

Original Article

Cite this article: Fu Y, Cai C, and Huang D (2020) First Mesozoic procercopids in mid-Cretaceous amber from northern Myanmar (Hemiptera: Cercopoidea). *Geological Magazine* 157: 506–512. <https://doi.org/10.1017/S0016756819001018>

Received: 20 March 2019
Revised: 23 July 2019
Accepted: 24 July 2019
First published online: 29 October 2019

Keywords:

Cicadomorpha; Procercopidae; Burmese amber; new taxa; palaeodiversity

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First Mesozoic procercopids in mid-Cretaceous amber from northern Myanmar (Hemiptera: Cercopoidea)

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Abstract

Two new genera and two new species of Procercopidae, *Paranthoscytina xiai* gen. et sp. nov., and *Burmocercopis lingpogensis* gen. et sp. nov., are described and illustrated based on two well-preserved specimens in mid-Cretaceous amber (c. 99 Ma) from northern Myanmar. Our discovery represents the first record of amber-entombed Procercopidae from the Mesozoic, widening the duration and biogeographic distribution of this extinct family. They also represent the latest record of Procercopidae, which fills the gap of Cercopoidea evolution during the mid-Cretaceous.

1. Introduction

The hemipteran superfamily Cercopoidea Leach, 1815, also known as froghoppers or spittlebugs, comprises more than 2600 described recent species (Hamilton, 2001; Dietrich, 2002; Bartlett *et al.* 2018). In addition to their extant diversity, three extinct families (i.e. Cercopionidae, Procercopidae and Sinoalidae) from the Mesozoic have been attributed to Cercopoidea. The extinct family Procercopidae Handlirsch, 1906, the earliest lineage of Cercopoidea, is widely accepted as a stem group of the superfamily (Evans, 1956; Shcherbakov & Popov, 2002). Procercopidae, originally established to accommodate *Procercopis* Handlirsch, 1906 from the Lower Jurassic of Germany, can be traced back from the Early Jurassic to the Early Cretaceous of Eurasia and Australia (Handlirsch, 1906–8; Hamilton, 1992). To date, nine valid genera of Procercopidae have been reported (Wang *et al.* 2012; Fu *et al.* 2018), which include *Procercopis* Handlirsch, 1906–8, *Procercopina* Martynov, 1937, *Sinocercopis* Hong, 1982, *Anthoscytina* Hong, 1983, *Cretocercopis* Ren, 1995, *Liassocercopis* Ansoerge, 1996, *Jurocercopis* Wang & Zhang, 2009, *Stellularis* D Chen *et al.* 2015 and *Titanocercopis* J Chen *et al.* 2015a.

Cretaceous procercopids with three genera and seven species are confined to Siberia and northern China. They include *Anthoscytina daica* Shcherbakov, 1988 from the Upper Jurassic to Lower Cretaceous Glushkovo Formation of Chita, Siberia, Russia; *Cretocercopis yii* Ren, 1995, *A. trinervus* Ren, 1995 and *A. pustulosus* Ren, 1995 from the Lower Cretaceous Lushangfen Formation of Beijing; *Stellularis aphthosa* (= *Anthoscytina aphthosa*) Ren *et al.* 1998, *S. macula* (= *A. macula*) Hu *et al.* 2014 and *S. longirostris* J Chen *et al.* 2015b, from the Lower Cretaceous Yixian Formation at Huangbanjigou, Beipiao City, Liaoning Province.

Here we report two new genera and species belonging to Procercopidae from mid-Cretaceous Burmese amber, representing the first record of the family from this deposit.

2. Geological setting

Two well-preserved adult specimens (XFY10103 and XFY10104) are derived from amber deposits in the Hukawng Valley of Kachin Province, c. 100 km southwest of the village of Tanai, in northern Myanmar (Yin *et al.* 2018; Fig. 1a) Grimaldi *et al.* (2002) and Ross *et al.* (2010) provided an overview of the amber deposit and its geological settings. The age of Burmese amber had been controversial for a long time, even considered as young as Miocene (Grimaldi *et al.* 2005). The redeposition age of Burmese amber based on the U–Pb dating of zircon crystals was considered to be the earliest Cenomanian (98.79 ± 0.62 Ma; Shi *et al.* 2012). In addition, available data suggest that the age of the Burmese amber was generally assigned to be around the Albian–Cenomanian boundary (Cruickshank & Ko, 2003; Ross *et al.* 2010; Rasnitsyn *et al.* 2016; Mao *et al.* 2018; Smith & Ross, 2018).



Fig. 1. (Colour online) Microphotograph of holotype (XFY10103) of *Paranthoscytina xiai* gen. et sp. nov., from mid-Cretaceous Burmese amber. (a) Lateral-dorsal aspect; (b) lateral-ventral aspect; (c) dorsal aspect; (d) showing details of head structure with three ocelli (white arrows) and pronotum; (e) showing details of pygofer and genitalia; (f) showing details of legs. Scale bars = 2 mm in (a–c); 1 mm in (d); 0.5 mm in (e, f).

Burmese amber harbours probably the most diverse Mesozoic palaeobiota (Ross, 2019). Among all the burmite bioinclusions, fossil insects are highly diverse. The number of species has risen exponentially over the past two decades (Ross, 2019). However, Auchenorrhyncha from Burmese amber are comparatively rare, with most of them belonging to Fulgoromorpha (or planthoppers) (Ross, 2019; Zhang *et al.* 2019). Recently, a few species of the infra-order Cicadomorpha (Cicadellidae, Sinoalidae and Tettigarctidae) have been reported from Burmese amber (Chen *et al.* 2018, 2019; Poinar & Brown, 2017; Fu *et al.* 2019; Wang *et al.* 2019).

3. Material and methods

Two well-preserved adult specimens (XFY10103 and XFY10104) are preserved in two clear yellowish amber pieces. The specimen XFY10104 also contains a thrip (Thysanoptera). Observations were made using an Olympus SZX7 microscope. Photographs were taken using a digital camera attached to a Zeiss Discovery V16 microscope; stacked using Helicon Focus 6 software; line drawings were drafted with CorelDraw X7 and Adobe Illustrator CC 2018 graphic software. The invert function in Photoshop CS6 software was used to invert colours of specimen images to show certain details more clearly. These specimens are deposited in the Lingpoge Amber Museum in Shanghai, China (Director: Fanguan Xia).

Wing venation terminology and cell nomenclature follow Bourgoïn *et al.* (2015) and Nel *et al.* (2012). The following standards were used for measurements: body length measured from the apex of the vertex to the apex of the abdomen; body width measured at the widest part of the abdomen; tegmen length

measured from the base to the apex of the tegmen; tegmen width measured at the widest part of the tegmen from costal margin to posterior margin. All measurements are presented in millimetres. The nomenclatural acts established herein are registered under Zoo-Bank LSID urn:lsid:zoobank.org:pub:A75E71C6-E325-4B99-A85F-F88189DC11A4.

4. Systematic palaeontology

Order HEMIPTERA Linnaeus, 1758

Suborder CICADOMORPHA Evans, 1946

Superfamily CERCOPOIDEA Leach, 1815

Family PROCERCOPIDAE Handlirsch, 1906–8

Genus *Paranthoscytina* Fu, Cai & Huang, gen. nov.

Type species Paranthoscytina xiai Fu, Cai & Huang, sp. nov., by original designation and monotypy.

Etymology. The generic name is prefixed *para-*, indicating that the new genus is similar to the genus of Procercopidae, *Anthoscytina* Hong, 1983. Gender: feminine. The genus is registered under LSID urn:lsid:zoobank.org:act:661347c-A497-4F56-B4EB-884F82EA1FAB.

Diagnosis. The new genus is characterized by the following characters: head triangular; pronotum longer than wide, much longer than head, lateral margins bulge outward at mid-length; metatibia with single strong lateral spine; tegmen with large punctation from base to apex, postcostal cell extremely broad, costal margin distinctly convex, veins ScR+R, MP and CuA leaving basal cell at common point, MP branching basal of bifurcation of CuA, a veinlet segmenting median cell, connecting MP₃₊₄ and CuA, cross-vein imp present; hind wing with cross-vein imp present.

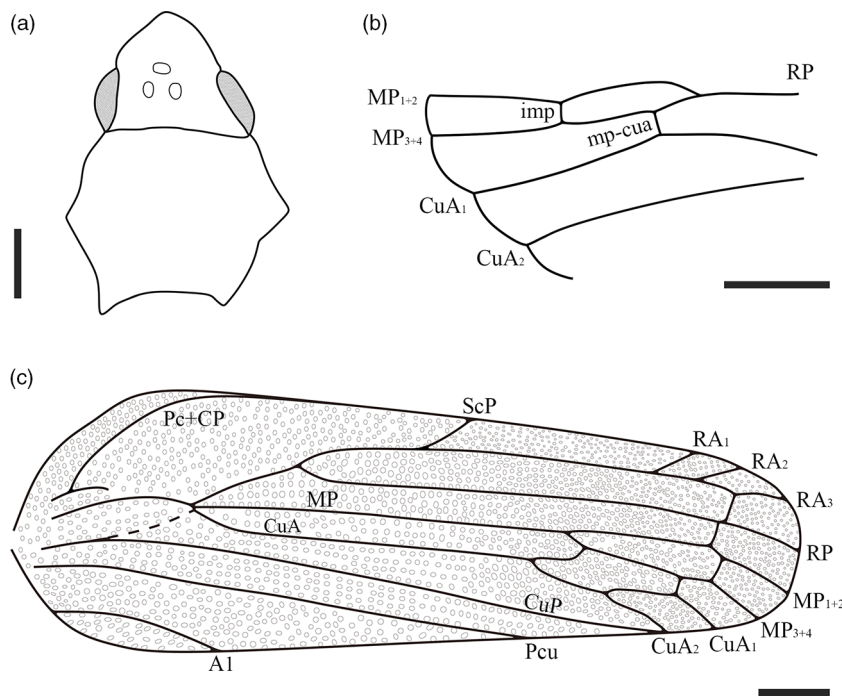


Fig. 2. Line drawings of *Paranthoscytina xiai* gen. et sp. nov. (a) Head and pronotum; (b) hind wing; (c) right tegmen. Scale bars = 1 mm in (a–c).

Remarks. The new genus resembles *Anthoscytina* Hong, 1983 by the metatibia with single lateral spine and several venation characters of tegmen such as radial area narrow, basal portion of ScP not reaching half of basal cell length, RP simple, MP varying from simple to three-branched, hind wing with MP two-branched. However, it differs from the latter by the following characters: (1) head triangular (head rounded apically in *Anthoscytina*); (2) pronotum expanded, much longer than head (pronotum often as long as head in *Anthoscytina*); (3) tegmen with postcostal cell wide, costal margin distinctly convex at one-fifth of tegmen length (postcostal cell relatively narrow, costal margin slightly arched at base in *Anthoscytina*); (4) vein ScR+R, MP and CuA leaving basal cell at common point (stem ScP+R+MP+CuA branching into ScP+R and MP+CuA leaving basal cell in *Anthoscytina*); (5) tegmen with MP branching basal of bifurcation of CuA (MP branching after or at the same level with bifurcation of CuA in *Anthoscytina*); (6) a veinlet segmenting median cell, connecting MP_{3+4} and CuA, and cross-vein imp present (the veinlet and imp absent in *Anthoscytina*); and (7) hind wing with cross-vein imp present (imp absent in *Anthoscytina*).

Paranthoscytina xiai Fu, Cai & Huang, gen. et sp. nov.

Etymology. The specific epithet is dedicated to Mr Fangyuan Xia, for his contribution to the study of this amber specimen. The species is registered under LSID [urn:lsid:zoobank.org:act:60020852-919C-472F-B611-41C975D734FD](https://zoobank.org/act:60020852-919C-472F-B611-41C975D734FD).

Holotype. XFY10103, male, deposited in the Lingpoge Amber Museum in Shanghai, China.

Locality and Horizon. Burmese amber, from deposits near Tanai village in the Hukawng Valley of northern Myanmar. Late Albanian.

Diagnosis. As for genus (see above) with some additional characters: body length c. 15 mm; tegmen with vein RA three-branched, RP single-branched; hind wing with MP two-branched.

Description. Body covered with punctures, length (including wings in repose) c. 15.2 mm (Fig. 1a, b, c); tegmen 11.6 mm long and 4.1 mm wide.

Head triangular (Figs 1d, 2a), c. 2.0 mm long and 2.5 mm wide from dorsal view; crown produced anteriorly; compound eye large, ovoid, located laterally; three ocelli on crown (Fig. 1d), with distance between lateral ocelli shorter than distance between ocellus and compound eye; median ocellus ovoid, lateral ocelli globular; postclypeus bulging, with distinct transverse grooves; rostrum obscure. Pronotum greatly expanded (Figs 1d, 2a), irregularly hexagonal, nearly 1.3 times as wide as head and 1.4 times as long as head; anterior margin straight; posterior margin slightly concave at middle length; lateral margins bulge outward at middle length. Mesonotum partly exposed, with mesoscutellum triangular, wider than long.

Tegmen (Fig. 2c) distinctly exceeds the tip of abdomen, length/width ratio c. 2.8, broadest at 0.17 of tegmen length, with large punctures from base to apex, densely covered with piliferous granules; costal margin thickened, convex at about basal 0.17 tegmen length; postcostal cell wide; basal cell nearly 0.22 times as long as tegmen length; basal portion of ScP slightly shifted from stem R+MP+CuA, not reaching half of basal cell length; Pc+CP partly visible; stem ScP+R branching into ScP+RA and RP reaching 0.36 of tegmen length; ScP+RA slightly longer than ScP+R, branching into ScP and RA slightly after mid-point of wing, distinctly basal of MP branching; RA with three terminals, connecting to RP by cross-vein ir; RP single-branched, straight, connected to MP_{1+2} by cross-vein rp-mp, slightly basal of ir; MP straight, with two branches, branching into MP_{1+2} and MP_{3+4} distinctly basal of bifurcation of CuA, reaching 0.70 of tegmen length; cross-vein imp present, nearly at same level as ir; CuA curved anteriorly, branching into CuA_1 and CuA_2 at same level as Pcu termination, reaching 0.76 of tegmen length; CuA emitting a veinlet at 0.70 of tegmen length, nearly straight at base and arched upward, connecting MP_{3+4} segmenting median cell; cross-vein mp-cua straight and short, connecting MP_{3+4} and CuA_1 ; CuP almost straight, terminating just basal of CuA_2 termination; Pcu almost straight, ending slightly after mid-point of wing, proximally well separated from A1; A1 arcuate. Hind wing partly visible (Fig. 2b); cross-vein

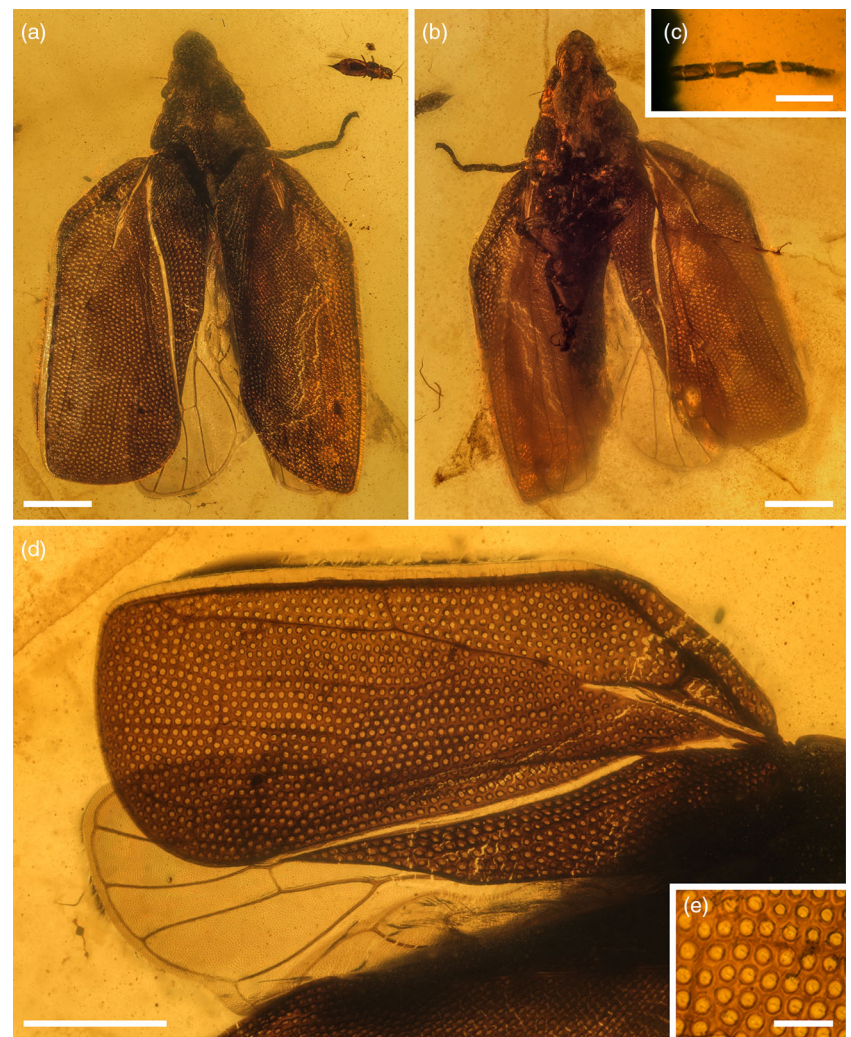


Fig. 3. (Colour online) Microphotograph of holotype (XFY10104) of *Burmocercopsis lingpogensis* gen. et sp. nov., from mid-Cretaceous Burmese amber. (a) Dorsal aspect; (b) ventral aspect; (c) showing details of antenna; (d) showing details of forewing and hind wing; (e) showing details of punctate. Scale bars = 1 mm in (a, b, d); 0.2 mm in (e); 0.1 mm in (c).

imp present; MP with two branches, connecting to CuA_1 by cross-vein mp-cua; CuA with two branches.

Leg covered with dense setae (Fig. 1f); profemur robust; protibia much more slender than profemur, c. 1.7 mm long, nearly twice as long as protarsus; metacoxae enlarged; metatrochanter cylindrical in shape; mesocoxa without a triangular meron, mesofemur c. 1.0 mm long and 0.41 mm wide; mesotibia nearly as long as protibia; mesotarsus slightly longer than protarsus, pretarsal claw sharp apically, arolium present; metafemur almost 1.3 times as long as mesofemur; metatibia almost 1.2 times as long as mesotibia, with a lateral spine (Fig. 1f), distinctly widened apically, armed with two rows of tiny teeth; tarsi trimerous, metatarsus almost 1.3 times as long as mesotarsus, widened apically, basal and second tarsomeres armed with two rows of apical teeth, teeth of apical row with subapical setae.

Abdomen tapered, segments II to VIII becoming successively narrower; genital valve and genital plates unclear; genital styles elongate, distinctly exceeding apex of pygofer; anal style exposed, relatively long (Fig. 1e).

Genus *Burmocercopsis* Fu, Cai & Huang gen. nov.

Type species. *Burmocercopsis lingpogensis* Fu, Cai & Huang, sp. nov., by original designation and monotypy.

Etymology. The name is a combination of the specimen's collection locality Burma (former name of Myanmar), and 'Cercopis',

the type genus of the superfamily Cercopoidea. Gender: masculine. The genus is registered under LSID urn:lsid:zoobank.org:act:E15AE53B-D24C-48D5-B6BE-F508BD249503.

Diagnosis. The new genus is characterized by the following characters: head relatively long, strongly produced anteriorly; antennal flagellum with at least six elongate flagellomeres; pronotum with posterior margin strongly convex at middle portion, arcuately W-shaped; mesonotum greatly concealed; metatibia without lateral spine; tip of tegmen truncated; tegmen covered with large punctate from base to apex, basal cell lance-shaped, with a short common stalk of MP+CuA closing it apically, base of CuA zigzagged, hypocostal carinae present, MP branching distinctly basal of bifurcation of CuA.

Remarks. The new genus differs distinctly from other known genera in Procercopidae by: (1) head strongly produced anteriorly (head relatively rounded apically in other genera); (2) specialized pronotum with posterior margin strongly convex, W-shaped (posterior margin of pronotum nearly straight or slightly concave at mid-length in other genera); (3) tegmen with ScP+R separated, short common stalk of MP+CuA closing basal cell, base of CuA zigzagged (stem ScP+R+MP+CuA branching into ScP+R and MP+CuA leaving basal cell, base of CuA slightly arched in other genera); (4) tip of tegmen truncated (tegmen elongated in other genera).

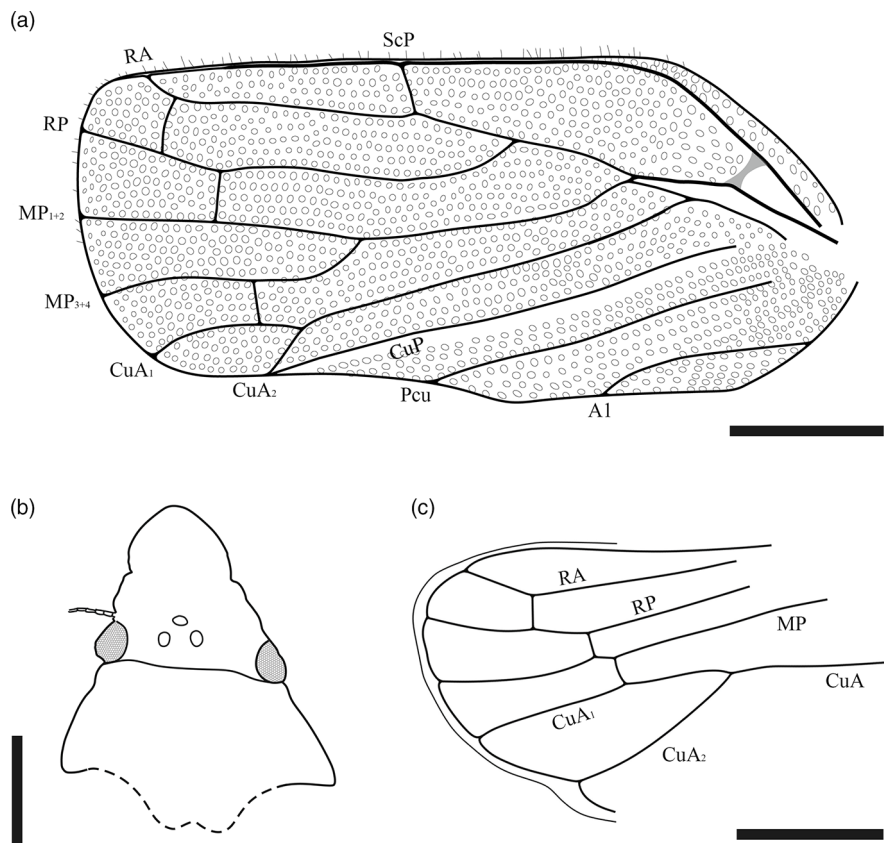


Fig. 4. Line drawings of *Burmoceropsis lingpogensis* gen. et sp. nov. (a) Left tegmen; (b) head and pronotum; (c) hind wing. Scale bars = 1 mm in (a–c).

Burmoceropsis lingpogensis Fu, Cai & Huang, gen. et sp. nov.

Etymology. From 'Lingpoge', indicating the amber is deposited in the Lingpoge Amber Museum in

Shanghai, China. The species is registered under LSID urn:lsid:zoobank.org:act:5A57C093-8405-4DD3-ACBD-6FA96F365F6E.

Holotype. XFY10104, male, deposited in the Lingpoge Amber Museum in Shanghai, China.

Locality and Horizon. Burmese amber, from deposits near Tanai village in the Hukawng Valley of northern Myanmar. Late Albian.

Diagnosis. As for genus (see above) with some additional characters: body length *c.* 5.2 mm; tegmen with vein RA and RP single-branched; hind wing with RA, RP and MP single-branched.

Description. Body covered with punctures, length (including wings in repose) 6.8 mm (Fig. 3a, b); tegmen 4.9 mm long and 2.2 mm wide.

Head subtriangular (Fig. 4b), 1.5 mm long, and 1.8 mm wide in dorsal view; crown distinctly produced anteriorly; compound eye large, ovoid; antenna partly visible (Fig. 3c); three ocelli on crown, ovoid (Fig. 4b); flagellum with at least six elongate flagellomeres, flagellomeres I–V becoming successively thinner; postclypeus bulging, with distinct transverse grooves, widest at middle; clypeus triangularly elongate; rostrum straight, extending to base of metacoxa, *c.* 1.3 mm long. Pronotum greatly expanded (Fig. 4b), nearly 1.5 times as wide as head, anterior margin nearly straight, posterior margin strongly convex at middle portion; mesonotum shortened.

Tegmen (Figs 3d, 4a) exceeds the tip of abdomen, length/width ratio *c.* 2.2, with large punctures from base to apex, densely covered with piliferous granules (Fig. 3e); costal margin with tiny spines;

postcostal cell wide; basal cell narrow, somewhat lance-shaped, *c.* 1.3 mm long and 0.15 mm wide, with a short common portion of MP+CuA closing it apically; hypocostal carinae wide, sclerotized; Pc+CP extremely long, extending to termination of RA; ScP+R branching into ScP+RA and RP reaching 0.45 of tegmen length; ScP+R slightly longer than ScP+RA; ScP+RA branching into ScP and RA basal of MP branching, reaching 0.58 of tegmen length; RA simple, connecting to RP by cross-vein ir; RP single-branched, connecting to MP₁₊₂ by cross-vein rp-mp; MP with two branches, branching into MP₁₊₂ and MP₃₊₄ distinctly basal of bifurcation of CuA, reaching 0.64 of tegmen length; cross-vein imp absent; CuA with two branches, branching into CuA₁ and CuA₂ reaching 0.71 of tegmen length, CuA₁ arcuate, more than twice as long as CuA₂; cross-vein mp-cua connecting MP₃₊₄ and CuA₁; CuP straight, terminating just basal of CuA₂ termination; Pcu almost straight, ending slightly after mid-point of wing; A1 simple, arcuate. Hind wing with peripheral membrane wide (Figs 3d, 4c); RA simple, connecting to RP by cross-vein ir; MP simple, connecting to CuA₁ by cross vein mp-cua; CuA with two branches.

Protibia more slender than profemur, covered with dense setae, *c.* 1.1 mm long; protarsus 0.47 mm long, pretarsal claw large, sharp apically, arolium obscure; mesofemur robust, 0.68 mm long and 0.24 mm wide; mesotibia slightly longer and wider than protibia; metafemur nearly as long as mesofemur; metatibia without lateral spine, distinctly widened apically, armed with a circle of apical teeth, totally at least 12 in number; metatarsus covered with setae, *c.* 0.50 mm long; tarsi trimerous, first and second tarsomeres armed with some apical, long, stout teeth. Abdomen narrow, tapered.

5. Discussion

The two new genera here described can be tentatively placed in the extinct family Procercopidae based on the combination of the following characters: body and tegmen entirely punctate; metatibia without lateral spine or with immovable lateral spine(s) arranged in a single row, no more than three in number; vein MP of tegmen with one to three terminals, branching after mid-length of tegmen; and hind wing with peripheric membrane (Wang *et al.* 2012). However, two new genera share some unique characters previously unknown in Procercopidae, including head produced anteriorly, pronotum greatly extended, mesonotum concealed, tegmen covered with large punctures, and vein MP of tegmen branching basal of bifurcation of CuA.

Paranthoscytina gen. nov. is probably related to *Anthoscytina* Hong, 1983, the largest genus of Procercopidae, reported from the Early Jurassic to the Early Cretaceous of northern Asia. However, some striking features of *Paranthoscytina* differentiate it from other procercopids, including tegmen with postcostal cell extremely broad, broadest near one-fifth of wing length; vein ScR+R, MP and CuA leaving basal cell at common point; a veinlet segmenting median cell; cross-vein imp present; and hind wing with cross-vein imp present. *Burmocercopis* gen. nov. bears the combination of characters also previously unknown in Procercopidae, including posterior margin of pronotum distinctly convex at mid-length, mesonotum greatly concealed; tip of tegmen truncated; ScP+R of tegmen separated, a short common stalk of MP+CuA closing basal cell, and base of CuA zigzagged.

Fossil record of Cercopoidea comprises all families except Machaerotidae from the Mesozoic to Miocene (Szwedo, 2018). Procercopidae was distributed worldwide and flourished in the Jurassic, but the contemporaneous Sinoalidae Wang *et al.* 2012 confined to NE China from the Middle to Late Jurassic. Cretaceous procercopids are relatively rare, including only three genera and seven species from the middle to high latitudes areas of the Northern Hemisphere. Our discovery of two new genera of procercopids from mid-Cretaceous Burmese amber represents the first record of Procercopidae from the Mesozoic amber, which extends the duration for nearly 25 Ma from the Early Cretaceous to mid-Cretaceous. It also represents the first record of procercopids from southern Asia, adding a significant distribution to the family Procercopidae. Additionally, the newly described species also provides important data for our knowledge of the documented palaeodiversity and morphological disparity of Cretaceous procercopids, increasing our understanding of the origin and evolution of the peculiar hemipteran family.

Acknowledgements. This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000, XDB18000000), the National Natural Science Foundation of China (41688103), and the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0706). We thank Mr Fangyuan Xia, Director of the Lingpoge Amber Museum, for his contribution to the study of the amber specimens.

References

- Ansorge J (1996) Insekten aus dem Oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paläontologische Abhandlungen* 2, 1–132.
- Bartlett CR, Deitz LL, Dmitriev DA, Sanborn AF, Soulier-Perkins A and Wallace MS (2018) The diversity of the true hoppers (Hemiptera: Auchenorrhyncha). *Insect Biodiversity: Science & Society* 2, 501–90.
- Bourgoin T, Wang R, Asche M, Hoch H, Soulier-Perkins A, Stroinski A, Yap S and Szwedo J (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology* 134, 63–77.
- Chen D, Yao YZ and Ren D (2015) A new species of fossil Procercopidae (Hemiptera, Cicadomorpha) from the Lower Cretaceous of Northeastern China. *Cretaceous Research* 52, 402–6.
- Chen J, Szwedo J, Wang B, Zheng Y, Wang Y, Wang X and Zhang HC (2018) The first Mesozoic frog hopper in amber from northern Myanmar (Hemiptera, Cercopoidea, Sinoalidae). *Cretaceous Research* 85, 243–9.
- Chen J, Wang B, Zhang HC, Wang XL and Zheng XT (2015b) New fossil Procercopidae (Hemiptera: Cicadomorpha) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *European Journal of Entomology* 112, 373–80.
- Chen J, Wang B, Zheng Y, Jiang H, Jiang T, Zhang JQ and Zhang HC (2019) A new sinoalid frog hopper in mid-Cretaceous Burmese amber, with inference of its phylogenetic position (Hemiptera, Cicadomorpha). *Cretaceous Research* 95, 121–9.
- Chen J, Zhang HC, Wang B, Zheng XT and Wang XL (2015a) High variability in tegminal venation of primitive cercopoids (Hemiptera: Cicadomorpha), as implied by the new discovery of fossils from the Middle Jurassic of China. *Entomological Science* 18, 147–52.
- Cruickshank RD and Ko K (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences* 21, 441–55.
- Dietrich CH (2002) Evolution of Cicadomorpha (Insecta, Hemiptera). *Denisia* 4, 155–70.
- Evans JW (1946) A natural classification of leaf-hoppers (Homoptera, Jassoidea). Part 1. External morphology and systematic position. *Transactions of the Royal Entomological Society of London* 96, 47–60.
- Evans JW (1956) Palaeozoic and Mesozoic Hemiptera (Insecta). *Australian Journal of Zoology* 4, 164–258.
- Fu YZ, Cai CY and Huang DY (2019) First hairy cicadas in mid-Cretaceous amber from northern Myanmar (Hemiptera: Cicadoidea: Tettigarctidae). *Cretaceous Research* 93, 285–91.
- Fu YZ, Huang DY and Engel MS (2018) A new species of the extinct family Procercopidae (Hemiptera: Cercopoidea) from the Jurassic of northeastern China. *Palaeoentomology* 1, 51–7.
- Grimaldi D, Zhang J, Fraser NC and Rasnitsyn A (2005) Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea). *Insect Systematics & Evolution* 36, 443–58.
- Grimaldi DA, Engel MS and Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361, 1–72.
- Hamilton KGA (1992) Lower cretaceous homoptera from the koonwarra fossil bed in Australia, with a new superfamily and synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America* 85, 423–30.
- Hamilton KGA (2001) A new family of froghoppers from the American tropics (Hemiptera: Cercopoidea: Epipygidae). *Biodiversity* 2, 15–21.
- Handlirsch A (1906–8) *Die Fossilen Insekten und die Phylogenie der rezenten Formen: ein Handbuch für Paläontologen und Zoologen*. Leipzig: Engelmann, 1430 pp.
- Hong YC (1982) *Mesozoic fossil insects of Jiuquan basin in Gansu Province*. Beijing: Geological Publishing House, 187 pp. (in Chinese).
- Hong YC (1983) *Middle Jurassic fossil insects in North China*. Beijing: Geological Publishing House, 223 pp. (in Chinese).
- Hu HJ, Yao YZ and Ren D (2014) New fossil Procercopidae (Hemiptera, Cicadomorpha) from the Early Cretaceous of Northeastern China. *Acta Geologica Sinica* 88, 725–9.
- Leach WE (1815) Entomology. In *The Edinburgh Encyclopaedia, Vol. 9, Part 1* (ed. D Brewster). Edinburgh: William Blackburn, 384 pp.
- Linnaeus C (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. **Tomus I**. Editio decima, reformata. Holmiae (= Stockholm): Laurentii Salvii, 824 pp.
- Mao Y, Liang K, Su YT, Li JG, Rao X, Zhang H, Xia FY, Fu YZ, Cai CY and Huang DY (2018) Various amberground marine animals on Burmese amber with discussions on its age. *Palaeoentomology* 1, 91–103.
- Martynov AV (1937) *Liassic insects from Shurab and Kysyl-Kiya. Part I: Various orders except Blattodea and Coleoptera*. Trudy Paleontologicheskogo Instituta, 179 pp. (in Russian).

- Nel A, Prokop J, Nel P, Grandcolas P, Huang DY, Roques P, Guilbert E, Dostál O and Szwedo J** (2012) Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology* **273**, 480–506.
- Poinar GJ and Brown A** (2017) A new genus of leafhoppers (Hemiptera: Cicadellidae) in mid-Cretaceous Myanmar amber. *Historical Biology*, published online 6 October 2017. doi: [10.1080/08912963.2017.1384472](https://doi.org/10.1080/08912963.2017.1384472).
- Rasnitsyn AP, Bashkuev AS, Kopylov DS, Lukashovich ED and Ponomarenko AG** (2016) Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research* **61**, 234–55.
- Ren D** (1995) Systematic palaeontology. Fossil insects. In *Fauna and Stratigraphy of Jurassic–Cretaceous in Beijing and the Adjacent Areas* (eds D Ren, L Lu, Z Guo and S Ji), pp. 47–120. Beijing: Seismic Publishing House (in Chinese with English abstract).
- Ren D, Yin JC and Dou WX** (1998) New planthoppers and froghoppers from the Late Jurassic of northeast China. *Acta Zootaxonomica Sinica* **23**, 281–8.
- Ross AJ** (2019) Burmese (Myanmar) amber checklist and bibliography (2018). *Palaeoentomology* **2**, 22–84.
- Ross AJ, Mellish C, York P and Crighton B** (2010) Burmese amber. In *Biodiversity of Fossils in Amber from the Major World Deposits* (ed. D Penney), pp. 208–35. Manchester: Siri Scientific Press.
- Shcherbakov DE and Popov YA** (2002) Superorder Cimicidea Laicharting, 1781 order Hemiptera Linné (1758) The bugs, cicadas, plantlice, scale insects, etc. In *History of Insects* (eds AP Rasnitsyn and DLJ Quicke), pp. 152–5. Dordrecht: Kluwer.
- Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei WY, Li QL and Li XH** (2012) Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research* **37**, 155–63.
- Smith RDA and Ross AJ** (2018) Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. *Transactions of the Royal Society of Edinburgh: Earth and Environmental Science* **107**, 239–47.
- Szwedo J** (2018) The unity, diversity and conformity of bugs (Hemiptera) through time. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **107**, 109–28.
- Wang B, Szwedo J and Zhang HC** (2012) New Jurassic Cercopoidea from China and their evolutionary significance (Insecta: Hemiptera). *Palaeontology* **55**, 1223–43.
- Wang B and Zhang HC** (2009) A remarkable new genus of Procercopidae (Hemiptera: Cercopoidea) from the Middle Jurassic of China. *Comptes Rendus Palevol* **8**, 389–94.
- Wang XD, Dietrich CH and Zhang YL** (2019) The first fossil Coelidiinae: a new genus and species from mid-Cretaceous Myanmar amber (Hemiptera, Cicadellidae). *Cretaceous Research* **95**, 146–50.
- Yin ZW, Cai CY and Huang DY** (2018) A potentially diverse fauna of spring-tail-hunting scydmaenines during the late Mesozoic (Coleoptera, Staphylinidae, Scydmaeninae). *Cretaceous Research* **90**, 163–7.
- Zhang X, Ren D and Yao YZ** (2019) A new family Jubisentidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea) from the mid-Cretaceous Burmese amber. *Cretaceous Research* **94**, 1–7.