocus*, the upper and base parts are both partly divided. The new genus *Neostenopsocus* **gen. n.** shows the intermediate condition, in which the upper and base parts are both partly divided.

As discussed above, several plesiomorphic features in Stenopsocidae are revealed, i.e., round vertex, presence of labral styli, broad pterostigma with a distinct posterior angle, straight Rsm on the forewing, glabrous anterior margin and CuP on the forewing, presence of two abdominal vesicles and the bilobed endophallus with weakly sclerotized portion. The new genus *Neostenopsocus* **gen. n.** is supported by several apomorphies: (i) forewing mostly transparent, (ii) abdomen with three ventral vesicles; (iii) endophallus with partly divided upper and base parts of minute sclerotized papillae.

5.2. Intergeneric phylogeny of Stenopsocidae

The present phylogenetic analyses confirm the monophyly of the family Stenopsocidae, which has been strongly supported based on the morphological characters and multi-loci phylogenetic studies (Yoshizawa, 2002; Yoshizawa et al., 2014). The paraphyly of *Stenopsocus* herein inferred agrees well with the previous result of the multi-loci phylogenetic study with less taxon sampling and a smaller dataset (Yoshizawa et al., 2014). However, Yoshizawa et al. (2014) did not reveal the sister group relationship between *Stenopsocus* and *Malostenopsocus* because these two genera are represented by only three species in this work. *Malostenopsocus* and *Stenopsocus*, herein recovered as sister group, share some similar characters: (i) head with bulbed vertex, (ii) absence of styli, (iii) abdomen with three ventral vesicles, (iv) forewing broad, with strongly curved posterior margin, (v) forewing CuP with one row of setae, (vi) genitalia generally weakly sclerotized, (vii) male endophallus complex with several areas composed of minute sclerotized papillae. As noted in Li (1993), *Malostenopsocus* can be distinguished from *Stenopsocus* based on: (i) basal membranous area of forewing with setae, (ii) posterior angle of pterostigma distinct, (iii) cell r5 in forewing with broad basal region (Rsm and Mm strongly curved), (iv) base part of endophallus without division. Thus, the generic status of *Malostenopsocus* is corroborated.

The phylogeny recovered a sister relationship between *Neostenopsocus* **gen. n.** and *Malostenopsocus* + *Stenopsocus*. This clade is supported by several apomorphies: (i) labrum with styli, (ii) abdomen with three ventral vesicles; (iii) endophallus with several lobes of minute sclerotized papillae. The genus *Graphopsocus* is estimated to be the sister group of all other stenopsocid taxa, as the stem branch of Stenopsocidae in the present study.

Herein, we propose a new classification scheme for the family Stenopsocidae based on our phylogenetic analysis of molecular data and re-evaluation of morphological characters. In this scheme, Stenopsocidae is classified into four genera: *Graphopsocus*, *Malostenopsocus*, *Neostenopsocus* **gen. n.**, and *Stenopsocus*.

6. Conclusion

We sequenced 20 new nearly complete mitochondrial genomes of Stenopsocidae, and reconstructed the intergeneric phylogeny of this family. A new genus, namely *Neostenopsocus* **gen. n.**, is proposed based on the molecular phylogeny herein inferred. Most species of Stenopsocidae were described from the Oriental realm, and it is likely that unknown genera and species are still to be discovered in this region. Future fieldwork and taxonomic studies based on morphological and molecular data could lead to further insight into the diversity and phylogeny of this family.

7. Conflict of interest statement

The authors declare no conflicts of interest.

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Supplementary Material 1

File S1

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