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ORIGINAL ARTICLE

[†]Cormopsocidae: a new family of the suborder Trogiomorpha (Insecta: Psocodea) from Burmese amber

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Abstract

Cormopsocidae **n. fam**. of the psocid suborder Trogiomorpha was proposed for a fossil species from mid-Cretaceous Burmese amber, *Cormopsocus groehni* **n. gen**. & **n. sp**. This family was estimated to be the sister group of all other trogiomorphan taxa, but the possibility of much deeper divergence (i.e., placement as a sister group of all Psocodea) could not be excluded. *C. groehni* retains many plesiomorphic features, which will contribute greatly to elucidating the ancestral state of Psocodea.

Key words: Cormopsocus groehni, new genus, new species, fossil, Cretaceous, Myanmar.

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INTRODUCTION

The insect order Psocodea (formerly known as two separate orders, Psocoptera and Phthiraptera) is composed of three suborders, Trogiomorpha, Troctomorpha (in which Phthiraptera are classified) and Psocomorpha (Lienhard & Smithers 2002; Yoshizawa & Johnson 2003). The morphological gaps between the suborders are very distinct, and thus, these three higher taxa have long been recognized (Roesler 1940). The monophyly of all suborders has been confirmed by morphological (Yoshizawa 2002; Ogawa & Yoshizawa 2018ab) and/or molecular data (Yoshizawa *et al.* 2006; Yoshizawa & Johnson 2010; Johnson *et al.* 2018). Among these suborders, the suborder Trogiomorpha is the sister taxon of all other psocodeans and is generally recognized as retaining the maximum of plesiomorphic conditions within the order (Smithers 1972; Mockford 1993; Lienhard 1998). Therefore, Trogiomorpha is one of the key taxa for elucidating the ground plan of Psocodea. The phylogenetic placement of Psocodea is controversial (Misof *et al.* 2014; Johnson *et al.* 2018); therefore, the estimation of the ancestral morphology of Psocodea will be a helpful contribution toward understanding the interordinal phylogeny.

Fossils provide fascinating information on organisms that existed in the past. When fossils represent deeply divergent extinct taxa, they may contribute to bridging the morphological gaps observed between extant groups. A significant example in insects is provided by the recent discovery of well-preserved specimens of the extinct family Archipsyllidae (Paraneoptera: Pancondylognatha) in mid-Cretaceous Burmese amber (Huang *et al.* 2016; Liang *et al.* 2016; Yoshizawa & Lienhard 2016) that bridge the morphological gap between chewing and sucking mouthparts observed in Psocodea and Thysanoptera + Hemiptera. However, for Psocodea, most of the available fossils of potentially deeply divergent taxa are impression fossils (Smithers 1972), from which only a limited amount of morphological data can be extracted. In contrast, amber fossils are often very well preserved, and detailed morphological information is available from them. However, most of the oldest known amber inclusions of Psocodea (i.e., from the Cretaceous) can be assigned to extant families or infraorders (Mockford *et al.* 2013) and thus have limited value for the estimation of the ancestral condition of taxa above the infraordinal level.

In this study, we describe a new genus and species of the suborder Trogiomorpha based on a specimen enclosed in mid-Cretaceous Burmese amber. After the detailed examination of this fossil specimen, we concluded that this species likely represents a sister group of the remaining trogiomorphans, or even of the entire order Psocodea. Therefore, we decided to establish a new family for this fossil species.

MATERIALS AND METHODS

A Cretaceous amber specimen collected in Myanmar (ca. 99 MYA Burmite: Shi *et al.* 2012) was at our disposal (Fig. 1). The amber was polished using Roxite (Iwamoto Mineral Co., Tokyo) after cutting and grinding. The amber piece was slide mounted using glycerol for observations. Observations were performed using an Olympus SZX16 (Olympus Imaging Corporation, Tokyo) binocular microscope and a Zeiss Axiophot (Carl Zeiss AG, Jena) light microscope. Photographs were taken using an Olympus E-M10II (Olympus Imaging Corporation, Tokyo) digital camera attached to the Olympus SZX16 or Zeiss Axiophot microscope. A confocal laser scanning microscope (CLSM: Leica TCS SP5, Wetzlar, Germany) was also used for observations. We used an excitation wavelength of 405 nm and an emission wavelength of 480–680 nm. Partially focused photographs were combined using Zerene Stacker (Zerene Systems LLC, WA) to obtain images with a high depth of field.

SYSTEMATICS

Order Psocodea Hennig, 1966 Suborder Trogiomorpha Roesler, 1940

Family Cormopsocidae new

Type genus. Cormopsocus Yoshizawa & Lienhard, **n. gen.** *Diagnosis.* See diagnosis of the type genus.

Genus Cormopsocus new

Type species. Cormopsocus groehni Yoshizawa & Lienhard n. sp.

Diagnosis. Within Trogiomorpha, this genus is characterized by a combination of the following features. Head (Fig. 2): postclypeus well bulged, bottom half exceeding bottom line of head capsule and located in front of oral region; lacinia well developed, with chisel-like shape, apically parallel sided and lacking distinct teeth; maxillary palpus four segmented, last segment long and tapering apically (Fig. 1); labial palpus two segmented, distal segment rounded; antenna shorter than forewing length (Fig. 1), flagellum composed of numerous short flagellomeres, each about as long as or shorter than length of pedicel, with secondary annulations (at least on distal segments, Fig. 2C). Legs (Fig. 1): tarsi three segmented; pretarsal claws symmetrical, with preapical tooth (Fig. 1C). Wings glabrous (Fig. 1). Forewing (Fig. 3A,C): anterior and posterior margins almost parallel; Sc well developed and strongly arched, ending at R1 vein; R1-Rs crossvein present; A2 vein absent; stigmapophysis absent; veins CuP

and A1 ending separately on wing margin; in-flight wing-coupling structure simple, composed of separate and almost straight spines. Hindwing (Fig. 3B): Sc vein well-developed, ending in distal part of anterior wing margin; A2 vein present. Terminalia (Fig. 4): paraproct lacking anal spine; paraproctal trichobothrial field well developed; paramere well developed and broad.

Etymology. As discussed below, this taxon is estimated here to represent the sister taxon of the remaining members of the suborder Trogiomorpha (i.e., divergent from the deepest position on the most basal branch of the psocodean tree of life) (see Introduction and Fig. 5). The generic name is the combination of *Kormos* (tree trunk in Greek) and *Psocus* (commonly used suffix for generic names of psocopterans).

Cormopsocus groehni n. sp.

Holotype. Male. Embedded in Burmite, early Cenomanian of the mid-Cretaceous, Hukawng Valley, northern Myanmar (to be deposited in the Museum of the Geolog.-Palaeontolog. Institut of the University of Hamburg, Germany, under specimen ID GPIH no. 4935, coll. Gröhn no. 11264).

Description of male holotype. Body extensively and darkly pigmented, except for pale membranous regions (Fig. 1).

Head (Fig. 2). Postclypeus well bulged, bottom half exceeding bottom line of head capsule and located in front of oral region; anteclypeus present; vertex rounded, strongly expanded dorsally; three ocelli arranged on flat frons; compound eye well developed. Antenna with 35 flagellar segments, distal segments with secondary annulations (Fig. 2C). Mouthparts: maxillary palpus four segmented (distal two segments missing on left side: Fig. 2AB); terminal segment long, approximately 6 times longer than width, broadened toward distal 1/3 and gradually narrowing apically (Fig. 1); labial palpus two segmented, second segment rounded but anteroposteriorly flattened (probably by deformation during fossilization).

Thorax (Figs 1, 2). Cervical sclerite well developed and swollen. Prothorax small, pronotum dorsally prominent. Pterothorax well developed.

Legs (Fig. 1). Tarsus three segmented; pretarsal claws symmetrical, nearly straight, with tiny preapical tooth and tiny hairs on ventral margin of distal half proximal to preapical tooth.

Wings. Forewing (Fig. 3A) transparent, basal end and center of basal radial cell faintly pigmented, pterostigma darkly pigmented; Sc vein forming large arc; pterostigma trapezoid, R1-Rs crossvein arising from its posterodistal corner; areola postica broad, CuA1 vein weakly curved; CuP and A1 veins separated at their end; A2 vein absent; in-flight wing-coupling structure composed of ca. 14 separate and almost straight spines (Fig. 3C); all rib-like structures between coupling structure and wing margin arranged transversally against CuP vein. Hindwing transparent, distal half lightly pigmented, with dark pigmentation along veins, as

shown in Fig. 3B (left hindwing), or along distal R1 vein and around M fork (right hindwing, Fig. 1); Sc vein well developed and very long, running nearly parallel with anterior wing margin, joining this margin slightly distal of half of wing length; A vein branching into two.

Terminalia (Fig. 4). Clunium simple, without ornamentation, posterodorsal margin slightly concave. Epiproct slightly concave dorsally, triangular. Paraproct simple, lacking anal spine, with six trichobothria arising from distinctly convex trichobothrial field. Hypandrium with simple rounded posterior margin. Paramere broad, apically with some setae, anterodorsal margin swollen; base of paramere and other phallosomal structures not visible.

Measurements (seen from the right side of the specimen, in mm). Body 1.44; antennal flagellomeres f1 0.09, f2 0.06, f3 0.06; right forewing 1.94; right hindwing 1.52; right hind femur 0.45; right hind tibia 0.55; right hind tarsomeres t1 0.20, t2 0.05, t3 0.07.

Etymology. The specific epithet is dedicated to Carsten Gröhn, who gave us the opportunity to examine this systematically important amber fossil.

DISCUSSION

Before justifying the establishment of a new family and discussing its systematic placement, the sex identification of the holotype specimen has to be discussed, as it is potentially controversial. The paired projections (pr in Fig. 4) protruding between the paraprocts (pt) and the ventral sclerite (hy) may be homologized with either the parametes (male) or the ovipositor valves (female) based on their position and superficial similarity. The identification of the segment, to which the ventral sclerite (hy in Fig. 4) covering the paired projections belongs, can provide decisive evidence (8th if female, 9th if male). However, the anterior abdominal segments of the holotype are badly damaged (Fig. 1), which prohibits an accurate count of the abdominal segments. The psocid clunium is composed of the 9th and 10th tergites, and the ventral sclerite of the holotype specimen seems to be continuous with the anteroventral margin of the clunium (Fig. 4), suggesting that it is not the 8th sternite. The following features also suggest that the paired projections and ventral sclerite represent the male parametes and hypandrium (9th sternum) (Fig. 4) (Badonnel 1934; Klier 1956; Yoshizawa 2005; Cheng & Yoshizawa 2019): the genital chamber formed by the ventral sclerite opens dorsally in the holotype specimen, as usually observed in males, while that formed by the subgenital plate (female genital chamber) almost always opens posteriorly; the ovipositors of psocids arise from the ventral end of the clunium, but the paired projections of the present specimen are located more dorsally with respect to the ventral margin of the clunium (cl in Fig. 4). Considering these features, the ventral sclerite and paired projections of the present specimen are identified here as the hypandrium and parameres, and the holotype of C. groehni is considered male.

The suborder Trogiomorpha is generally considered to be the group retaining the

maximum of plesiomorphic conditions in Psocodea (Smithers 1972; Mockford 1993; Lienhard 1998). Although its monophyly is unambiguously supported by molecular data (Yoshizawa et al. 2006; Yoshizawa & Johnson 2010; Johnson et al. 2018), there are only a few morphological autapomorphies supporting this suborder (Yoshizawa et al. 2006): partial reduction of the subgenital plate, only covering the basal part of the ovipositor, and partial reduction of the ovipositor valves, frequently composed of only the external one (Yoshizawa et al. 2006). Both apomorphies are female characters and cannot be used for deciding a male's placement in this suborder. Therefore, all similarities observed between C. groehni and other trogiomorphans are plesiomorphic: ventrally expanded postclypeus; two-segmented labial palpus; antenna with more than 20 articles; well-developed and arched Sc and presence of R1-Rs crossveins in forewing; absence of stigmapophysis; simple in-flight wing-coupling system composed of separate spines (Yoshizawa et al. 2006; Ogawa & Yoshizawa 2018ab). Based on these features of Trogiomorpha, most of which are diagnostic characters, C. groehni is tentatively placed in this suborder (Fig. 5: solid arrow), although the possibility cannot be excluded that this species belongs to a more basal clade outside of Trogiomorpha (Fig. 5: broken arrow accompanied by a question mark). As discussed above, it might be possible that the holotype of C. groehni is a female. If our current morphological interpretations and sex determination are wrong (i.e., if the paired projections and the ventral sclerite actually represent the female ovipositor valves and subgenital plate, respectively), then C. groehni can be assigned to the stem branch of Trogiomorpha based on the reduction of the ovipositor valves (apomorphy) and the presence of a well-developed subgenital plate (plesiomorphy). Its assignment to either Psocomorpha or Troctomorpha, the other psocid suborders, can clearly be excluded as the clade composed of these suborders is supported by the following two apomorphies in the forewing: rib-like structures arranged vertically against CuP vein between the wing-coupling structure and the wing margin (Ogawa & Yoshizawa 2018a) (ribs are transverse against CuP in Cormopsocidae: Fig. 3C) and presence of the stigmapophysis on the R vein (Ogawa & Yoshizawa 2018b) (stigmapophysis absent in Cormopsocidae).

Within Trogiomorpha, *C. groehni* strongly resembles the species of Prionoglarididae (Fig. 5) in its glabrous forewing with a well-developed and strongly arched Sc vein and R1-Rs crossvein (e.g., Lienhard 1998, 2004, 2011; Azar *et al.* 2017). Both venation characteristics are also observed in †Empheriidae and †Archaeatropidae (Baz & Ortuño 2000, 2001), and the latter is also observed in some Psyllipsocidae (Fig. 5), thus probably representing the ancestral condition of Trogiomorpha. The monophyly of Prionoglarididae is still controversial (Yoshizawa *et al.* 2006, 2018, 2019: as indicated by dotted lines in Fig. 5), but morphologically, the long antenna composed of 15 segments at most (i.e., 13 flagellomeres) and the broadened and rounded forewing (both are apomorphic and unique to Prionoglarididae within Trogiomorpha) could support its monophyly (Mockford 1993; Lienhard 1998, 2007;

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Yoshizawa *et al.* 2006; Nico Schneider, personal communication: numerous specimens of *Prionoglaris stygia* examined, intact antennae never more than 15-segmented). *C. groehni* has short antennae with a large number of flagellomeres and narrow wings (Fig. 1); therefore, this species is clearly excluded from this family.

Furthermore, the strongly developed and very long Sc vein of the hindwing is very characteristic of *C. groehni* (Fig. 3B). In Trogiomorpha, the hindwing Sc vein is usually reduced (or short even if clearly present, never reaching the distal half of the wing) (Smithers 1972; Lienhard 2007, 1998). The strong development of the Sc vein is apparently a plesiomorphic condition. Thus, based on this character state, this species can be excluded from the clade composed of all other trogiomorphans. In this context, we interpret the probably apomorphic glabrous forewing veins in *C. groehni* and Prionoglarididae (see above) as being due to homoplasy because this condition is also highly homoplasious within the suborder Psocomorpha (Yoshizawa 2002).

As discussed above, a slight ambiguity remains regarding the exact phylogenetic placement of *C. groehni* (within or outside of Trogiomorpha: Fig. 5). However, in both cases, it is obvious that *C. groehni* cannot be assigned to any of the established families, and the establishment of a new family for this fossil species is therefore appropriate. The discovery of a female specimen of this species or its relatives would be key for unambiguously determining the systematic placement of this family, through which it would also be possible to clarify whether the plesiomorphic conditions observed in *C. groehni* can be attributed to the ancestral Trogiomorpha or to the ancestral Psocodea.

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- Figure 1 (A–B) Habitus of *Cormopsocus groehni* n. sp. from right (A)- and left (B)-side views.(C) Third tarsal segment and pretarsal claw of the right hind leg (indicated by an arrowhead in A). Scale 0.5 mm for A and B, 0.1 mm for C.
- Figure 2 (A) CLSM image (composition of inverse images) of the head of *Cormopsocus* groehni n. sp. (B) Ditto, mouthparts enlarged, and lacinia highlighted in red. (C) Flagellomere of the distal half of the right antenna. Abbreviations: ac, anteclypeus; cs, cervical sclerite; cx1, procoxa; e, eye; fl, first flagellomere; fr, frons; lc, lacinia; lp, labial palpus; lr, labrum; md, mandible; mp, maxillary palpus; oc, ocelli; p, pedicel; pc, postclypeus; pg, paraglossa; pm, prementum; pn, pronotum; s, scape; st, stipes; T1, prothorax; v, vertex. Scale 0.1 mm for A and B, 0.02 mm for C.
- Figure 3 Wings of *Cormopsocus groehni* **n. sp.** (A) Right forewing. (B) Left hindwing (flipped). (C) In-flight wing-coupling system on the right forewing (arrow heads indicate the rib-like structure). Scale 0.5 mm for A and B, 0.1 mm for C.
- Figure 4 Terminalia of *Cormopsocus groehni* n. sp., male. (A) Right-side view, CLSM image (composed of inverse images). (B) Ditto, line drawing. Abbreviations: cl, clunium; ep, epiproct; hy, hypandrium (9th sternum); pr, paramere; pt, paraproct; tf, trichobothrial field. Scale 0.1 mm.
- Figure 5 Dated molecular phylogeny of Trogiomorpha according to Yoshizawa *et al.* (2019) and possible placement of Cretaceous fossil taxa indicated by arrows. The phylogenetic relationships between Prionoglaridinae and Speleketorinae (subfamilies of the family Prionoglarididae) are ambiguous; thus, alternative relationships (monophyly/paraphyly of Prionoglarididae) are indicated by broken lines (Yoshizawa *et al.* 2006, 2018, 2019). The position of the arrowheads only indicates the association with a branch, and the age scale is not valid for them.



Fig1 209x177mm (300 x 300 DPI)

С

T1

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Fig2

215x128mm (300 x 300 DPI)

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Fig4 187x135mm (300 x 300 DPI)

