



First record of adult Dorytocidae — *Dorytocus jiaxiaoe* Song, Szwedo & Bourgoin sp. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea) from mid-Cretaceous Kachin amber

Zhi-Shun Song^a, Chen-Ling Zhang^a, Hao-Yuan Xi^a, Jacek Szwedo^{b, *},
Thierry Bourgoin^{c, **}

^a Institute of Insect Resources and Biodiversity, School of Life Sciences, Chemistry & Chemical Engineering, Jiangsu Second Normal University, Nanjing, 210013, China

^b Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, Department of Invertebrate Zoology and Parasitology, University of Gdańsk, 59, Wita Stwosza Street, PL80-308 Gdańsk, Poland

^c Institut Systématique Evolution Biodiversité (ISYEB), UMR 7205 MNHN-CNRS-Sorbonne Université-EPHE-Univ. Antilles, Muséum National D'Histoire Naturelle, 57 Rue Cuvier, CP 50, F-75005, Paris, France

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ABSTRACT

A new species, *Dorytocus jiaxiaoe* Song, Szwedo & Bourgoin sp. nov., from the mid-Cretaceous Burmese amber is described and illustrated. This species represents the first record of the adult of the extinct family Dorytocidae. The supplementary description for the fourth-instar nymph of *Dorytocus ornithorhynchus* Emeljanov & Shcherbakov is provided. The morphological peculiarities of the new fossil species are briefly discussed, and family diagnosis is now based on the combination of both adult and nymph characters.

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1. Introduction

The planthoppers, or Fulgoromorpha, constitute a very diversified unit of some 13 900 species divided into 21 extant families plus 13 fossils ones (Song et al., 2019; Brysz and Szwedo, 2019; Luo et al., 2020b; Bourgoin, 2021). They belong to one of the old hemipteran lineages known from fossils since the Early Permian, some 258 Ma (Shcherbakov, 2002; Szwedo et al., 2004; Szwedo, 2018; Brysz and Szwedo, 2019), while calibration molecular phylogenies estimate now Fulgoromorpha to have separated from other Hemiptera during the Carboniferous (Moscovian: 310 Ma (Johnson et al., 2018)

or Viséan around 335 Ma (Dietrich et al., 2019; Bucher and Bourgoin, 2019 and in prep.). Eleven families are currently already reported from the Cretaceous (Szwedo et al., 2004; Luo et al., 2020b; Bourgoin, 2021), including three extant families: Achilidae (Cockerell, 1917; Hamilton, 1990; Szwedo, 2004), Cixiidae (Fennah, 1987; Martins-Neto, 1989; Ren et al., 1998; Szwedo, 2001; Martins-Neto and Szwedo, 2007), and Dictyopharidae (Emeljanov, 1983); and eight fossil ones: Dorytocidae (Emeljanov and Shcherbakov, 2018), Jubisentidae (Zhang et al., 2019; Shcherbakov, 2020), Katlasidae (Luo et al., 2020b), Lalacidae (Martins-Neto, 1988; Hamilton, 1990; Ren et al., 1995; Zhang, 2002), Mimarachnidae (Shcherbakov, 2007b, 2017; Szwedo, 2008; Szwedo and Ansorge, 2015; Zhang et al., 2018; Jiang T. et al., 2018, 2019, 2020a; Fu et al., 2019; Luo et al., 2020a), Neazoniidae (Szwedo, 2007, 2009), Perforissidae (Shcherbakov, 2007a; Peñalver

* Corresponding author.

** Corresponding author.

E-mail addresses: jacek.szwedo@biol.ug.edu.pl (J. Szwedo), thierry.bourgoin@mnhn.fr (T. Bourgoin).

and Szwedo, 2010; Szwedo et al., 2013; Zhang et al., 2017), and Yetkhatidae (Song et al., 2019).

The extinct family Dorytocidae was described based on nymphs of three different instars (II, III, and V) from mid-Cretaceous Burmese amber (Emeljanov and Shcherbakov, 2018). The dorytocid species exhibit so far, the longest cephalic process in all the extinct planthopper families, which is comparable to the longest “noses” of extant fulgorid (Fulgoridae, e.g. *Pyrops* Spinola, 1839 and *Zanna Kirkaldy*, 1902) or dictyopharid planthoppers (Dictyopharidae, e.g. *Lappida Amyot & Audinet-Serville*, 1843, *Hasta Kirkaldy*, 1906, and *Madagascaritia* Song & Liang, 2016). The shape of this enormous snout, as well as dark-mottled colouration and the carinate dorsum of dorytocid nymphs, was considered masquerading thorn, like some treehoppers, which can hide from predators in the mid-Cretaceous tropical forest while the dorytocids dwelt on the bark of the trees (Emeljanov and Shcherbakov, 2018).

This family is similar to Cretaceous Perforissidae in the structures of the pronotum and abdominal segments IX and X in nymphs, and Dorytocidae have been suggested as “descendants of Perforissidae” and even of the Jurassic Fulgoridiidae (Emeljanov and Shcherbakov, 2018), all belonging to the pre-cixioid group (Shcherbakov, 2007a). The family Fulgoridiidae Handlirsch, 1939 is a paraphyletic assemblage, which needs a full revision, as most of the species reported are based on the tegmen adpressions, the hind wings or body structures are rarely preserved and available for examination (Bourgoin and Szwedo, 2007; Szwedo, 2010; Brysz and Szwedo, 2019). Dorytocidae is somewhat more derived than Perforissidae due to having asetigerous tibial pectens and a ‘modern-looking’ snout (Emeljanov and Shcherbakov, 2018).

While studying samples from Cretaceous Myanmar amber, we discovered the first record of adult Dorytocidae, representing a new species *Dorytocus jiaxiaoe* Song, Szwedo & Bourgoin sp. nov., and the fourth-instar nymph of *D. ornithorhynchus* Emeljanov & Shcherbakov, 2018. The morphological peculiarities of the new fossil species are briefly discussed, and the diagnostic characters of Dorytocidae are suggested and improved based on the combination of characters of adults.

2. Material and methods

The material examined, Burmese amber, comes from deposits in the Hukawng Valley of Myanmar. The mining area is located at Noiye Bum, near Bum, close to Tanai Village (26°21'33.41"N, 96°43'11.88"E; palaeocoordinates 12.4°N, 93.8°E) (Kania et al., 2015; Thu and Zaw, 2017; Westerweel et al., 2019; see the locality in Fig. 1 of Jiang T. et al., 2019). These deposits were investigated and dated in detail by Cruickshank and Ko (2003) and Shi et al. (2012), which currently date the deposit to the earliest Cenomanian (ca. 98.8 ± 0.63 Ma). A slightly older age was postulated (Albian by Ross et al., 2010; late Albian by Zheng et al., 2018; Albian/Cenomanian boundary by Rasnitsyn et al., 2016), due to the fact that the amber show evidence of redeposition (Grimaldi and Ross, 2017; Mao et al., 2018; Smith and Ross, 2018). Over the last 100 years, and particularly in the past two decades, Kachin amber has received worldwide scientific interest; nearly 600 families of invertebrates, vertebrates, protists, plants, and fungi have been reported (Ross, 2019, 2020a, b; Yu et al., 2019). The Burma Terrane was part of a Trans-Tethyan island arc and stood at a near-equatorial southern latitude at about 95 Ma, suggesting island endemism for the Kachin amber biota (Westerweel et al., 2019), but Kachin amber still gives us new insights into the very important period of formation of modern faunistic complexes at mid-Cretaceous biotic re-organization times (Szwedo and Nel, 2015) and they are the ideal materials for studying the Cretaceous

Terrestrial Revolution, which is marked by the radiation of angiosperms, social insects, and early mammals (Lloyd et al., 2008; Yamamoto et al., 2016; Bao et al., 2019; Zhao et al., 2020).

The specimens studied in the course of this work are deposited in Zoological Collection, Jiangsu Second Normal University, Nanjing, China (JSSNU). The piece of amber containing the specimen was cut with a razor blade, polished with sand papers of different grain sizes and diatomite mud, and mounted on transparent plastic slides. Fourier Transformed Infrared Spectra (FT-IR) spectra of the amber specimen (Figs. S1A, B and S2A, B) were obtained at the Jiangsu Key Laboratory of Bifunctional Molecule, JSSNU, with Nicolet iS5 Spectrometer. Spectra were registered with resolution 4 cm⁻¹, baseline correction and advanced ATR correction were applied. Reference curve numbers in the collection archives are stored as registration number of the specimen, with suffix ‘IR’. This procedure must be regarded now as recommended for the museum material, especially holotypes, as proposed by Szwedo and Stroński (2017). It gives spectroscopic characteristics and confirmation of the identity of the tested material, by diagnostic fingerprints at wavenumbers 2929, 2862, 1720, 1458, 1357, 1027 and 972 cm⁻¹ (Kosmowska-Ceranowicz, 2015; Bai et al., 2020; Jiang X. et al., 2020b).

Observations, measurements, photography, and illustrations were conducted under a Leica M205C optical stereomicroscope with a drawing tube and a Canon EOS 5D Mark IV digital camera. Some final images were compiled from multiple photographs using Helicon Focus 6 image stacking software and improved with the Adobe Photoshop CC.

The morphological terminology and measurements used in this study follow mostly Anufriev and Emeljanov (1988), with Bourgoin et al. (2015) for the tegminal venation.

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758
 Infraorder Fulgoromorpha Evans, 1946
 Superfamily Fulgoroidea Latreille, 1807
 Family Dorytocidae Emeljanov & Shcherbakov, 2018
 Dorytocidae Emeljanov and Shcherbakov, 2018: 3

Type genus: *Dorytocus* Emeljanov & Shcherbakov, 2018, by original designation.

Emended diagnosis. The family may be distinguished by the following combination of characters of adults: body medium sized; cephalic process elongate, extremely compressed laterodorsad; vertex narrow in front of anterior margin of pronotum, posterior plane mostly beneath pronotum, median carina absent; frons wider than vertex, intermediate carinae absent, median carina foliaceous and complete; anteclypeus without lateral carinae; compound eyes long oval, mostly below pronotum; pronotum long inverted V-shaped, very high in middle and inclining laterad, anterior central disc covering posterior plane of vertex and extremely produced forwards, far beyond anterior margin of eyes, posterior margin deeply angulately concave, median carinae paired, completely independent, strongly foliaceous; mesonotum with three carinae, lateral carinae sharp, nearly straight and convergent anteriorly; tegmina macropterous and membranous; venation simple, veins reduced and faint; transverse veinlets invisible; costal area narrow, without veinlets; stem ScP+R forked basally, Sc+RA and RP straight and subparallel anteriorly; MP forked at about fourth apex; CuA forked at about fourth base; clavus open; Pcu and A₁ connected to form stem Pcu+A₁ near subapex of clavus, not reaching posterior margin; basal cell large; hindwings large, veins developed and thick, without transverse veinlets; anal area folding inside along A₁,

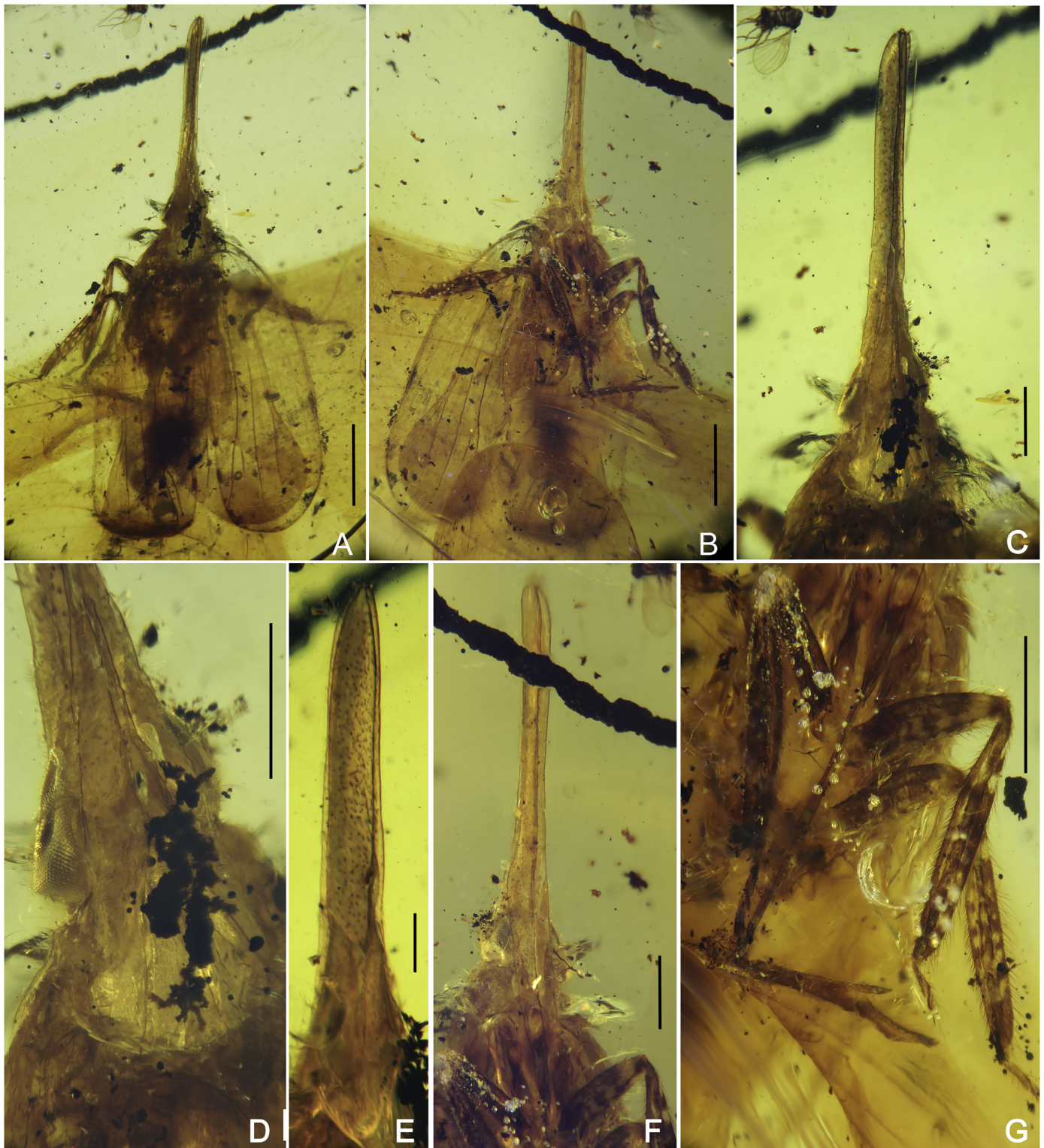


Fig. 1. *Dorytocus jiaxiaoa* sp. nov., holotype (JSSN-2020001; please see the editor correction Figure 1 and 2 captions -JSSNU-2019002-). Note that as per standardization double hyphen will not be retained in the text. Kindly check and advise whether we can retain the text as -JSSNU-2020001- to proceed further. →U-2019002). A, dorsal view; B, ventral view; C, head, pronotum and mesonotum, dorsal view; D, pronotum and mesonotum, dorsal view; E, head, laterodorsal view; F, head, ventral view; G, rostrum, fore and middle legs. Scale bars: 2 mm for A, B, 1 mm for C–G.

A₂ present; fore coxae long, beyond apex of clypeus; fore and middle coxae and femora flattened and dilated, without spine; fore and middle tibiae foliaceous and lanceolate; hind tibiae without lateral spines, apical teeth asetigerous; apical teeth of hind tarsomeres I and II setigerous (with long and thick subapical setae).

Dorytocidae may be distinguished by the following combination of characters of nymphs: median carina of pronotum double; lateral carinae of mesonotum running along posterior margin of pronotum; discs of mesonotum and metanotum with sensory pits; fore and middle tibiae foliaceous; dorsum of abdomen carinate, without

wax-pore plates, with long segments IX and X not retracted between lateral lobes of segment VIII (modified after Emeljanov and Shcherbakov 2018).

Diversity and distribution. Dorytociidae is an extinct Fulgoroidea family and comprises one genus *Dorytocus* Emeljanov & Shcherbakov, 2018, known so far from mid-Cretaceous Burmese amber inclusions.

Genus ***Dorytocus*** Emeljanov & Shcherbakov, 2018

Dorytocus Emeljanov and Shcherbakov, 2018: 3.

Type species: *Dorytocus ornithorhynchus* Emeljanov & Shcherbakov (2018), by original designation.

Diagnostic characters. Diagnostic characters of the genus may refer to familial diagnosis above for adult and nymph.

Diversity and distribution. The genus *Dorytocus* is now comprised of two species, including *Dorytocus jiaxiaoe* Song, Szwedo & Bourgoin sp. nov. in this study, all known so far from mid-Cretaceous Burmese amber inclusions.

Remarks. *Dorytocus* was erected by Emeljanov and Shcherbakov (2018) based on nymphs of three different instars (II, III, and V) of *D. ornithorhynchus* from mid-Cretaceous Burmese amber. We first describe and illustrate the adult dorytociids based on the new species *D. jiaxiaoe* sp. nov.

Key to the species of *Dorytocus*.

1. Cephalic process very elongate, length from anterior margin of eyes to apex nearly five times longer than longitudinal length of eyes.....
..... *Dorytocus jiaxiaoe* Song, Szwedo & Bourgoin sp. nov.
- Cephalic process relatively short, length from anterior margin of eyes to apex no more than four times longer than longitudinal length of eyes.....
..... *Dorytocus ornithorhynchus* Emeljanov & Shcherbakov

Dorytocus jiaxiaoe Song, Szwedo & Bourgoin sp. nov. (Figs 1, 2)
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Diagnosis. The new species may be distinguished from *D. ornithorhynchus* by the longer head which is extremely elongate, more than twice longer than pronotum and mesonotum combined.

Description. Total length (from tip of tegmina to apex of head) 12.74 mm; body length (excluding tegmina) 11.76 mm; head length (from posterior margin of eyes to apex of cephalic process) 5.20 mm, width (including eyes) 0.97 mm; vertex maximum width in front of eyes 0.58 mm and minimum width at apex 0.08 mm; eyes length 0.93 mm; frons length 6.59 mm, maximum width in front of eyes 0.52 mm; tegmina length 7.06 mm, width 2.45 mm.

General colour (Fig. 1A, B) ochraceous. Head with vertex, frons, and clypeus ochraceous, eyes dull ochraceous, rostrum with apex black, lateral surface in front of eyes with numerous small black spots. Pronotum and mesonotum pale ochraceous. Tegmina hyaline, veins reduced and very faint, apical margin and several small patches near terminal CuA fuscous. Hindwings hyaline, apical third brown. Legs fuscous, marked with pale brown; coxa pale brown; femora and tibiae marked with numerous pale brown speckles; tarsi and claws brown; tips of apical spines on hind tibiae and tarsi black. Abdomen mostly dissolved, dorsally and ventrally ochraceous.

Head (Figs 1C–F, 2C, D) extremely compressed laterodorsad, produced anteriorly into an elongate cephalic process, length from posterior margin of eyes to apex more than twice longer than pronotum and mesonotum combined. Cephalic process with dorsal part more compressed laterodorsad than ventral one, so it becomes a very high trapezoid (truncated arrow) in cross section and lateral areas visible laterodorsally in dorsal view (Fig. 1C); lateral area at base separated from preocular area by a longitudinal carina. Vertex (Figs 1C–E, 2C) narrow in front of apex of pronotum; posterior plane broad, mostly beneath pronotum, with lateral carinae distinctly ridged, widest at base, gradually convergent forwards apex of pronotum, then narrowly subparallel and sulcate; posterior margin invisible. Frons (Figs 1F, 2D) narrow and elongate, but compared to vertex, wider; lateral carinae foliaceous, intermediate carinae absent, median carina complete and strongly foliaceous. Postclypeus and anteclypeus cuneate, converging anteriorly, slightly convex medially; lateral and median carinae of postclypeus foliaceous; anteclypeus extremely compressed laterally, without lateral carinae, median carina strongly foliaceous. Rostrum long, basal segment slightly longer than distal one, surpassing middle coxae, distal one reaching to middle of hind femora. Compound eyes long, compressed dorsoventrad, not much projecting laterally, mostly below pronotum. Ocelli indiscernible, perhaps absent. Antennae small, pedicel globose, with several sensory plaque organs.

Pronotum and mesonotum (Fig. 1D) more or less dissolved partly, some margins and carinae invisible. Pronotum (Figs 1D, 2C) long inverted V-shaped, little longer than mesonotum, very high in middle and inclining laterad, covered with sparse long setae; anterior central disc extremely produced forwards and covering posterior plane of vertex and most compound eyes; anterior margin angulately convex at about 30°, far beyond anterior margin of eyes; lateral margin indistinct, uniting with anterior and post-ocular margins; posterior margin deeply angulately concave at about 30°, incision surpassing middle of eyes; intermediate carinae nearly complete and slightly divergent posteriorly; median carinae paired, completely independent, strongly foliaceous and high, and convergent forwards. Mesonotum (Figs 1D, 2C) strongly arched, covered with long setae, with three sharp carinae: lateral carinae nearly straight and convergent anteriorly.

Tegulae present. Tegmina (Fig. 2A, E) macropterous, membranous, hyaline, with numerous long setae on dorsal surface; venation simple, veins reduced and very faint, subparallel; transverse veinlets invisible. Costal margin more or less arched near base, nearly straight posteriorly; costal area narrow, without transverse veinlets; stem ScP+R forked basally, Sc+RA and RP straight and subparallel anteriorly, ScP+RA forked at subapex, RP without branch; MP forked at about fourth apex; CuA forked at about fourth base, CuA₂ forked in middle; clavus open, CuP not reaching posterior margin; claval veins Pcu and A₁ connected to form stem Pcu+A₁ near subapex of clavus, not reaching posterior margin. Basal cell (Fig. 2E) faint, large. Polygonal net of transverse veinlets present at apex, but very faint (Fig. 2A).

Hind wings (Fig. 2B, F) large, membranous and hyaline, with extremely dense short setae on apical third of dorsal surface, making it look coriaceous; veins developed and thick; transverse veinlets absent. ScP+R bifurcated at third apex, branches ScP+RA and RP straightly reaching apical margin; MP without branching; CuA bifurcating CuA₁ and CuA₂ near apical third and posterior to ScP+R; CuP and Pcu unbranched, running close and parallel at their base; anal area folding inside along A₁, A₂ present.

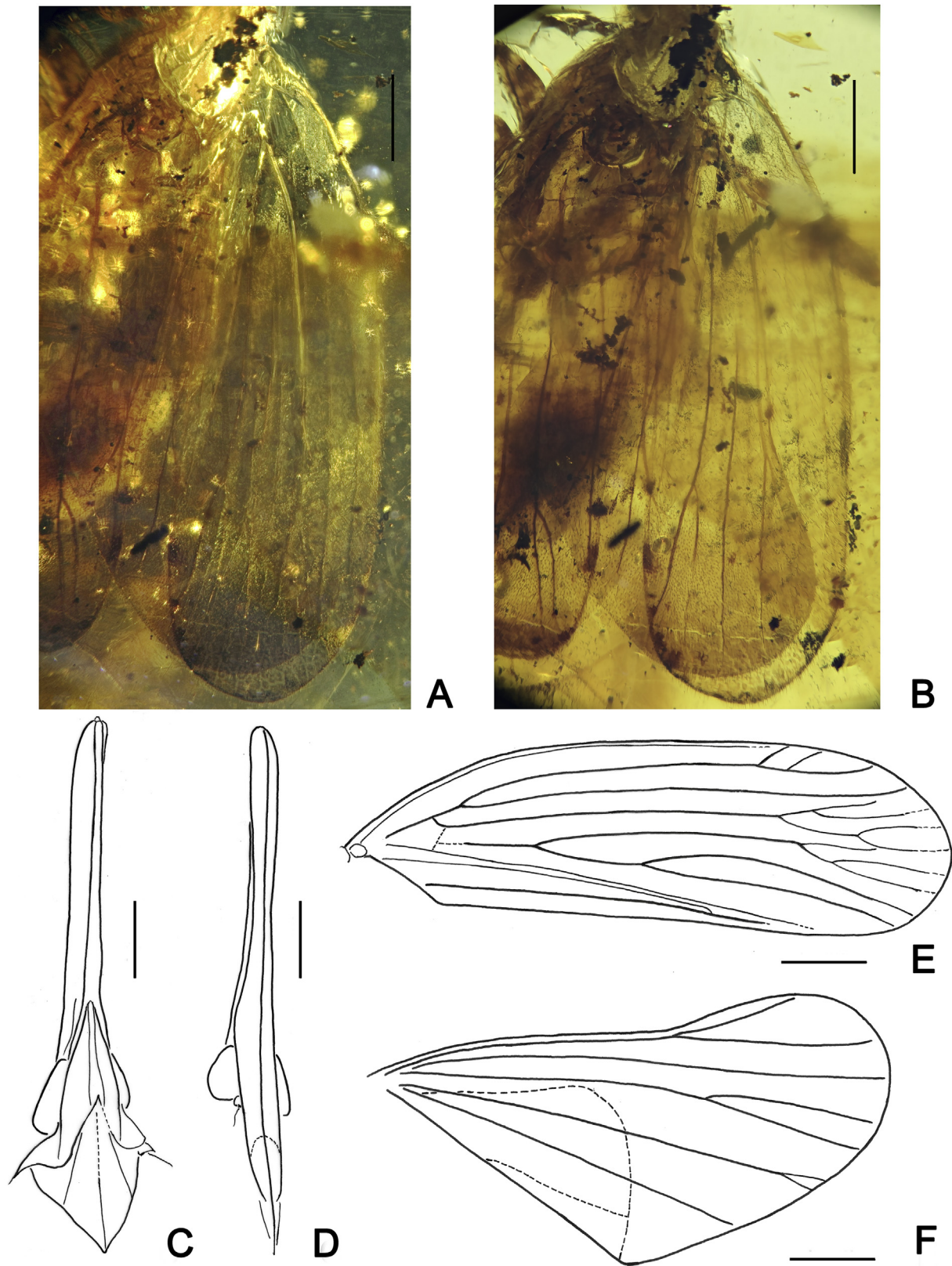


Fig. 2. *Dorytocus jiaxiaoa* sp. nov., holotype (JSSNU-2019002). A, right tegmen and hindwing, dark background; B, right tegmen and hindwing; C, head, pronotum and mesonotum, dorsal view; D, head, ventral view; E, right tegmen; F, right hindwing. Scale bars: 1 mm.

Legs (Fig. 1G) elongate; fore and middle coxae flattened, dilated, and elongate; fore coxae beyond apex of clypeus; fore and middle femora flattened and dilated, without spine; fore and middle tibiae foliaceous and lanceolate; fore and mid tarsi three-segmented. Hind legs mostly missing, a broken hind tibia thin, terete, without lateral spine, apical teeth missing.

Abdomen with genitalia mostly damaged. Sex unknown.

Type material examined. Holotype, a nearly complete specimen (No. JSSNU-2019002), sex unknown because of the abdomen with genitalia mostly damaged, is deposited in Zoological Collection, Jiangsu Second Normal University, Nanjing, China (JSSNU). The piece of amber containing the holotype and eight Diptera specimens was ground and polished to a $20.8 \times 17.8 \times 8.0$ mm compressed cube (Fig. S1C, D). Reference FTIR curves JSSNU-2019002IR (Fig. S1A, B), compared with those published in Kosmowska-Ceranowicz (2015).

Etymology. The new species is named after Ms. Jia Xiao, founder and curator of Longyin Hupo Amber Museum, Kunming, China, who kindly offered the type specimen for this study.

Type locality and stratigraphic horizon. Hukawng Valley, Kachin, Myanmar. Mid-Cretaceous (lowermost Cenomanian).

Remarks. The adult *Dorytocus* sp. specimen exhibits a very long cephalic process constituting more than third of the body length (with wings). It might be conspecific with *D. ornithorhynchus* (Emeljanov and Shcherbakov, 2018), which description was only based on nymphal characters.

Emeljanov and Shcherbakov (2018) stated that each *D. ornithorhynchus* instar (II, III, V) was ca. 1.4 times longer than the previous one, but they could not estimate how long the head would have been in an adult *D. ornithorhynchus*. Based on our observation for *Doryphorina* sp. (Dictyopharidae) which has a very long cephalic process as well, the length of head between the fifth-instar nymph and the adult is not obviously different. Accordingly, the cephalic process of adult *D. ornithorhynchus* is estimated as relatively shorter than in *D. jiaxiaoe* sp. nov., with a length from anterior margin of the eyes to the apex no more than four times longer than the longitudinal length of the eyes, approximately equal to the fifth-instar nymph. *Dorytocus jiaxiaoe* sp. nov. is therefore erected herein as a new species in this study based on the longer cephalic process, as provided in the key above.

Dorytocus jiaxiaoe sp. nov. possesses the longest cephalic process in all known plan topper taxa. Although long cephalic process occur with great disparities in various planthopper families, such as Fulgoridae and Dictyopharidae (Urban and Cryan, 2009; Song et al., 2016, 2018), the elongate head of *D. jiaxiaoe* sp. nov. is obviously different, and also from other Cretaceous planthoppers including *Jaculistilus oligotrichus* Zhang, Ren & Yao (2018) (Mimarachnidae) also recently described from Burmese amber (Zhang et al., 2018).

***Dorytocus ornithorhynchus* Emeljanov & Shcherbakov (2018)** (Figs 3, 4)

Dorytocus ornithorhynchus Emeljanov and Shcherbakov (2018): 4.

Description of instar IV nymph. Total length more than 6.17 mm; head length (from posterior margin of eyes to apex of cephalic process) 2.96 mm, width (including eyes) 0.89 mm; vertex maximum width in front of eyes 0.42 mm and minimum width at apex 0.03 mm; eyes length 0.69 mm; frons length 3.04 mm, maximum width below eyes 0.37 mm; pronotum length in middle (from median incision of posterior margin to anterior margin) 0.81 mm.

General colour (Figs. S3A and B) pale ochraceous. Head with frons, and clypeus dull ochraceous, eyes pale ochraceous, rostrum with apex black, lateral surface in front of eyes dark brown. Thorax dorsally pale ochraceous. Legs fuscous, marked with pale brown; coxa pale brown; femora and tibiae marked with numerous pale brown speckles; tarsi and claws brown; tips of apical spines on hind tibiae and tarsi black. Abdomen dorsally and ventrally pale ochraceous, mottled with dark brown.

Most morphological characters similar to instar V. Body strongly convex in thorax, which suggests the specimen maybe close to molting stage. Cephalic process (Fig. 3B) similar to instar V, narrow and elongate, length from anterior margin of eyes to apex about 3.6 times longer than longitudinal length of eyes, which the proportion is slightly less than instar V (nearly four times longer than longitudinal length of eyes). Vertex (Fig. 3A, B) narrow in front of apex of pronotum; lateral carinae ridged, widest at base, gradually convergent forwards, narrowly sub-parallel in front of apex of pronotum; median carina present at basal two thirds. Frons (Fig. 4A–C) narrow and elongate, but wider than vertex; lateral carinae foliaceous, area between lateral carinae with median carina strongly convex and median carina extremely foliaceous; about 25 sensory pits of two longitudinal rows between lateral and median carinae from base to apex except an oval area on subapical area. Postclypeus and anteclypeus cuneate, converging anteriorly, slightly convex medially; lateral and median carinae of postclypeus foliaceous; anteclypeus extremely compressed laterally, without lateral carinae, median carina strongly foliaceous. Rostrum long, basal segment slightly longer than distal one, surpassing middle coxae; distal one reaching abdominal segment VII. Compound eyes (Figs 3F, 4C) compressed dorsoventrad, projecting laterally. Antennae (Fig. 3E) small, pedicel globose, sensory plaque organs discernible.

Pronotum (Fig. 3B, D, F) long inverted V-shaped, strongly convex, very high in middle and inclining laterad; anterior margin angulately produced at about 30° , far beyond anterior margin of eyes, apex distinctly incurved ventrad; jugal carinae (Emeljanov and Shcherbakov, 2018) distinct; posterior margin deeply angulately concave at about 30° , incision reaching anterior margin of eyes, uniting median carinae forwards; median carinae paired, completely independent, an additional carina between median carinae from base to apex which it is the real ecdysial line. Disc with about 24 sensory pits varying in size between median carinae and jugal carinae: 12 big pits along median carinae and posterior margin, and 12 pits varying in size along jugal carinae; four big pits along outer margin of paranotal lobes. Mesonotum (Fig. 3C) strongly arched, tegmina pads slightly beyond posterior margin of metanotum, much shorter than hind wing pads; about ten sensory pits varying in size between median carina and lateral carinae; five pits outside lateral carinae; four big pits along outer margin of tegmen pads. Metanotum (Fig. 3C) strongly arched, hind wing pads reaching middle of tergite III; five pits (three small pits in anterior row and two ones posteriorly) in discal area and three pits on hind wing pads.

Legs (Fig. 4D, E) similar to instar V, fore and middle coxae long, flattened and dilated, and long; fore coxae far beyond apex of clypeus; fore and middle femora flattened and dilated, without spine; fore and middle tibiae foliaceous and lanceolate; fore and mid tarsi two-segmented, tarsomere II more than twice longer than tarsomere I. Hind tibiae (Fig. 4E, F) thin, terete, without lateral spine, with six asetigerous apical teeth. Hind tarsomeres missing.

Abdomen (Fig. 4G) nine-segmented, not ten mentioned by Emeljanov and Shcherbakov (2018); distinctly arched dorsad, and tapered posteriorly from segment III. Tergites I–VIII (the remaining missing) foliaceous laterally; median carina sharp and high,

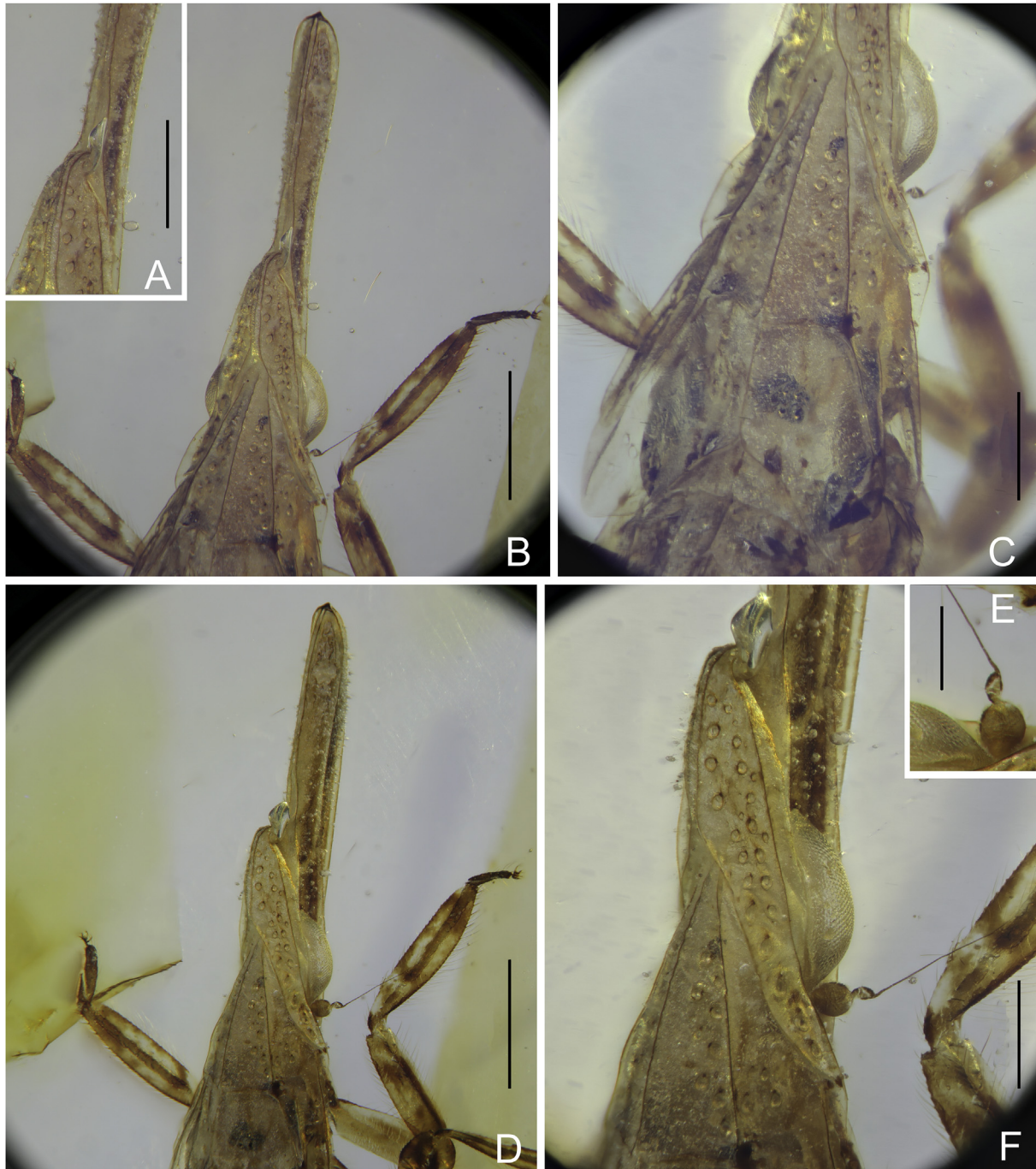


Fig. 3. *Dorytocus ornithorhynchus*, fourth-instar nymph (JSSNU-2020001). A, apex of pronotum; B, head, pronotum and mesonotum, dorsal view; C, mesonotum and metanotum; D, head, pronotum and mesonotum, dorsolateral view; E, antenna; F, pronotum and mesonotum, lateral view. Scale bars: 0.5 mm for A, C, F; 1 mm for B, D; 0.2 mm for E.

intermediate carinae distinct, lateral carinae obscure. Tergites II–VII with one small pit between median carina and intermediate carinae, and two to three lateral pits. Wax-secreting plates absent.

Material examined. A nearly complete specimen (No. JSSNU-2020001), gender unknown, is deposited in Zoological Collection, JSSNU. The piece of amber containing the specimen was ground and

polished to a $19.0 \times 8.6 \times 4.5$ mm compressed cube (Fig. S2C, D). Reference FTIR curves JSSNU-2020001IR (Fig. S2A, B, C).

Remarks. Descriptions of the sensory pits of *D. ornithorhynchus* are mainly based on the second and third instars nymphs because the holotype, a fifth-instar nymph is less well preserved. We here supplement some descriptions based on our fourth-instar specimen.



Fig. 4. *Dorytocus ornithorhynchus*, fourth-instar nymph (JSSNU-2020001). A, apex of head, ventral view; B, head, ventral view; C, base of head, ventral view; D, fore and middle legs; E, rostrum, hind legs. F, abdomen, caudal view; G, abdomen, dorsal view. Scale bars: 0.5 mm for A, C–G; 1 mm for B.

4. Discussion

Seven plesiomorphies and four apomorphies for Dorytocidae were suggested by Emeljanov and Shcherbakov (2018). The new species *Dorytocus jiaxiaoa* sp. nov. represents the first report of the adult Dorytocidae in the mid-Cretaceous amber of Myanmar. It provides more diagnostic characters for this family and will allow in the future easier and further comparative analyses with the other planthopper families. The adult Dorytocidae can be separated from most fossil and extant planthopper families by the extremely produced pronotum which is long inverted V-shaped, covering posterior plane of vertex and eyes; the paired median carinae of pronotum; the tegmina having simple, reduced and faint veins which they have little with few branches; the missing transverse veinlets; the elongate fore coxae; and the hind tibiae lacking lateral spine.

The frons exhibits only one primary median carina, similar to most extinct Cretaceous families, e.g., Lalacidae, Mimarachnidae, Perforissidae, and Yetkhatidae, and extant basal 'cixiid-like' families, e.g., Cixiidae and many Delphacidae, which the character of which is considered a plesiomorphic character of Dorytocidae (Emeljanov and Shcherbakov, 2018). The family Jubisentidae newly described from Burmese amber shows intermediate carinae ('lateral carinae' in Zhang et al., 2019) on frons, forming a median area. However, these intermediate carinae of frons remain weak and incomplete (Zhang et al., 2019) and new specimens from Burmese amber, especially nymphs, show that these carinae are absent, implying that Jubisentidae's intermediate carinae on frons may be secondary (Song et al., in prep.). A newly described species *Psilargus anufrievi* Shcherbakov (2020) from mid-Cretaceous Burmese amber, representing a subfamily Psilarginae Shcherbakov, 2020 of Jubisentidae, also supported it (Shcherbakov, 2020). One primary median carina on frons should be herein considered as characteristic of the 'cixiid-like' families.

The pronotum of both nymphs and adults of Dorytocidae is extremely produced forwards and covers the posterior plane of the vertex and the compound eyes. This character is also shared with Perforissidae and Jubisentidae, but the pronotum of Dorytocidae is long inverted V-shaped and more elongate, and its anterior margin is angularly convex at about 45° and far beyond the anterior margin of the eyes. The median carinae of pronotum of adult Dorytocidae is paired, completely independent, and distinctly ridged, like in the nymphs. This character is also present in some Mimarachnidae species (e.g., *Burmissus raunoi* Shcherbakov, 2007a,b and *Jaculistilus oligotrichus*). The shape and double median carinae of the pronotum might be good autapomorphies for Dorytocidae.

In Dorytocidae, the lateral spines of the hind tibiae are absent, and the apical teeth of the hind tarsomeres I and II (hind tarsal pectens) are setigerous, as in two other Cretaceous families Jubisentidae and Perforissidae. The apical teeth of the hind tibiae (hind tibial pectens) are asetigerous, like all extant planthoppers, contrarily to Perforissidae and Jubisentidae (Emeljanov and Shcherbakov, 2018; Zhang et al., 2019).

Like Jubisentidae, Dorytocidae have the long and foliaceous fore and middle legs including coxae, which are considered to contribute to camouflage and mimicry (Emeljanov and Shcherbakov, 2018; Shcherbakov, 2020).

Sensory pits in dorytocid nymphs are present between median carina and lateral carinae on mesonotum, which their arrangement is similar to Perforissidae (Shcherbakov, 2007a,b) and Jubisentidae (Song et al., in prep.).

Considered as belonging to the pre-cixioid group, Dorytocidae were suggested in a gradist vision as "descendants of Perforissidae", being more derived than Perforissidae in having asetigerous tibial

pectens and a modern-looking snout (Emeljanov and Shcherbakov, 2018). More taxa might be found in the future that will be able to enrich or modify the set of diagnostic features of this family.

Diversity of planthoppers in Burma ambers in the Kachin area is quite noticeable (Bourgoin, 2021). They are now represented by Cixiidae (Luo et al., 2021), Dorytocidae, Jubisentidae, Katlasidae, Mimarachnidae, Neazoniidae, Perforissidae and Yetkhatidae. This remarkable diversity currently might be put in relation with the specificity of Kachin area paleoenvironmental and its topographic characteristics as being considered to be an island or an archipelago at this Cretaceous period (Rasnitsyn and Öhm-Kühnle, 2018; Xing et al., 2018; Westerweel et al., 2019; Morley et al., 2020).

5. Conclusion

Dorytocidae is a new example of the great diversity of the planthopper lineages from mid-Cretaceous amber of Myanmar. The taxa of the family present unique combination of characters observed also among various other planthopper families. Fossils, like Dorytocidae point the need of further and deeper morphological investigations at the higher levels of the planthopper classification, to better document and structure the phylogenetic investigations about fossil and extant planthopper taxa.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.104863>.