

A new remarkable cimicoid genus and species (Hemiptera, Heteroptera, Cimicomorpha) from mid-Cretaceous Burmese amber, with implications for its aberrant male genitalia

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Abstract

A new genus and species of cimicoid true bug, *Ecpaglocoris ditomeus* Yamada & Yamamoto, **gen. et sp. nov.**, is described and illustrated from mid-Cretaceous (Cenomanian–Albian) amber in the Kachin State of northern Myanmar (Burma). This new fossil genus and species is reminiscent of members of Anthocoridae by the strongly flattened and elongated body, four-segmented labium, distinct costal fracture and presence of fossula spongiosa on fore tibiae, but should not be ascribed to this family. The new taxon cannot be placed in any extant cimicoid families, based upon hemelytral, male genital and other morphological structures. Based on the hemelytral membrane venation and presence of dorsal laterotergites on abdominal segments I to VIII, it can be assumed that this new genus belongs to the extinct family Vetanthocoridae. *Ecpaglocoris ditomeus* **gen. et sp. nov.** has aberrant male genitalia characterised by sickle-shaped left and right parameres and grooves running throughout the paramere. This characteristic indicates that traumatic insemination occurred in this genus. The peculiar combination of male genital characteristics seen in *Ecpaglocoris* **gen. nov.** prevents its placement in any of the extant cimicoid families.

Key Words

Cenomanian, Cimicoidea, male genital morphology, Myanmar, traumatic insemination, Vetanthocoridae

Introduction

Cimicoidea, a morphologically and ecologically diverse group in the suborder Heteroptera, is currently represented by seven extant families based on the concepts of Ford (1979), Schuh and Štys (1991), Schuh et al. (2009), Weirauch et al. (2019) and Schuh and Weirauch (2020): Anthocoridae Fieber, 1836; Cimicidae Latreille, 1802; Curaliidae Schuh, Weirauch & Henry, 2008; Lasiochilidae Carayon, 1972; Lyctocoridae Reuter, 1884; Plokiophilidae China, 1953; and Polycetenidae Westwood, 1874. In addition, the extinct family Vetanthocoridae Yao, Cai & Ren, 2006 is treated as a member of this superfamily (Tang

et al. 2016; Schuh and Weirauch 2020). Popov (2016) established a monotypic fossil family Taimyrocoridae to accommodate the new species *Taimyrocoris sukatshevae*, based on specimens from Late Cretaceous amber of the Taimyr Peninsula in Far North Russia and classified the taxon as belonging to Cimicoidea. However, this family has been overlooked by subsequent authors, including in a comprehensive review of the heteropteran classification and natural history by Schuh and Weirauch (2020). Based on Popov's description and figures, the superfamily placement of Taimyrocoridae may be agreed upon; however, this decision may be controversial because of the difficulty in interpreting morphological details.

The fossil records of cimicoid true bugs currently extend from the Middle Jurassic to Oligocene for species found in China, Mongolia, Siberia, Myanmar (Burma), Ukraine, the Baltics and Germany (e.g. Statz and Wagner (1950); Yao et al. (2006); Shcherbakov (2007); Engel (2008); Popov (2016); Tang et al. (2016); Schuh and Weirauch (2020)). A total of 28 genera and 38 species from six families (Anthocoridae, Cimicidae, Lyctocoridae, Plokiophilidae, Taimyrocoridae and Vetanthocoridae) have been reported to date, with most described as members of Anthocoridae from Eocene Baltic amber (Popov 2003; Popov et al. 2011a, 2011b; Schuh and Weirauch 2020). In Vetanthocoridae, 12 genera and 16 species in two tribes are known from the Middle Jurassic to Lower Cretaceous in China (Tang et al. 2016) and they are represented only by compression fossils. Recently, *Pubivetanthocoris carnalis* Tang, Wang & Yao, 2022 was described from mid-Cretaceous Kachin amber of northern Myanmar — this was the first observation of amber inclusion of Vetanthocoridae (Tang et al. 2022).

Observations of the structure of male genitalia are crucial for diagnosing and placing specific groups of Cimicomorpha; however, these structures are not visible in most compression or impression fossils. Even in amber fossils, male genitalia are seldom visible at perfectly clear angles. In Cimicoidea, the details of male genitalic morphology remain unknown, except for those of *Lyctoferus* Popov, 2003 (Anthocoridae) from Eocene Baltic and Ukrainian ambers (Popov 2003) and *Quasicimex* Engel, 2008 (Cimicidae) from Kachin amber (Engel 2008).

The current study reports a well-preserved cimicoid true bug amber fossil from the Hukawng Valley in the Kachin State of northern Myanmar, which is here-in described as a new genus and species, *Ecpaglocoris ditomeus* gen. et sp. nov. Although the external appearance of this cimicoid species mostly resembles that of Anthocoridae members, the hemelytral membrane venations and presence of dorsal laterotergites on abdominal segments I to VIII reasonably place it in the family Vetanthocoridae. Therefore, this amber inclusion represents the second discovery of the family Vetanthocoridae in mid-Cretaceous amber, revealing a new genus and species with novel morphological data on male genitalia. This well-preserved amber fossil enables a series of detailed morphological observations on the male genitalia in *E. ditomeus* gen. et sp. nov. and it provides new insights into male genital morphology and phylogenetic relationships within Cimicoidea.

Materials and methods

The amber specimen used in this study was obtained from the Noije Bum Hill of the Hukawng Valley in the State of Kachin, northern Myanmar (Burma). A variety of clastic sedimentary deposits, thin limestone beds and abundant coal and carbonaceous materials have been recognised at the mine and the occurrence of amber is associated with

a narrow horizon in fine-grained facies (Cruickshank and Ko 2003). Burmese amber from the Kachin State or recently called “Kachin amber”, had been previously considered as being of the Eocene age (Chhibber 1934), but Cruickshank and Ko (2003) suggested a much older Cretaceous age. Based on uranium-lead (U-Pb) dating of zircons of the surrounding sedimentary matrix, amber dates have recently been established as the earliest Cenomanian (98.79 ± 0.62 Ma) (Shi et al. 2012). However, the amber deposits of Kachin may possibly be slightly older (Balashov 2021) and, thus, we here adopted the mid-Cretaceous age (i.e. Cenomanian–Albian) for the amber from the Hukawng Valley.

Regarding recent conflicts in Myanmar (e.g. Sokol (2019); Poinar and Ellenberger (2020); Peretti (2021)), the Kachin amber piece used in this study has been collected before the control of the amber mining areas in the Kachin State started in November 2017 and that we follow the recommendations by Haug et al. (2020). The sole specimen used in this study was legally purchased from an Italian amber dealer on 2 January 2018; it was mined before 2017.

An amber piece containing an inclusion was prepared for cutting, grinding and polishing by the third author. The amber piece is a small, flattened, semicircular or sub-rectangular polished prism of approximately $12 \times 7 \times 4.5$ mm in size. Observations were performed using a binocular microscope (stereoscopic zoom microscope SMZ1500; Nikon). Photographs (Figs 1, 2, 4A, B) were taken using a digital camera (EOS 80D; Canon) attached to an extreme macro-lens (MP-E 65 mm, F2.8, 1–5 \times ; Canon) and a flash light (Macro Twin Lite MT-24 EX; Canon). Line drawings (Figs 3, 4C, D) were prepared principally using an eyepiece grid. The software Helicon Focus 7.7.5 was used for image stacking. All digital images were edited and assembled using Adobe Photoshop CC 2022. The type specimen is deposited the American Museum of Natural History, New York, USA (AMNH), under the registered number of AMNH Bu-SY33. The terminology generally follows Carayon (1972) and Schuh and Weirauch (2020). This publication is registered in ZooBank under: urn:lsid:zoobank.org:pub:6A3587A7-9E57-40AC-B9FD-753EDDBA73C5.

Systematic palaeontology

Superfamily Cimicoidea Latreille, 1802

Family Vetanthocoridae Yao, Cai & Ren, 2006

Genus *Ecpaglocoris* Yamada & Yamamoto, gen. nov.

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Type species. *Ecpaglocoris ditomeus* Yamada & Yamamoto, sp. nov., by original designation.

Etymology. The genus name is a combination of the Greek *ekpaglos* (= wondrous, astounding) and *koris* (= bug), referring to this new fossil bug possessing unique male genitalia amongst Cimicoidea; gender masculine.

Diagnosis. Body (Fig. 1) elongated, dorsoventrally flattened; head (Figs 1, 3A) porrect; labium (Figs 1D, 2B, C) reaching middle of mesosternum; pronotum (Figs 1A, C, 3A) with pair of long erect setae near antero-lateral and postero-lateral angles and a pair of similarly long setae behind anterior margin; pronotal callus flat, with longitudinal shallow groove on the mid-line; hemelytral membrane (Fig. 3D) with 10 or more long, slightly curved veins; a very long trichobothrium (Figs 2E, 3D, E) present on middle of corium-membrane boundary; ostiolar peritreme (Figs 2F, 3F) slightly curved forward at apex, distinctly continued to a fine carina which reaches anterior margin of metapleura; fore femur (Figs 2G, 3G) extremely enlarged; fore tibia (Figs 2G, 3G) strongly expanded towards apex, bearing 4–5 long, stout spines and 4–5 small teeth on ventral side and with greatly developed fossula spongiosa at apex; middle and hind tibiae (Figs 1B, D, 3H, I) with several long, stout spines, lacking fossula spongiosa; dorsal laterotergites (Fig. 2D) not fused with mediotergites on abdominal segments I to VIII; pygophore (Fig. 4A–C) symmetrical, longer than combined length of abdominal sterna VII and VIII in ventral view, very broadly connected to abdominal segment VIII; proctiger well-developed; parameres (Fig. 4) symmetrical, orientated anteriorly, very slender and long, moderately curved, acute towards apex, with groove running throughout the paramere.

Differential diagnosis. The new genus *Ecpaglocoris* differs from the genus *Pubivethanocoris* Tang, Wang & Yao, 2022 by the head shorter than pronotum (in *Pubivethanocoris*, slightly longer than pronotum); vertex wider than twice the width of an eye in dorsal view (in *Pubivethanocoris*, narrower than the width of an eye); lateral margin of pronotum not membranous, only carinated at antero-lateral angle (in *Pubivethanocoris*, membranous, flattened and widely carinated); hemelytra parallel-sided (in *Pubivethanocoris*, strongly curved); PCu and R+M absent on hemelytra (in *Pubivethanocoris*, present); and fore tibia strongly expanded towards apex (in *Pubivethanocoris*, slender, not expanded).

Description. Male. Body elongated, dorsoventrally flattened.

Head (Figs 1, 3A) porrect, slightly shorter than width across eyes; three pairs of long, erect trichobothria (cephalic macrosetae) on each side of anterior clypeus, near front margin of each eye and each side of vertex between eye and ocellus; antecular region slightly longer than length of eye in dorsal view; eyes prominent, exceeding level of dorsal and ventral surfaces of head in lateral view; ocelli situated between eyes in front of an imaginary line that passes through posterior margin of eyes; vertex wider than twice the width of an eye in dorsal view; postocular region constricted, demarcated by transverse shallow furrow; neck long, smooth, highly polished. Antennal segment I (Figs 1, 3A) stout, exceeding apex of head, with a few short setae; prepedicellite present between segments I and II; segment II (Figs 1, 2A, 3B) stout, slightly thickened towards apex, about as long as head width across

eyes, covered with suberect setae that are much shorter than width of the segment, intermixed with long setae that are longer than width of the segment; segments III and IV (Figs 1, 2A, 3B) filiform, much narrower than maximum width of segment II, equal in length, about 0.7 times as long as segment II, sparsely covered with long erect setae intermixed with short procumbent setae, longest setae much longer than twice the width of the respective segment. Labrum short, rounded at apex, not wholly covering labial segment I. Labium (Figs 1D, 2B, C, 3C) long, reaching middle of mesosternum, weakly curving; segment I visible, much shorter than the other segments; segment II stout, basally narrowed, approximately eye length long; segment III extremely long, slightly thickened near base and gradually narrowed towards apex, approximately 3.6 times as long as segment II; segment IV much slender, half as long as segment III.

Pronotum (Figs 1A, C, 3A) nearly trapezoidal, shallowly depressed postero-medially, sparsely covered with tiny punctures, with pair of long erect setae near antero-lateral and postero-lateral angles and with pair of similarly long setae behind anterior margin; anterior margin slightly concave; lateral margin strongly angulate antero-laterally in dorsal view, densely covered with short setae; lateral carinae strongly expanded at antero-lateral angle; collar absent; callus flat, with longitudinal shallow groove on the mid-line; posterior margin deeply concave. Scutellum (Fig. 1A, B) large, sub-equilateral, mesal length longer than basal width, weakly depressed through middle, sparsely covered with short procumbent setae, with a pair of long erect setae near lateral margin base. Hemelytra (Figs 1A, B, 3D) parallel-sided, surpassing apex of abdomen, overall covered with short procumbent setae; claval suture, medial fracture and costal fracture clearly visible; distal end of medial fracture not contiguous with costal fracture; costal margin slightly sinuate. Membrane (Figs 1A, B, 3D) with a cross vein running along corium-membrane boundary and 10 or more long, slightly curved veins radiating posteriorly from it; stub (processus corial) present at distal end of a cross vein; a very long trichobothrium (Figs 2E, 3D, E) present on middle of corium-membrane boundary, the length much longer than three times that of other setae on hemelytron. Mesosternum wide, coarse, mesally with longitudinal carina. Metasternum extremely swollen, obtuse at apex. Metepisternum wide, overall occupied by evaporatorium surrounding the metathoracic scent gland. Metathoracic scent gland (Figs 2F, 3F) with a wide ostiolar peritreme; ostiolar peritreme curved slightly forward at apex, distinctly continued to a fine carina that reaches anterior margin of metapleura while gently curving; median furrow running throughout the ostiolar peritreme. Fore femur (Figs 2G, 3G) extremely enlarged, unarmed, much thicker than width of middle femur; fore tibia (Figs 2G, 3G) strongly expanded towards apex, bearing 4–5 long, stout spines and 4–5 small teeth on ventral side, with well-developed fossula spongiosa at apex; middle coxae widely separated from each other; middle tibia

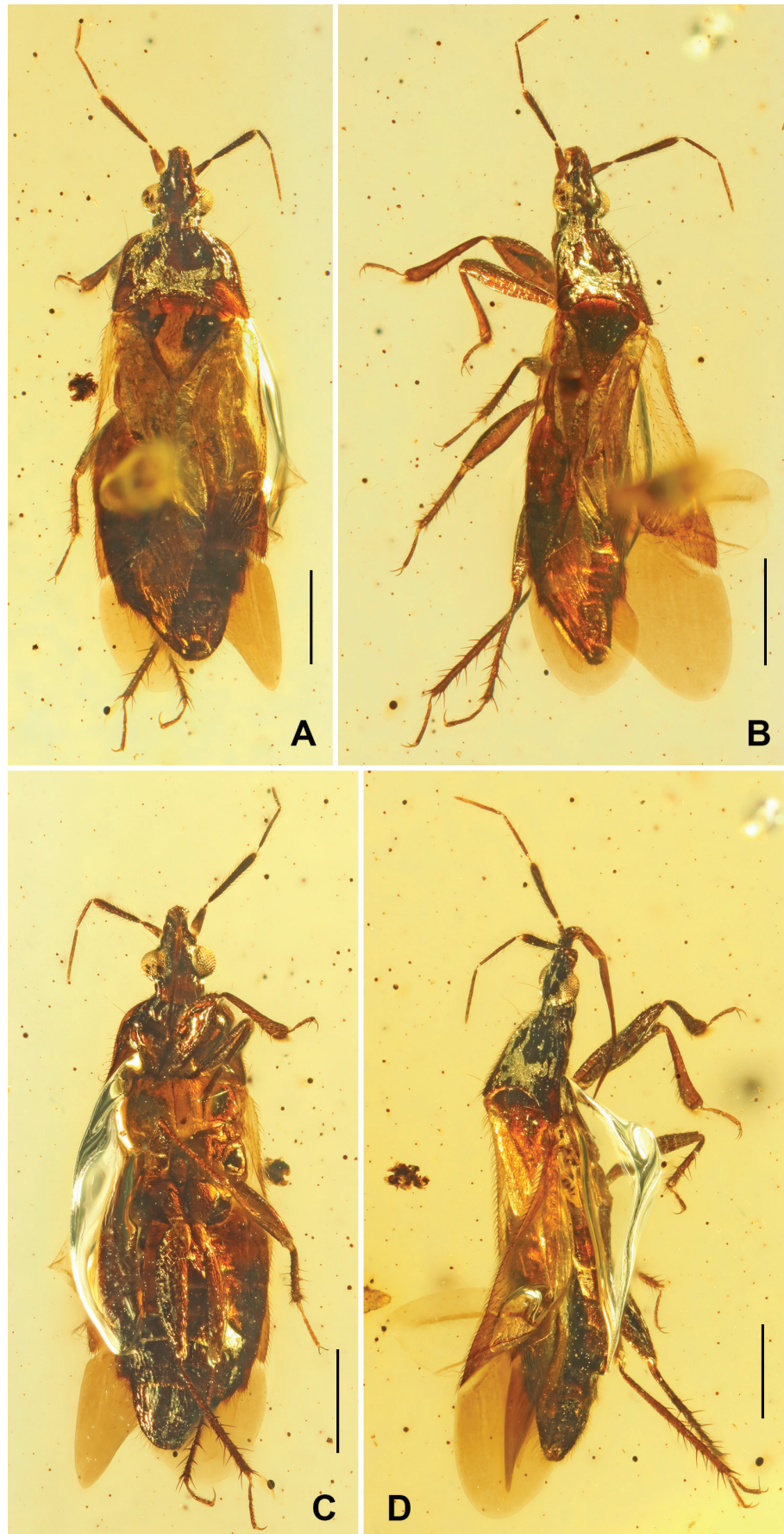


Figure 1. General habitus of *Ecpaglocoris ditomeus* gen. et sp. nov., male, holotype (AMNH Bu-SY33). **A.** Dorsal view; **B.** Left laterodorsal view; **C.** Ventral view; **D.** Right laterodorsal view. Scale bars: 0.5 mm.

(Figs 1B, 3H) expanded towards apex, covered with several long, stout spines on apical two-thirds and with tibial comb at apex, lacking fossula spongiosa; hind coxae proximate with each other; hind femur thickened, slightly narrower than width of fore femur, equal to hind tibia; hind tibia (Figs 1B–D, 3I) nearly cylindrical, densely covered with long, stout spines on apical three-fourths, with small tibial comb at apex, lacking fossula spongiosa. Tarsus three-segmented. Pretarsus of each leg with long, slender, symmetrical claws.

Abdomen (Figs 1C, D, 2D) lateroventrally covered with dense short setae; lateral margins of sterna VI–VIII densely covered with short, suberect setae intermixed with thickly setae; dorsal laterotergites (Fig. 2D) not fused with mediotergites on abdominal segments I to VIII; sterna II and III broad, and VIII very narrow.

Male genitalia (Fig. 4): Pygophore (Fig. 4A–C) symmetrical, large, longer than combined length of abdominal sterna VII and VIII in ventral view, very broadly connected to abdominal segment VIII, dorsally depressed, posteriorly narrowed and rounded in dorsal view, densely covered with short, erect setae along outer margin and on posteroventral surface, lacking long trichobothria; proc-tiger well-developed; parameres (Fig. 4) symmetrical, arising from near mid-line of dorsocaudal part of pygophore, orientated anteriorly, very slender and long, moderately curved, acute towards apex, with groove running throughout paramere.

Ecpaglocoris ditomeus Yamada & Yamamoto, sp. nov.

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Figs 1–4

Type material. Holotype: male, a well-preserved adult in Kachin amber, with the registered number AMNH BU-SY33 (deposited in AMNH).

Etymology. The species epithet is named for the Greek *di* (= two, double) and *tomeus* (= knife, cutter), referring to the slender, sickle-shaped left and right parameres in male genitalia.

Type locality and horizon. Noiye Bum Hill, Hukawng Valley, Kachin State, northern Myanmar; mid-Cretaceous (Cenomanian–Albian).

Diagnosis. As in generic diagnosis.

Description. Male. Body 3.1 mm long, pale to dark brown (Fig. 1), sparsely covered with procumbent setae.

Head (Figs 1, 3A) uniformly dark brown, 0.35 mm in length excluding neck, 0.39 mm in width across eyes; eye length 0.15 mm, width 0.08 mm, in dorsal view. Antennae (Figs 1, 2A, 3B) dark brown, segments I and IV tinged pale brown; lengths of segments I–IV (mm): 0.18, 0.38, 0.28 and 0.28. Labium (Figs 1D, 2B, C) pale brown; lengths of segments II–IV (mm): 0.15, 0.54 and 0.27.

Pronotum (Figs 1A, C, 3A) uniformly dark brown; anterior width 0.25 mm, approximately 0.65 times as wide as mesal pronotal length; basal width 0.74 mm, approximately three times as wide as anterior width.

Scutellum (Fig. 1A, B) somewhat paler than pronotum. Hemelytra (Figs 1A, B, 3D) generally pale brown, but cuneus apically tinged with dark brown; embolial margin 1.06 mm, about three times as long as cuneal margin; embolium approximately 0.6 times as wide as maximum width of endocorium; cuneal margin 0.34 mm; membrane semi-transparent. Venter of thorax (Fig. 1C) uniformly dark brown. Legs (Figs 1B–D, 2G, 3G–I) generally pale brown, femora tinged dark brown; lengths of femur, tibia and tarsus of fore leg (in mm): 0.6, 0.5 and 0.28; middle leg: 0.5, 0.44 and 0.25; hind leg: 0.8, 0.8 and 0.46, respectively.

Abdomen (Figs 1C, D, 2D) brown to dark brown.

Female. Unknown.

Discussion

Family placement of *Ecpaglocoris*

This new genus and species is reminiscent of members of Anthocoridae and can be unambiguously placed in Cimicoidea (Heteroptera: Cimicomorpha), based on the following characters: labium with four segmented; costal fracture distinct, delimiting cuneus; hemelytral membrane without closed cell; fossula spongiosa present at least on fore tibiae; absent ventral laterotergites; and insertion of paramere shifted to near mid-line of pygophore (Schuh et al. 2009; Weirauch et al. 2019; Schuh and Weirauch 2020).

However, the new genus *Ecpaglocoris* has the following unusual characteristics in membrane venation, dorsal laterotergites on abdomen and male genitalia, which are not observed in either Anthocoridae or other families of Cimicoidea: membrane with a cross vein running along the corium-membrane boundary and 10 or more long veins radiating from it (Fig. 3D) (in Cimicoidea, 4–5 free veins, rarely with one long closed cell without emanating veins); dorsal laterotergites not fused with mediotergites on abdominal segments I to VIII (Fig. 2D) (in Cimicoidea, on abdominal segments I to III or I and II); pygophore symmetrical (Fig. 4A–C) (in Cimicoidea, except for Plokiophilidae, asymmetrical); left and right parameres symmetrical, with groove (Fig. 4C, D) (in most Cimicoidea, asymmetrical; in a part, non-grooved).

Excepting the unusual membrane venation and male genitalia features, some morphological features of *Ecpaglocoris* gen. nov. are observed in the anthocorid genera *Scoloposcelis* Fieber, 1864 (Tribe Scolopini), *Xylocoris* Dufour, 1831 (Xylocorini) and *Blaptostethus* Fieber, 1860 (Blaptostethini). The characteristics shared by *Ecpaglocoris* gen. nov. and *Scoloposcelis* include: body elongated and dorsoventrally flattened; pronotum shallowly depressed postero-medially, with flat callus; hemelytra parallel-sided; and fore- and hind femora enlarged. However, *Scoloposcelis* is also characterised by femora with small teeth on the ventral side, ostiolar peritreme not continuing to a fine carina and males with

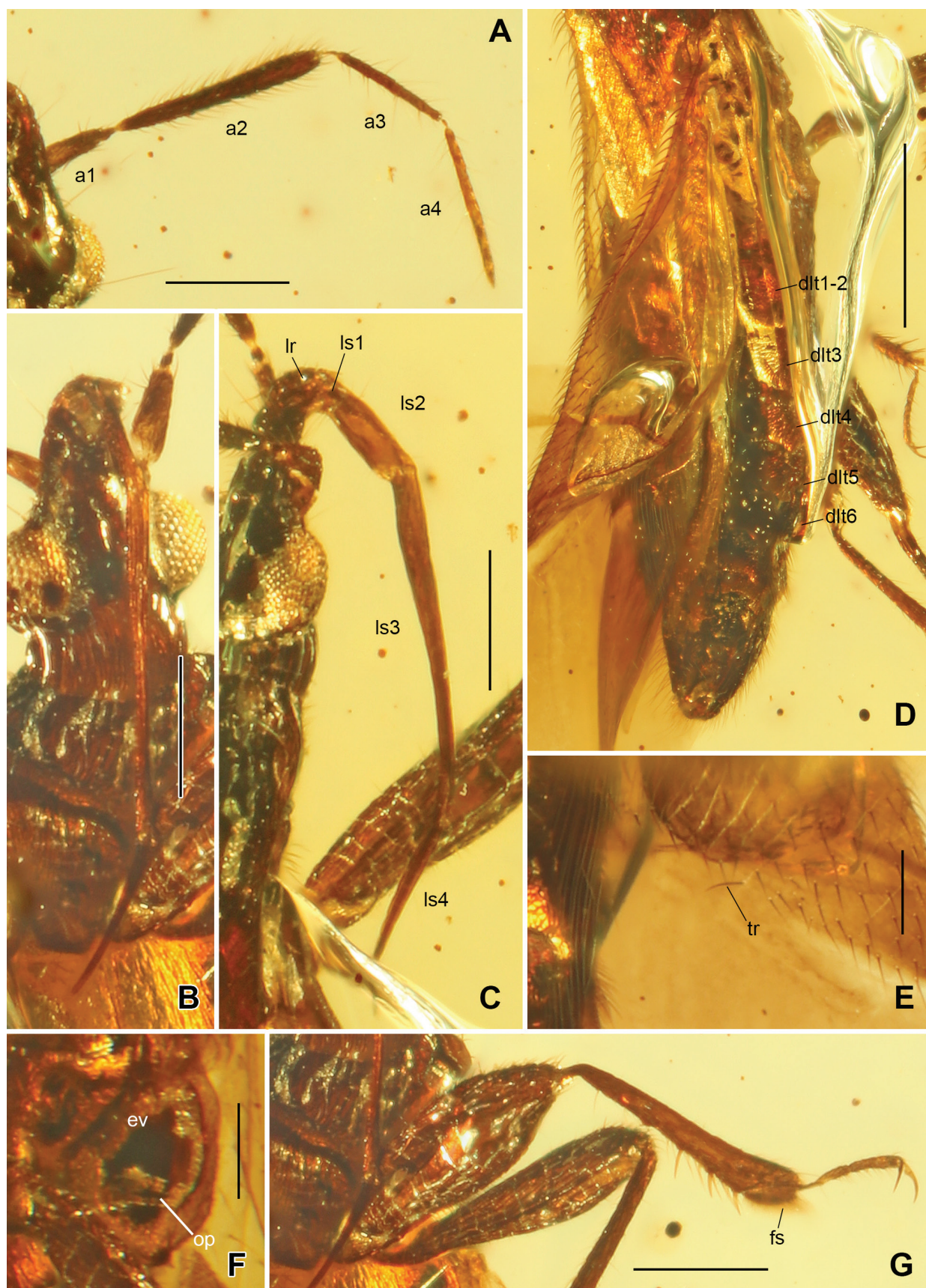


Figure 2. *Ecpaglocoris ditomeus* gen. et sp. nov., male, holotype (AMNH Bu-SY33). **A.** Right antenna, laterodorsal view; **B, C.** Labium, ventral (**B**) and right lateral (**C**) views; **D.** Thorax and abdomen, right laterodorsal view; **E.** Trichobothrium on corium-membrane boundary of right hemelytron; **F.** Ostiolar peritreme and evaporatorium, left lateroventral view; **G.** Right fore-leg, outer view. Abbreviations: a1–4, antennal segment 1–4; dlt1–6, dorsal laterotergite 1–6; ev, evaporatorium; fs, fossula spongiosa; lr, Labrum; ls1–4, labial segment 1–4; op, ostiolar peritreme; tr, trichobothrium. Scale bars: 0.5 mm (**D**); 0.2 mm (**A–C, E–G**).

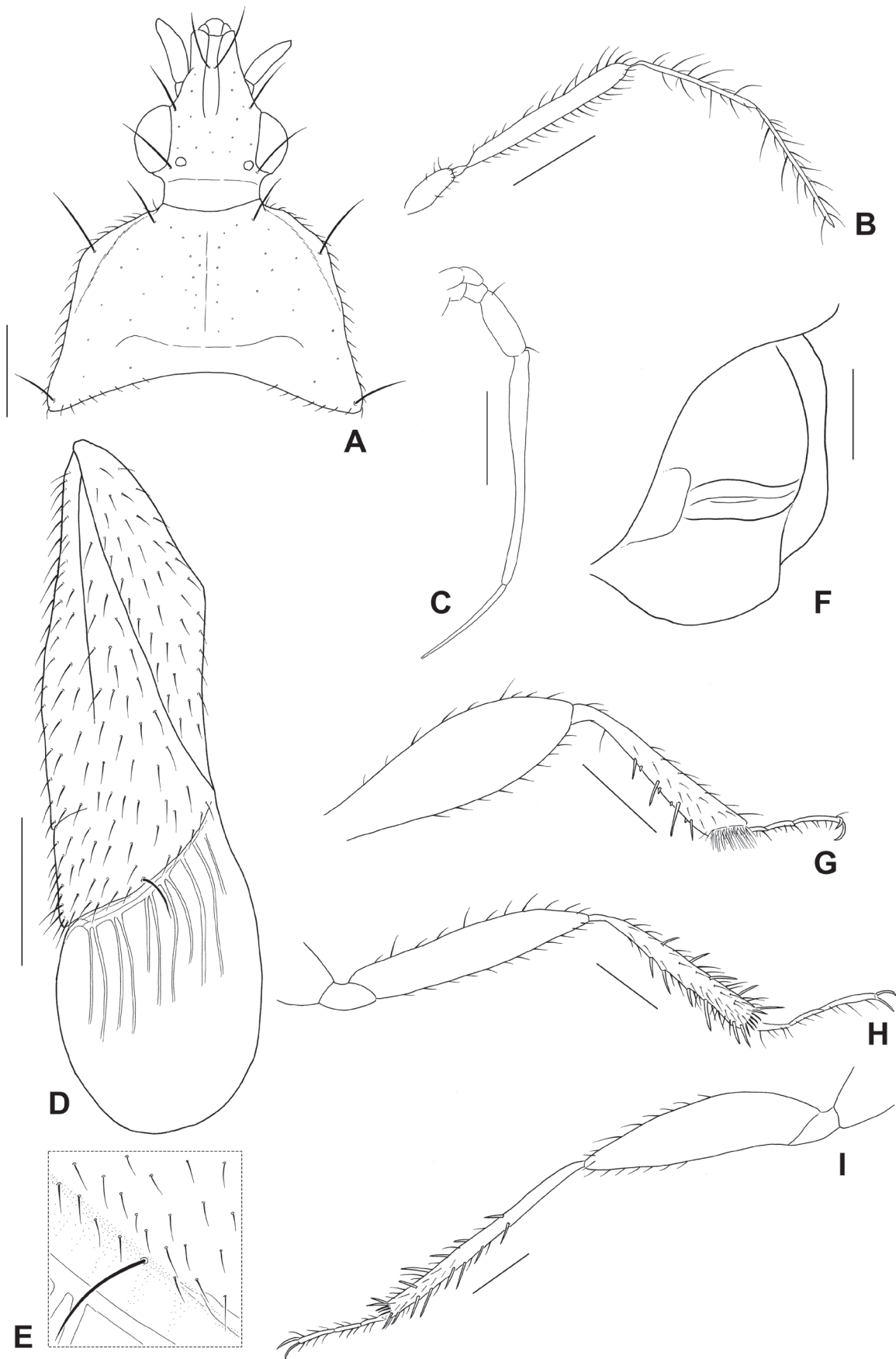


Figure 3. *Ecpaglocoris ditomeus* gen. et sp. nov., male, holotype (AMNH Bu-SY33). **A.** Head and pronotum, dorsal view; **B.** Right antenna, laterodorsal view; **C.** Labium, lateral view; **D.** Left hemelytron, as seen in situ, not flattened; **E.** Trichobothrium on corium-membrane boundary of right hemelytron; **F.** Ostiolar peritreme and evaporatorium, left lateroventral view; **G.** Right fore-leg, outer view; **H.** Right middle leg, outer view; **I.** Right hind leg, inner view. Scale bars: 0.5 mm (**D**); 0.2 mm (**A–C, F–I**).

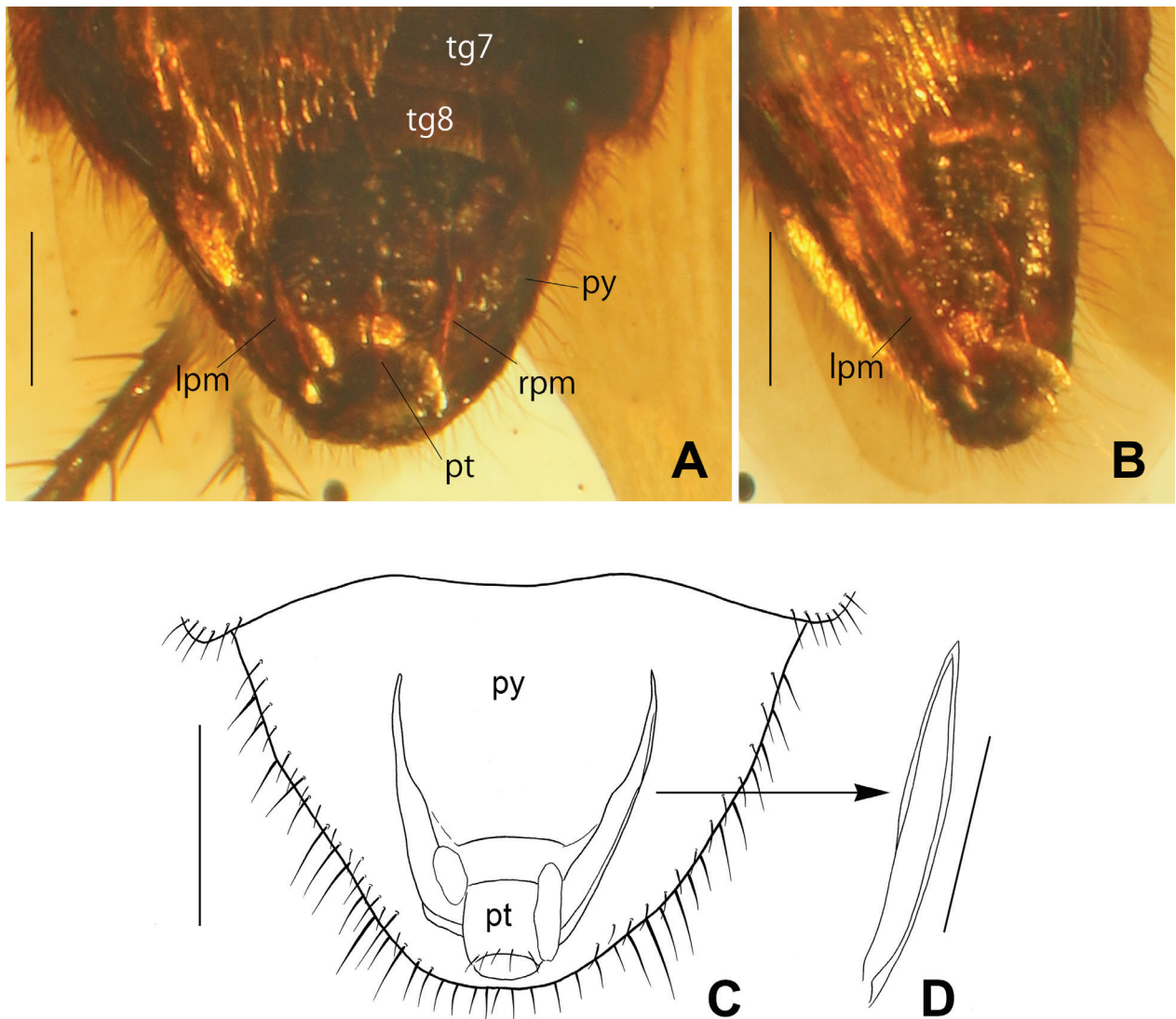


Figure 4. *Ecpaglocoris ditomeus* gen. et sp. nov., male, holotype (AMNH Bu-SY33). **A, B.** Apex of abdomen, dorsal (**A**) and left laterodorsal (**B**) views; **C.** Pygophore with parameres, dorsal view; **D.** Right paramere, right lateral view. Abbreviations: lpm, left paramere; pt, proctiger; py, pygophore; rpm, right paramere; tg7–8, tergite 7–8. Scale bars: 0.1 mm.

opening(s) of uradenia (paired abdominal glands) on either abdominal sternum 4 or 5, which is also an autapomorphy of Scolopini (e.g. Carayon (1972); Schuh and Slater (1995)). *Ecpaglocoris* gen. nov. lacks femoral teeth and an opening of uradenia on the abdominal sternum and it has an ostiolar peritreme continuing to a fine carina (Figs 2F, 3F). *Ecpaglocoris* gen. nov. has leg characteristics similar to those of *Xylocoris* and *Blaptostethus* as follows: each tibiae bearing several long, stout spines that are as long as or longer than the width of the tibia (Figs 1B–D, 2G, 3G–I); fore tibia expanded towards the apex, with developed fossula spongiosa at the apex (Figs 1B–D, 2G, 3G). However, the fossula spongiosa is also present on the middle and hind tibiae in *Xylocoris* and *Blaptostethus*, but it is absent in *Ecpaglocoris* gen. nov. (e.g. Carayon (1972); Schuh and Slater (1995)). This new genus is characterised by a combination of morphological features found in some anthocorid taxa of different tribes, but lacks synapomorphies in each genus (tribe) in Anthoc-

oridae. Considerable differences in male genitalia are recognised between the new genus and anthocorid groups. The superficial morphological similarities between these taxa may represent the convergence of habits and habitats.

Although symmetrical male genitalia in *Ecpaglocoris* gen. nov. are also found in Microphysoidea (Joppeicidae and Microphysidae) and Naboidea (Medocostidae, Nabidae and Velocipedidae), which are closely related to Cimicoidea, all these groups possess a conspicuous paramere insertion on the left side of the pygophore and the various-shaped paramere, which is never sickle-like in shape (Schuh and Štys 1991; Schuh et al. 2009; Schuh and Weirauch 2020). These features clearly distinguish *Ecpaglocoris* gen. nov. from both the superfamilies. In addition, Microphysoidea has reduced or no evaporatorium in the metapleuron and two-segmented tarsi and Naboidea has a membrane with 2–3 short or elongate cells usually with numerous emanating veins. The new genus may belong to neither Microphysoidea nor Naboidea.

Of the above-mentioned unusual features in *Ecpaglocoris* gen. nov., membrane venation and dorsal laterotergites on the abdomen are also recognised in the extinct family Vetanthocoridae. Tang et al. (2016) re-evaluated Vetanthocoridae as a member of Cimicoidea and suggested two synapomorphies to support the monophyly of the family, based on their phylogenetic analysis: antennal segments III and IV smooth without setae and 10 or more simple longitudinal veins on the hemelytral membrane. However, the former was not considered a synapomorphic character for the family by Tang et al. (2022), because *Pubivetanthocoris carinalis* Tang, Wang & Yao, 2022, described as the first record of the Vetanthocoridae from Kachin amber, has antennal segments III and IV with discrete setae. However, the membrane venation and dorsal laterotergites on the abdomen found in Vetanthocoridae and *Ecpaglocoris* gen. nov. clearly distinguish both taxa from Recent cimicoids and can be regarded as important diagnostic features for Vetanthocoridae. Thus, we should place *Ecpaglocoris* gen. nov. in the family Vetanthocoridae.

Relationships within Vetanthocoridae

Although *Ecpaglocoris* gen. nov. is best placed in Vetanthocoridae, the genus has several remarkable characteristics amongst the vetanthocorid genera: body very small (Fig. 1) (in Vetanthocoridae, 4.3–13.7 mm vs. 3.1 mm); hemelytra parallel-sided (Fig. 1A) (in Vetanthocoridae, generally curved-sided); embolar fracture on hemelytra absent (Figs 1A, B, 3D) (in Vetanthocoridae, present); a very long trichobothrium present on the middle of the corium-membrane boundary (Figs 2E, 3D, E) (in Vetanthocoridae, absent; at least not confirmed in the descriptions of all members); and fore tibia strongly expanded towards apex (Figs 2G, 3G) (in Vetanthocoridae, generally straight) (Yao et al. 2006; Tang et al. 2016, 2022). Based only on the condition of antennal segments III and IV (both distinctly narrower than segment II) (Yao et al. 2006; Tang et al. 2022), *Ecpaglocoris* gen. nov. can be assigned to the tribe Vetanthocorini; however, the above-mentioned distinctive characters are all exceptional in Vetanthocoridae. Therefore, the tribal placement of this new genus cannot be determined yet.

Limited information is available regarding the male genital features of Vetanthocoridae. Based on the figures by Yao et al. (2006: pp. 10, 17), *Vetanthocoris decorus* Yao, Cai & Ren, 2006 and *Collivetanthocoris rapax* Yao, Cai & Ren, 2006 may have symmetrical and well-developed pygophores. Shcherbakov (2007) also indicated that the family Vetanthocoridae has symmetrical male genitalia; however, no detailed discussion was provided. The general appearance of pygophore from the ventral aspect in *E. ditomeus* gen. et sp. nov. is relatively similar to those of *V. decorus* and *C. rapax*; however, it is not possible to determine whether they have the same characteristics owing to limited morphological information available from their fossils.

Male genitalic morphology

Male genitalia and insemination mechanisms are the most important characteristics for determining the family level systematic position within Cimicoidea. Asymmetrical male genitalia are one of the peculiarities of all extant Cimicoidea, except for Plokiophilidae. Sinistral asymmetry affects the pygophore and parameres, indicating that the right paramere is usually completely lost. Asymmetry, as seen in parameres, occurs in many groups that appear to be distantly related, judging by other characters, including Nepomorpha, Dipsocoridae, Schizopteridae and Miroidea (Ford 1979; Weirauch et al. 2019). Male genital asymmetry has arisen independently of several evolutionary lineages. Symmetrical male genitalia in *Ecpaglocoris* gen. nov. and Plokiophilidae are clearly plesiomorphic within the Cimicoidea.

Traumatic (haemocoelic) insemination is the most prevalent mating strategy in the true bug infraorder Cimicomorpha, where it occurs in at least seven families (Carayon 1966, 1972, 1977; Ford 1979; Tatarnic et al. 2014). With some exceptions, the members of Cimicoidea practise traumatic insemination. Male genitalic characteristics associated with these insemination mechanisms include: 1) aedeagus (endosoma) with sclerotised organ (needle-like acus) and 2) copulatory left paramere. The former is found in Lyctocoridae and Plokiophilidae, as well as in several other non-cimicoid heteropterans (Nabidae: Prostematinae). Their paramere has no grooves because the aedeagus itself serves as an intromittent organ. The latter is found in Anthocoridae, Cimicidae and Polycetenidae. Their paramere itself functions as an intromittent organ and has a distinct groove with an acute apex, which serves as a guide for the membranous aedeagus. The paramere of some Lasiochilidae species has a similar condition with those of three families, but its function is unknown (Carpintero 2014). Although the grooved paramere is also seen in *Coridromius* (Miridae), suggesting an independent derivation for traumatic insemination, it can be regarded as a unique condition within the Cimicoidea. The parameres of *Ecpaglocoris* gen. nov. are sickle-shaped and possess a groove throughout the paramere (Fig. 4). Due to the male genitalic structure of this new fossil genus, they have very significant differences from the extant species which have traumatic insemination and no direct behavioural evidence showed in the amber specimen. Although the possibility of this new fossil species mating by traumatic insemination is existing, based on their male genitalic characteristics, our insight is completely speculative.

The mating posture of *E. ditomeus* gen. et sp. nov. might be quite different from that of other cimicoid groups. Available evidence suggests that its posture is presumably almost the same as that of other heteropterans with symmetrical male genitalia, showing that the male takes its place under the female (Ceratocombidae, Melber and Köhler 1992; Aradidae, Schuh and Weirauch 2020) or that the male places the dorsal side of the tip of the abdomen

under the tip of the female abdomen (Nepidae, Larsén 1938; Joppeicidae, Davis and Usinger 1970). Whereas, another hypothesis can predict that *E. ditomeus* gen. et sp. nov. also practised the most common “male-above” position for genital coupling in cimicoid members with grooved parameres. In this case, the male bends his abdomen from the female’s right (or left) side and inserts his paramere into a certain part of the ventral side of the abdomen (e.g. Péricart (1972); Huber et al. (2007); Tatarnic et al. (2014)). In the case of *E. ditomeus* gen. et sp. nov., the mating posture may be an alternating two-sided position because it has double parameres as an intromittent organ.

Male genital asymmetry in Recent Cimicoidea is overwhelmingly directional (sinistrally curved) (Huber et al. 2007; Schuh and Weirauch 2020). Directional asymmetry is also seen in females of Cimicoidea, because traumatic insemination often occurs via a specific copulatory site (Carayon 1977). Their morphological modifications are thought to have evolved through a mating strategy in association with sexually antagonistic types of behaviour (e.g. Parker (1979); Arnqvist and Rowe (2005)); however, no hypothesis explains why sinistral male genitalia are dominant over symmetry in Cimicoidea.

According to Schuh et al. (2009), Jung et al. (2010), Jung and Lee (2012) and Weirauch et al. (2019), cimicoid groups with grooved paramere (Anthocoridae, Cimicidae, Polyctenidae and some Lasiophilidae) do not form a monophyletic group, placing Lasiophilidae as a base for the remaining Cimicoidea. Thus, the grooved paramere occurs separately in the superfamily and that their possession has no strong systematic significance, at least within Cimicoidea. *Ecpaglocoris* gen. nov. also has grooved parameres; however, owing to the combination of the unique characters mentioned above, it is unlikely that this genus would be closely related to these taxa with grooved parameres. Within Heteroptera, *Ecpaglocoris* gen. nov. is characterised by plesiomorphic symmetrical pygophore and parameres and a unique grooved paramere. This peculiar combination of male genital characteristics prevents their placement in any of the extant cimicoid families. If this characteristic is recognised in members of the Vetanthocoridae, it could undoubtedly be a synapomorphy in this extinct family.

Conclusions

Although our investigation of these *Ecpaglocoris* gen. nov. characteristics produced unexpected results and produced doubt that this taxon belongs to Cimicoidea, we are reasonably certain that it should be placed in this superfamily, based on salient characteristics. Consequently, *Ecpaglocoris* gen. nov. can be assigned to the extinct family Vetanthocoridae because of the presence of venation of the hemelytral membrane and dorsal laterotergites on abdominal segments I to VIII, which are unique amongst the extant cimicoid taxa. In extant Heteroptera, the parameres of the species that are used as the intro-

mittent organ are all strongly asymmetrical, never symmetrical. However, the male genitalia of *Ecpaglocoris ditomeus* gen. et sp. nov. is characterised by a combination of plesiomorphic (symmetrical pygophore and paramere) and unique (a groove that runs throughout the paramere) characteristics within Heteroptera. The characteristics of the parameres indicate that traumatic insemination was practised in this genus. If this characteristic in the male genitalia is recognised in the members of Vetanthocoridae, it could undoubtedly be a synapomorphy in the extinct family. Since relationships amongst the family level taxa within Cimicoidea remain controversial, assessment of the phylogenetic position of *Ecpaglocoris* gen. nov. or Vetanthocoridae requires detailed phylogenetic studies to rigorously evaluate the monophyly of the currently-recognised family level groups in extant Cimicoidea.

Data availability

The single material (holotype) is deposited in the American Museum of Natural History, New York, USA (AMNH). All data and results are presented in the main text and figures. Higher-resolution images are also available through the Zenodo repository (<https://doi.org/10.5281/zenodo.7472713>).

Author contributions

KY, SY and YT conceived the study. YT and SY prepared for cutting, grinding and polishing an amber piece containing an inclusion. KY identified and described the specimen. SY produced the photos. KY edited and assembled the figures. KY, SY and YT prepared the paper and contributed to the editing.

Competing interests

The authors declare that they have no conflict of interest.

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