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## New data on fossil mimarachnids (Hemiptera, Fulgoromorpha, Fulgoroidea) in mid-Cretaceous Burmese amber

YANZHE FU<sup>1,2</sup> & DIYING HUANG<sup>2\*</sup>

<sup>1</sup>University of Chinese Academy of Science, Beijing 100049, China

<sup>2</sup>State Key Laboratory of Palaeobiology and Stratigraphy, Center for Excellence in Life and Palaeoenvironment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

✉ [yzfu@nigpas.ac.cn](mailto:yzfu@nigpas.ac.cn); <https://orcid.org/0000-0002-7819-1703>

✉ [dyhuang@nigpas.ac.cn](mailto:dyhuang@nigpas.ac.cn); <https://orcid.org/0000-0002-5637-4867>

\*Corresponding author.

### Abstract

Mimarachnidae is an extinct planthopper family of the superfamily Fulgoroidea, with ten genera from the Cretaceous of Eurasia. Here, we describe a new genus, *Cretodorus* **gen. nov.** and two new species, *Cretodorus granulatus* **sp. nov.** and *C. angustus* **sp. nov.**, on the basis of four specimens from the mid-Cretaceous amber of northern Myanmar. This remarkable genus can be separated from all other mimarachnids as follows: moderately elongate head, anteriorly protruded pronotum with straight lateral carinae, and unbranched MP of tegmen. Additionally, a new species of *Burmissus* Shcherbakov, 2017, *Burmissus latimaculatus* **sp. nov.**, is described from the same Burmese amber, and the morphological characters of *Burmissus szwedoi* Luo, Jiang, Wang & Xiao, 2020 are supplemented for pronotum, clypeus, rostrum, and legs. These new discoveries enrich the palaeodiversity of mimarachnid planthoppers to fifteen species, ten of which are described from the mid-Cretaceous Burmese amber, suggesting that this extinct family remained highly diverse during this period.

**Keywords:** Mimarachnidae, *Cretodorus* **gen. nov.**, *Burmissus*, Mesozoic, Myanmar

### Introduction

The hemipteran lineage Fulgoromorpha (planthoppers) is a group of diverse phytophagous insects, recorded since the early Permian (Shcherbakov & Popov, 2002; Szwedo *et al.*, 2004; Szwedo, 2018). This infraorder includes Permian Coleoscytoidea Martynov, 1935 (Coleoscytidae Martynov, 1935); Permian and Triassic Suriokocixioidea Shcherbakov, 2000 (Suriokocixiidae Shcherbakov, 2000); and Fulgoroidea Latreille, 1807, known since the Jurassic, currently comprising 21 extant and 11 extinct families (Szwedo, 2018; Bourgoïn, 2020).

Cretaceous planthoppers are distributed among three extant families (Cixiidae Spinola, 1839, Achilidae Stål, 1866, and Dictyopharidae Emeljanov, 1983) and eight extinct families (Lalacidae Hamilton, 1990, Neazoniidae Szwedo, 2007, Perforissidae Shcherbakov, 2007a, Mimarachnidae Shcherbakov, 2007b, Dorytocidae Emeljanov & Shcherbakov, 2018, Jubisentidae Zhang, Ren & Yao, 2019, Yetkhatidae Song, Szwedo & Bourgoïn, 2019, and Katlasidae Luo, Jiang & Szwedo, 2020) (Szwedo, 2018; Song *et al.*, 2019; Bourgoïn, 2020). The well-preserved fossil material from the Cretaceous provides a chance to explore the relationships and early evolution of the ‘cixiid-like’ group.

The extinct Fulgoromorpha family Mimarachnidae, one of the so called ‘cixiid-like’ groups, is considered to be the earliest recognized spider-mimic planthoppers because of the spider-like dark silhouette and black eyespots with pupils on tegmina (Shcherbakov, 2007b; Bourgoïn & Szwedo, 2008; Szwedo & Ansoerge, 2015). Mimarachnidae currently comprise ten genera from the Early Cretaceous through mid-Cretaceous of Japan, Russia, Spain, and Myanmar, with poorly known relationships (Fujiyama, 1978; Shcherbakov, 2007b; Szwedo, 2008; Szwedo & Ansoerge, 2015; Shcherbakov, 2017; Zhang *et al.*, 2018; Jiang *et al.*, 2018, 2019). They include *Nipponoridium* Fujiyama, 1978, *Mimarachne* Shcherbakov, 2007b, *Saltissus* Shcherbakov, 2007b, *Mimamontsecia* Szwedo & Ansoerge, 2015, *Chaloricidulum* Szwedo & Ansoerge, 2015, *Burmissus* Shcherbakov, 2017, *Dachibangus* Jiang, Szwedo & Wang, 2018, *Jaculistilus* Zhang, Ren & Yao, 2018, *Mimaplax* Jiang, Szwedo & Wang, 2019, and *Ayaimatum* Jiang & Szwedo, 2020.

Herein, we report a new genus with two species, and a new species of *Burmissus* preserved in Burmese amber from Kachin.

## Material and methods

The six planthopper specimens described herein come from the Hukawng Valley of Kachin Province in northern Myanmar (locality as indicated in Yin *et al.*, 2018: figure 1A). The Burmese amber preserves the most diverse Cretaceous terrestrial palaeobiota with over one thousand species recorded to date (Ross, 2019, 2020). Its age was commonly assigned to be around the Albian–Cenomanian boundary (Cruickshank & Ko, 2003; Ross *et al.*, 2010; Shi *et al.*, 2012; Rasnitsyn *et al.*, 2016; Mao *et al.*, 2018; Smith & Ross, 2018).

The amber pieces containing the inclusions were cut, shaped, and polished manually, as described in Azar *et al.* (2003) and Sidorchuk & Vorontsov (2018). Photographs were taken with a Zeiss AxioZoom V16 stereoscope. Epifluorescence images were captured with the Zeiss Axio Imager 2 light microscope combined with a fluorescence imaging system. Helicon Focus 6 software packages were utilized for stacking and processing the different images. Line drawings were drafted with Adobe Illustrator CC 2018 graphic software. The material studied here is deposited in the Nanjing Institute of Geology and Palaeontology (NIGPAS), Chinese Academy of Sciences, Nanjing, China.

The venational nomenclature follows the proposals presented by Nel *et al.* (2012) and Bourgoïn *et al.* (2015). Measurements are taken as maximum distances across structures. Vein abbreviation: ScP, subcosta posterior; Pc+CP, precosta + costa posterior; ScP+R, subcostal posterior + radius; RA, radius anterior branch; RP, radius posterior branch; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; Pcu, postcubitus; A1, first anal vein.

## Systematic palaeontology

### Order Hemiptera Linnaeus, 1758

### Suborder Fulgoromorpha Evans, 1946

### Superfamily Fulgoroidea Latreille, 1807

### Family Mimarachnidae Shcherbakov, 2007b

### Genus *Burmissus* Shcherbakov, 2017

**Type species.** *Burmissus raunoi* Shcherbakov, 2017; by original designation.

*Burmissus szwedoi* Luo, Jiang, Wang & Xiao, 2020 (Fig. 1)

**Material.** NIGP173208, adult male, embedded in a piece of transparent yellowish amber.

**Type locality and horizon.** Amber mine located near

Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, northern Myanmar; mid-Cretaceous.

**Remarks.** *Burmissus szwedoi* was described on the basis of a single incomplete specimen with ventral characters of head invisible, pronotum almost completely blocked, and legs missing (Luo *et al.*, 2020). Herein we provide more detailed morphological characters of *B. szwedoi* based on an amber specimen from Myanmar. It is reasonable to assign these two specimens to the same species (*B. szwedoi*) based on a series of characters, including identical size, venation and color pattern of tegmina, and head, mesonotum structures.

The original description in Luo *et al.* (2020) indicated that Pc+CP submerged to margin at nearly 2/3 of the tegmen length, and the line drawings (figures 1B, 3A of Luo *et al.*, 2020) showed that Pc+CP submerged to margin at about 0.56 of the tegmen length. But it is in fact almost extending to the apex of ScP+RA by examined the type specimen (NIGP172207). Additionally, the basal cross vein mp-cua represented by dashed in the line drawing (figure 3A of Luo *et al.*, 2020) actually is not a vein. Tapered posterior angle of pronotum about 60° probably is due to the fact that difference of three-dimensional angle of amber. It should not be regarded as a diagnostic character.

**Supplemental description.** Head with clypeus punctate, postclypeus with distinct median carina, length 2.67 mm and width 3.75 mm; anteclypeus narrow and elongate; rostrum extended to apex of abdomen. Pronotum sub-hexagonal, punctate, length 1.32 mm and width 3.85 mm; widest at posterolateral lateral angle; anterior margin sinuous, anterolateral margin with dark strips, length about 1.4× as long as posterolateral margin; posterior margin concave medially, widely W-shaped; anterolateral angle roundly wide; posterolateral angle 70–85°; median carinae paired, reaching anterior margin and posterior margin; two lateral carinae strongly arcuate; middle transverse furrows between median- and lateral carinae. Metatibia distinctly widened apically, armed with row of five apical teeth; metatarsus with tarsomeres length (in mm): 1.77/0.65/0.75, basi- and midtarsomere widened apically, each with row of five apical teeth.

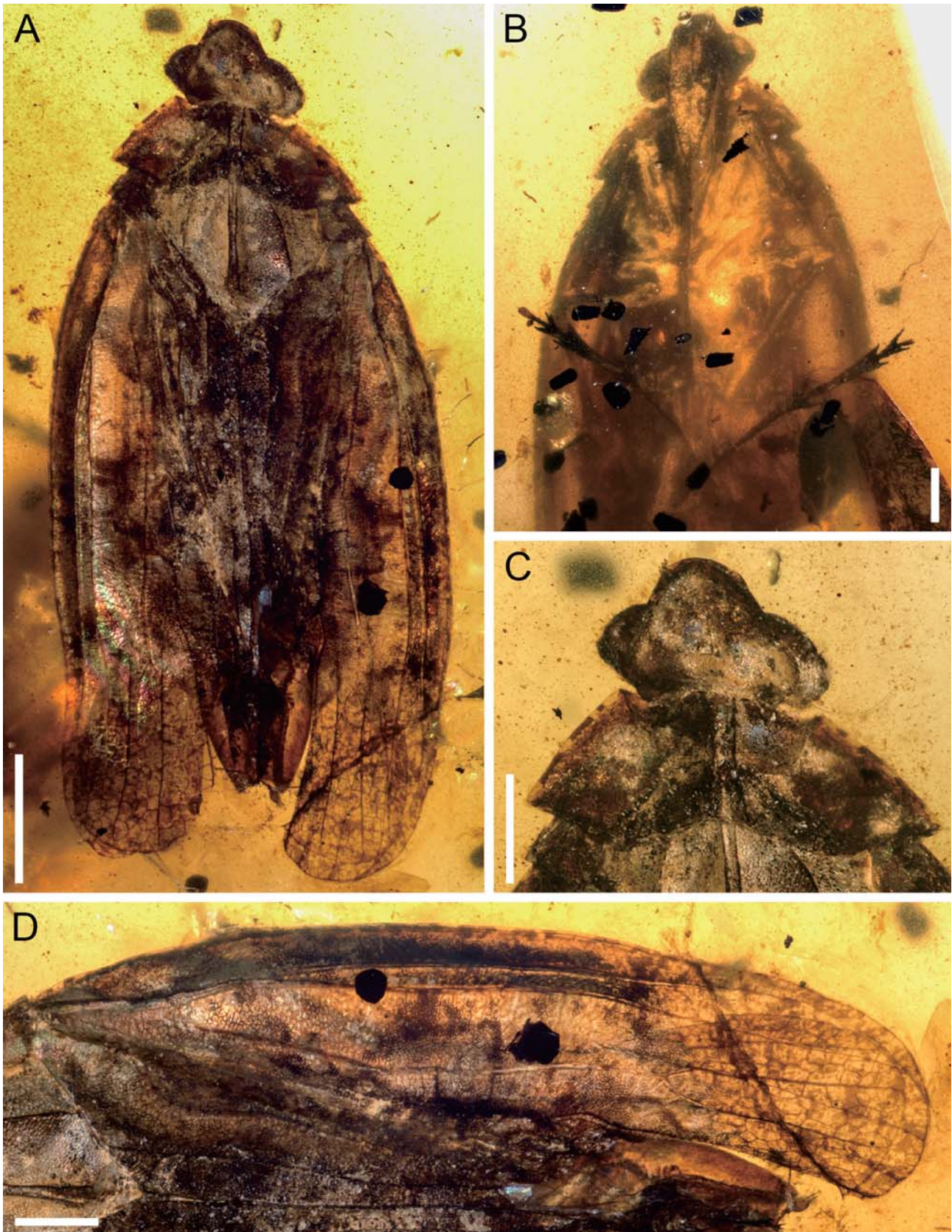
### *Burmissus latimaculatus* sp. nov.

(Fig. 2)

**Material.** Holotype, NIGP172396, embedded in a piece of transparent yellowish amber; inclusion incomplete: ventral characters of head capsule, legs, and abdomen missing, gender unknown.

**Etymology.** The specific epithet refers to the wide range of dark color bands on tegmen.

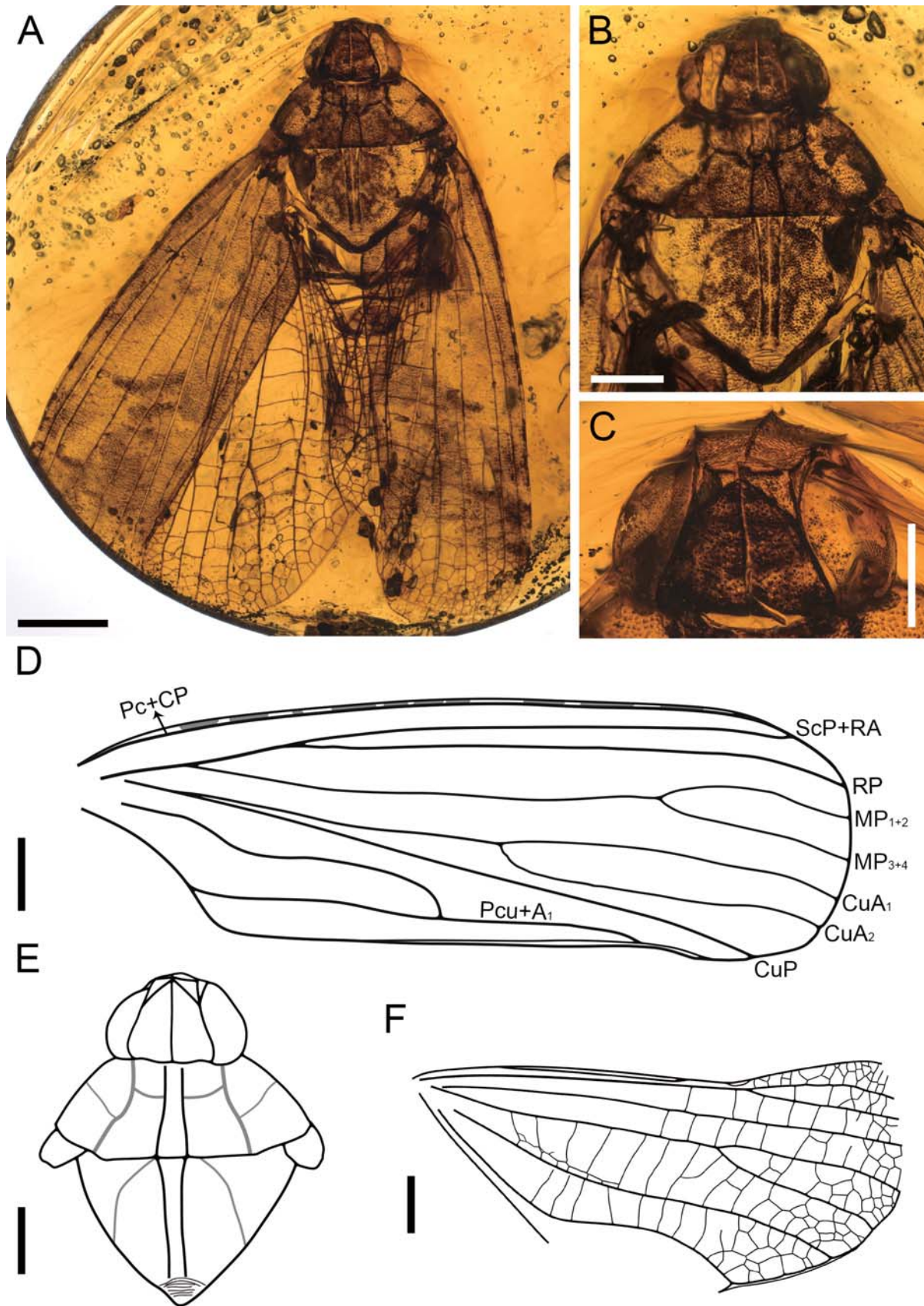
**Diagnosis.** Head rounded, frons with median carina,



**FIGURE 1.** *Burmissus szwedoi* (NIGP173208). **A**, General habitus in dorsal view. **B**, General habitus in ventral view. **C**, Head and pronotum in dorsal view. **D**, Left tegmen. (Scale bars = 2 mm in **A**; 1 mm in **B–D**).

anterior margin of compound eyes almost reaching vertex; pronotum with posterior margin straight, lateral

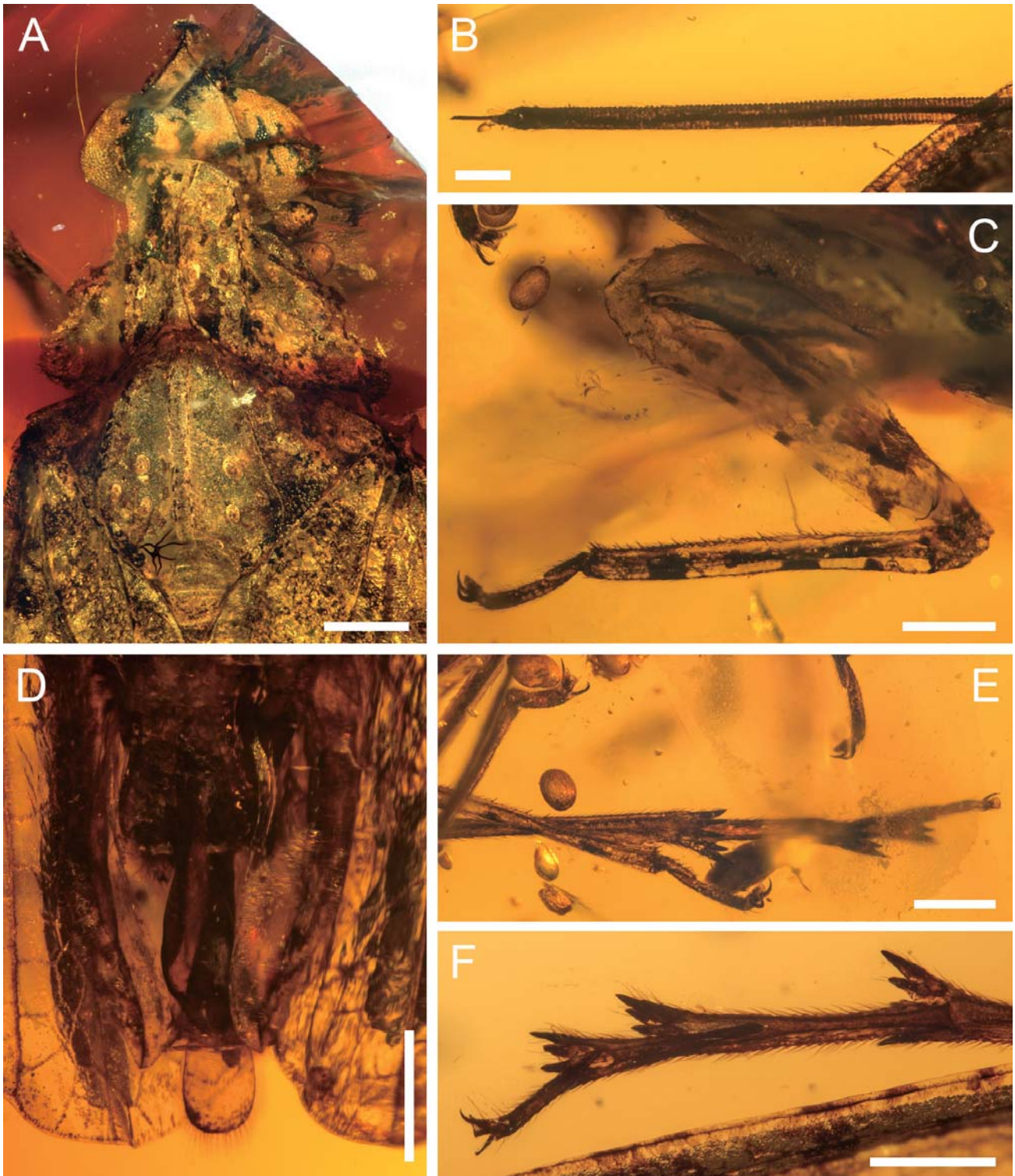
furrows present; mesonotum with doubled, wide spaced median carinae slightly diverging anteriorly, two lateral



**FIGURE 2.** The holotype (NIGP172396) of *Burmissus latimaculatus* sp. nov. **A**, General habitus. **B**, Head, pronotum and mesonotum. **C**, Detailed head. **D**, Line drawing of forewing. **E**, Line drawing of head, pronotum and mesonotum. **F**, Line drawing of hind wing (Scale bars = 2 mm in **A**; 1 mm in **B**, **D–F**; 0.5 mm in **C**).



**FIGURE 3** *Cretodorus granulatus* sp. nov., holotype (NIGP173209). General habitus. **A**, Dorsal view. **B**, Ventral view. **C**, Lateral view. (Scale bars = 2 mm).



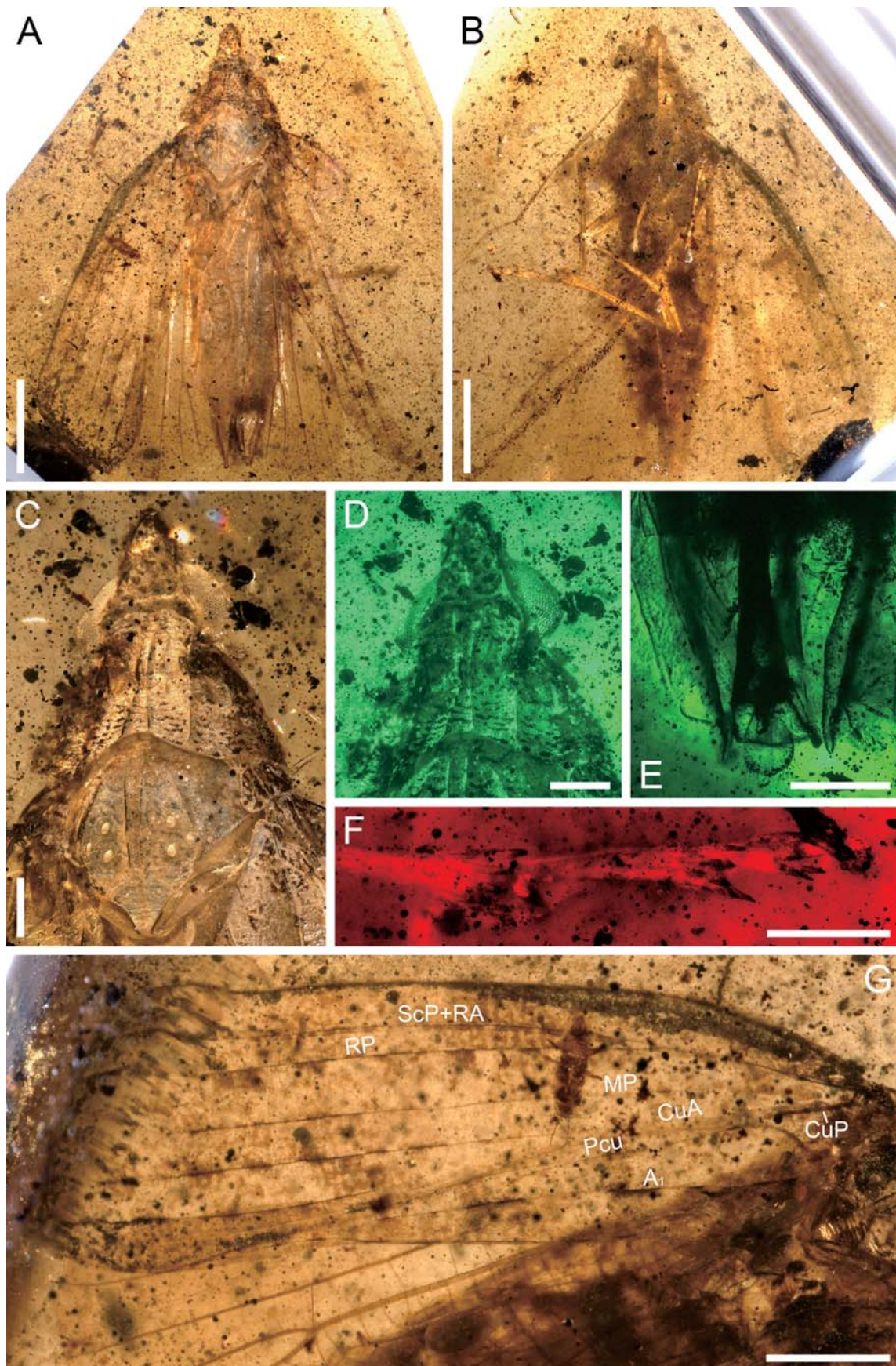
**FIGURE 4** Enlargements of the holotype of *Cretodorus granulatus* **sp. nov.** **A**, Head, pronotum and mesonotum in dorsal view. **B**, Detailed rostrum. **C**, Fore leg. **D**, Male terminalia in ventral view. **E**, Legs. **F**, Metatarsus. (Scale bars = 0.5 mm in **A**, **C–F**; 0.2 mm in **B**).

carinae strongly curved, converging anteriorly; tegmen with wide range of irregular dark color bands on clavus and postmedian section, wing-coupling fore fold (WCFF) long, between last third of free portion of  $A_1$  and tornus; hind wing with stem CuA forked slightly basad of ScP+R fork.

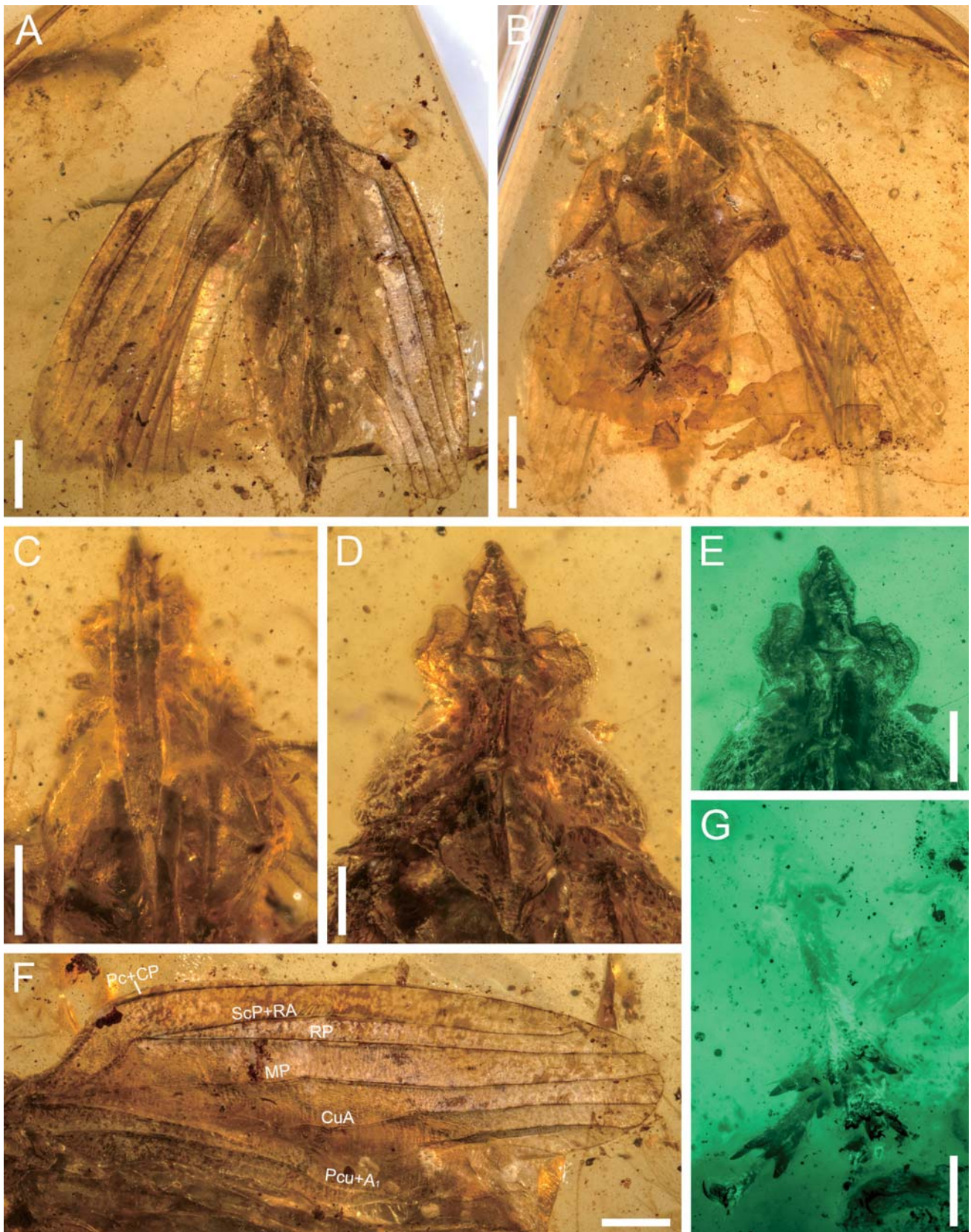
**Type locality and horizon.** Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, northern Myanmar; mid-Cretaceous.

**Description.** Total length (including wings in repose) ca. 13.9 mm (Fig. 2A).

*Head* (Figs. 2B, C, E). Head length 1.36 mm, width

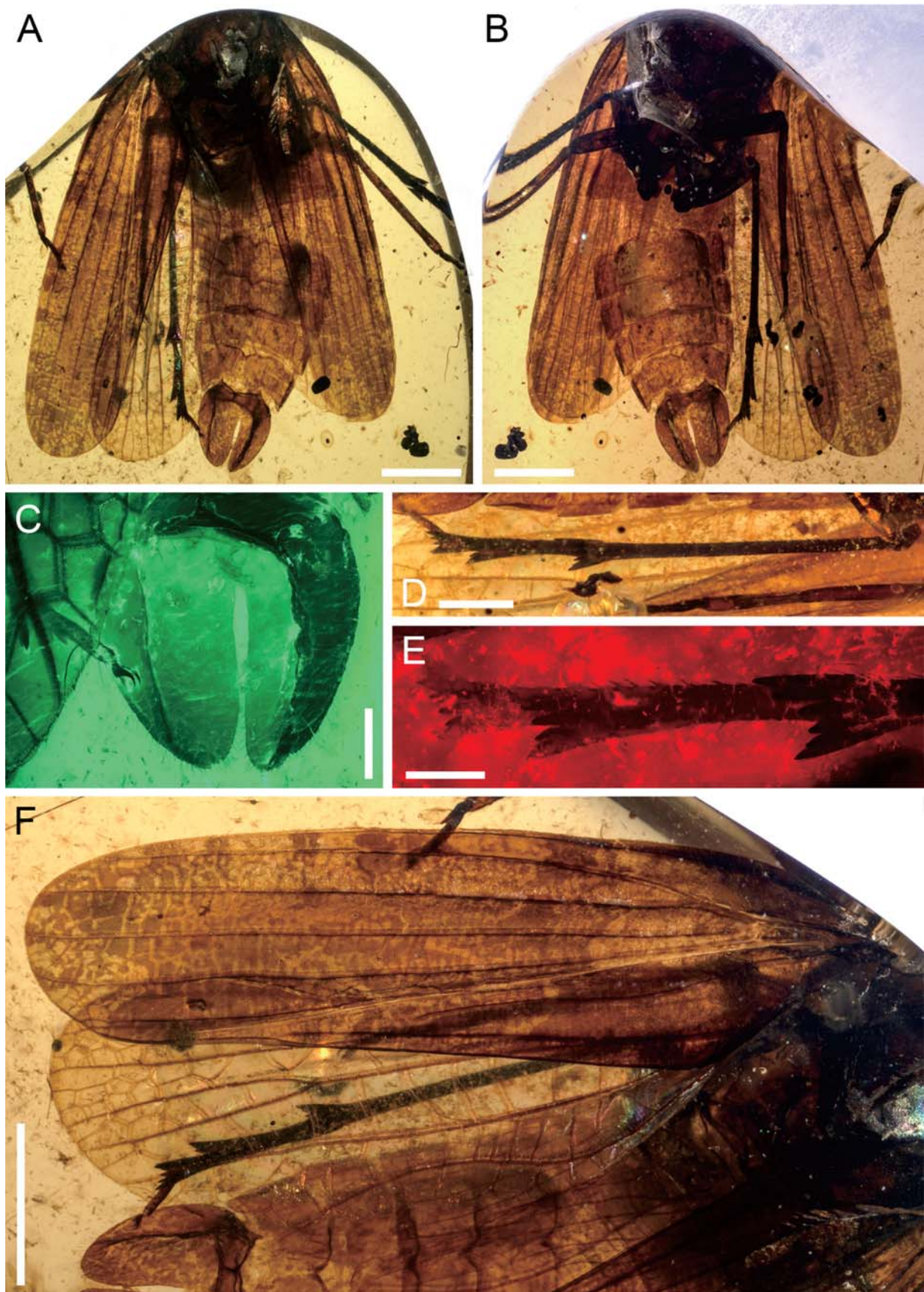


**FIGURE 5** *Cretodorus granulatus* sp. nov., paratype (NIGP173210). **A**, Dorsal view, showing the general habitus. **B**, Ventral view, showing the general habitus. **C**, Head, pronotum and mesonotum in dorsal view. **D**, Head and pronotum, under green fluorescence. **E**, Male terminalia in dorsal view, under green fluorescence. **F**, Metatarsus, under red fluorescence. **G**, **Right** forewing. (Scale bars = 2 mm in **A**, **B**; 1 mm in **G**; 0.5 mm in **C–F**).

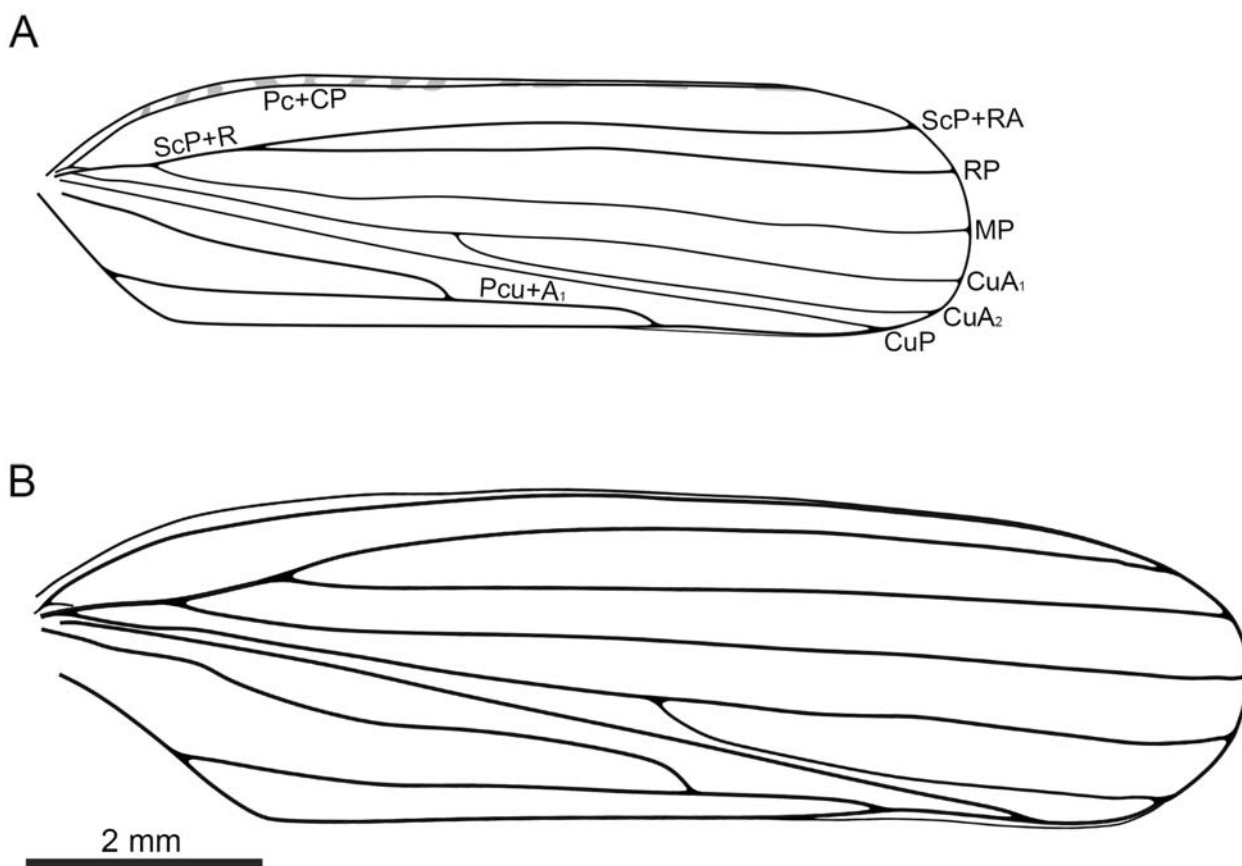


**FIGURE 6** *Cretodorus granulatus* sp. nov., paratype (NIGP173211). **A**, Dorsal view, showing the general habitus. **B**, Ventral view, showing the general habitus. **C**, Head in ventral view. **D**, Head, pronotum and mesonotum in dorsal view. **E**, Head and pronotum, under green fluorescence. **F**, **Left** forewing. **G**, Metatarsi, under green fluorescence. (Scale bars = 2 mm in **A**, **B**; 1 mm in **C**, **F**; 0.5 mm in **D**, **E**, **G**).





**FIGURE 7** The holotype (NIGP173212) of *Cretodorus angustus* sp. nov. from the mid-Cretaceous Burmese amber. **A**, Dorsal view, showing the general habitus. **B**, Ventral view, showing the general habitus. **C**, Pygofer and metatarsus, under green fluorescence. **D**, Legs. **E**, Part of metatibia and metatarsus, under red fluorescence. **F**, **Right** forewing and hind wing. (Scale bars = 2 mm in **A**, **B**, **F**; 1 mm in **D**; 0.5 mm in **C**, **E**).



**FIGURE 8** Line drawings of forewing of *Cretodorus* gen. nov. **A**, *Cretodorus granulatus* sp. nov. **B**, *Cretodorus angustus* sp. nov.. Scale bars: 2 mm.

including compound eyes 2.07 mm in dorsal view; vertex sub-pentagonal, adjacent to compound eyes; frons with lateral edges converging anteriad, single median carina extending on clypeus; compound eyes large, bulging; postclypeus punctate, with distinct median carina.

*Thorax* (Fig. 2B, E). Pronotum sub-hexagonal, length 1.47 mm, width 3.75 mm; densely punctate; anterolateral margin slightly gibbous, length about 1.5× as long as posterolateral margin; posterior margin straight; anterolateral angle roundly wide; posterolateral angle subacutely rounded; posterior angle obtuse; median carinae doubled, reaching posterior margin, converging anteriad and faint before with anterior margin; two lateral carinae strongly arcuate, reaching anterior and posterior margin; anterior transverse furrow between median- and lateral carinae, and two lateral furrows sub-parallel to posterolateral margin, between anterolateral margin and lateral carinae. Mesonotum densely punctate, slightly bigger on lateral lobes than on disc; anterior of median carina converging posteriad and then parallel to each other, faint before mesoscutellum; two lateral carinae strongly converging anteriad; mesoscutellum triangular, transversely wrinkled. Tegula small, punctate.

*Tegmen* (Fig. 2D). Length 10.9 mm and width 3.3

mm, ratio about 3.3; with network of veinlets, forming irregular polygonal cells, becoming widened in apical portion; coriaceous, surface with irregular markings mainly on clavus and postmedian section, and several dark strips on costal area; costal margin smoothly arched, broadest at 0.79 of tegmen length; tornus distinct; posterior margin almost straight; claval margin curved; Pc+CP sub-parallel to costal margin and submerged to margin just before terminal ScP+RA; stem ScP+R straight, forked at basal 0.28 of tegmen length; ScP+RA simple, reaching margin at anteroapical angle; RP diverging from ScP+RA distally; stem MP forked distinctly apicad of CuA fork nearly at basal 3/4 of tegmen length; stem CuA separated from CuP slightly basad of stem ScP+R+MP fork; CuA<sub>2</sub> curved basally and approaching CuP, then sinuous and sub-parallel to CuA<sub>1</sub>; CuP straight; claval veins Pcu and A<sub>1</sub> fused basad of CuA fork; free portion of Pcu strongly sinuous; free portion of A<sub>1</sub> about 1.2× as long as claval stalk Pcu+A<sub>1</sub>; Pcu+A<sub>1</sub> bent distally, reaching WCFF.

*Hind wing* (Fig. 2F). Membranous; cells of polygonal net much larger than on tegmen; costal margin smoothly arched, then curved just basad of stem ScP+R fork; ScP+R forking into ScP+RA and RP nearly at same level of WCFF; ScP+RA arched medially; RP simple, straight;

MP unbranched, sub-parallel to RP; CuA forked slightly basad of ScP+R fork, with two terminals; CuP and Pcu strongly sinuous.

***Cretodorus* gen. nov.**

**Type species.** *Cretodorus granulatus*; by present designation.

**Etymology.** The generic name is formed from the prefix “creto-”, referring to the Cretaceous, and the Greek ‘dory’, indicating its produced, spear-like head; gender masculine.

**Diagnosis.** Differs from other mymarachnids by the following combination of features: head moderately elongate, anterior margin of vertex produced, acutely angled in middle; rostrum extremely long, distinctly beyond tip of tegmina (as in *Burmissus* and *Jaculistilus*, but rostrum just reaching metacoxae in *Mimaplax* and *Ayaimatum*, slightly exceeding metacoxae in *Chalidoridulum*); pronotum ridged, protruded anteriorly, distinctly longer than head, with two straight lateral carinae, parallel to each other; tegmen with stem CuA emerged from stem ScP+R+MP (CuA separated from CuP in *Burmissus*, *Mimaplax* and *Ayaimatum*); tornus indistinctive; longitudinal veins simple, straight and parallel to each other, ScP+RA, RP and MP unbranched (longitudinal veins more sinuous and multi-branched in other genera).

***Cretodorus granulatus* sp. nov.**

(Figs 3–6)

**Material.** Holotype, NIGP173209, well-preserved adult male, embedded in a piece of transparent, orange amber (Figs. 3, 4). Paratypes, NIGP173210 and NIGP173211 (Figs. 5, 6).

**Etymology.** The specific epithet refers to the mesonotum covered with six granulas.

**Diagnosis.** Body length 8.9–10.5 mm; pronotum with irregularly arranged granules; mesonotum with two sets of rounded granules arranged in triangle; metatibio-metatarsal formula (apical teeth) 5: 5: 5; tegmen length 7.5–8.0 mm, length/width about 3.4–3.5, with postcostal cell and radical cell distinctly wider than C1 cell, claval veins Pcu and A<sub>1</sub> fused basad of mid length of tegmen, slightly basad of CuA fork.

**Type locality and horizon.** Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, northern Myanmar; mid-Cretaceous.

**Description.** Body length *ca.* 10.5 mm in the holotype (Fig. 3); paratypes: Body length *ca.* 9.5 mm in NIGP173210 (Figs. 5A, B), 9.0 mm in NIGP173211 (Figs. 6A, B); tegmen length about 7.6 mm and width 2.2 mm in NIGP173210 and NIGP173211 (Figs. 5G, 6F). The following measurements are based on the holotype.

**Head** (Figs. 4A, 5C, D, 6C, D, E). Head width including compound eyes 1.39 mm in dorsal view; central anterior margin of vertex distinctly projecting in front of eyes; compound eyes large, bulging, anterior margin nearly at half of the head length on middle; frons elongate, with lateral edges converging anteriorly; postclypeus with distinct median carina; anteclypeus foliaceous, narrow; rostrum (Fig. 4B) long, beyond tip of tegmina.

**Thorax** (Figs. 4A, 5C, D, 6D). Pronotum extended, punctate, with irregularly arranged granules; length 1.47 mm and width 1.89 mm, about 1.36× as wide as head; narrow anteriorly, divergent posteriorly, with central disc elevated; anterior margin protruded anteriorly, slightly gibbous; posterior margin arcuately concave; median carinae doubled, converging medially from posterior margin, then diverging anteriorly to anterior margin; two longitudinal lateral carinae very straight, not extending to eyes. Mesonotum densely punctate, with two sets of rounded granules arranged in triangle between median carinae and lateral carinae; paired median carinae almost parallel to each other, slightly diverging anteriorly; two lateral carinae slightly incurved anteriorly toward median carina; mesoscutellum transversely wrinkled. Tegula subtriangular, punctate. Legs with rows of short bristles along, with irregular rectangular dark color bands, especially profemora and protibiae (Fig. 4C); segments length in mm (femur/tibia/tarsus): prothoracic leg 2.39/2.21/0.72, mesothoracic leg 1.97/2.66/0.73, metathoracic leg 1.62/3.64/1.83; protarsi and mesotarsi with claw hooked, with tip sharp, longer than arolium (Fig. 4C, E); metatibiae distinctly widened apically, with five apical teeth with subapical setae (Figs 4F, 5F, 6G); metatarsus setose, basi- and midtarsomere widened apically, each with five apical teeth (Figs 4F, 5F, 6G).

**Tegmen** (Fig. 8A). Length *ca.* 7.97 mm; mottled; with network of veinlets, forming irregular polygonal cells; costal margin arched; apical margin rounded; posterior margin straight; costal area narrow, with several small dark bands; postcostal cell distinctly wider than C1 cell; ScP short; Pc+CP submerged to margin at 0.83 of tegmen length; ScP+R straight, ScP+RA reaching margin at anteroapical angle; RP sub-parallel to MP; radial cell distinctly wider than C1 cell; stem CuA separated from stem ScP+R+MP at base, forked at 0.45 of tegmen length; CuP straight; Pcu and A<sub>1</sub> fused slightly basad of CuA fork; free portion of Pcu slightly sinuous; claval stalk Pcu+A<sub>1</sub> bent distally, reaching WCFF; free portion of A<sub>1</sub> about 1.7× as long as Pcu+A<sub>1</sub>. Hind wing membranous, transparent; cells of polygonal net much larger than on tegmen; RP and MP unbranched, straight; CuA forked late, with two terminals.

**Abdomen.** Male terminalia (Figs 4D, 5E) with two symmetrical lobes covering most of genital structures; pygofer translucent, with middle carinae; anal tube

with apex oval, with long setae apically; anal styles and aedeagus invisible.

***Cretodorus angustus* sp. nov.**

**Material.** Holotype, NIGP173212, embedded in a piece of transparent, yellowish amber.

**Etymology.** The specific name, from the Latin for narrow, refers to the narrow tegmen.

**Type locality and horizon.** Amber mine located near Noiye Bum Village, Tanai Township, Myitkyina District, Kachin State, northern Myanmar; mid-Cretaceous.

**Diagnosis.** The new species differs from the type species by the following combination of features: pro- and mesonotum without granules; metatibio-metatarsal formula (apical teeth) 6: 6: 6; tegmen slender, length about 10.5 mm, length/width about 3.8, postcostal cell narrow, widest just as wide as C1 cell, claval veins junction apicad of mid length of tegmen, slightly apicad of CuA fork, Pcu+A<sub>1</sub> very short.

**Description.** Head and pronotum missing, preserved length ca. 11.7 mm (Fig. 7A, B), estimated complete total length over 14.0 mm.

**Thorax.** Mesonotum with two adjacent median carinae, elevated, diverging anteriorly; two lateral carinae converging anteriorly; mesoscutellum triangular, transversely wrinkled. Tegula obscure. Legs (Fig. 7D) with rows of short bristles along, segments length in mm (femur/tibia/tarsus): mesothoracic leg 2.41/4.18/1.06, metathoracic leg 1.97/4.81/2.63. mesotarsi with claw large, hooked, sharp apically; metacoxae cylindrical; metatibiae widened apically, with six apical teeth (Figs. 7D, E); metatarsus (Figs. 7E, F) with tarsomeres length (in mm): 0.57/0.75/1.31, basi- and midtarsomere widened apically, each with six apical teeth, apical tarsomere thin, with tarsal claw small.

**Tegmen** (Figs. 7F, 8B). Length 10.45 mm and width 2.75 mm, ratio about 3.8; with network of veinlets, forming irregular polygonal cells; surface with a wide range of markings; costal margin smoothly arched, broadest at 0.20 of tegmen length; apical margin rounded; posterior margin straight; postcostal cell widest just as wide as C1 cell; Pc+CP long, submerged to margin just before terminal ScP+RA; stem ScP+R short, forked at basal 0.28 of tegmen length; ScP+RA arched basally, then nearly straight; RP very straight, sub-parallel to and MP; stem CuA separated from stem ScP+R+MP at base, forked nearly at half of tegmen length; CuA<sub>2</sub> curved basally and approaching CuP; CuP straight; Pcu and A<sub>1</sub> fused slightly apicad of CuA fork; free portion of Pcu sinuous; claval stalk Pcu+A<sub>1</sub> short, bent distally; free portion of A<sub>1</sub> about 2.7× as long as Pcu+A<sub>1</sub>. Hind wing membranous, transparent (Fig. 7F); cells of polygonal net much larger

than on tegmen; stem ScP+R forked nearly at same level of wing-coupling fore fold; MP unbranched, sub-parallel to RP; CuA with two terminals, forked at same level or slightly basad of ScP+R fork; Pcu strongly sinuous.

**Abdomen.** Abdomen slightly exceeding tip of tegmina; pygofer (Fig. 7C) lobes foliaceous, broad, with tiny setae, carinae present.

## Discussion

*Burmissus* previously included two species known only from the mid-Cretaceous amber of northern Myanmar. The new species, *Burmissus latimaculatus* sp. nov., described above can be assigned to this genus based on the diagnosis provided by Shcherbakov (2017) and emended by Luo *et al.* (2020) with slight modifications: anterior margin of compound eyes distinctly exceeding half of head length on middle; pro- and mesonotum with double median carina; tegmen slender, without eyespots, costal area extremely narrow, postcostal cell narrow, most of longitudinal veins are not obviously curved or sinuous, ScP+RA and RP simple, MP two-branched, CuA forked apicad of claval veins junction.

The discovery of new material with completely preserved pronotum structure is crucial and provides several detailed morphological features that have never been observed in *Burmissus*. *Burmissus latimaculatus* has the pronotum with straight posterior margin, and lateral furrows sub-parallel to posterolateral, between anterolateral margin and lateral carinae, which can be readily distinguished from other species (W-shaped posterior margin, and lateral furrows absent in *B. raunoi* and *B. szwedoi*) (Shcherbakov, 2017; Luo *et al.*, 2020). Additionally, *B. latimaculatus* can be differentiated from the two other species mainly as follow: 1) head rounded, anterior margin of compound eyes almost reaching vertex, with long median carina extending on clypeus (head triangular, anterior margin with a sharp angle in dorsal view, and anterior margin of compound eyes reaching 2/3 of frons length in *B. szwedoi*, and median carina absent in *B. raunoi* and *B. szwedoi*); 2) characteristic coloration on tegmen (tegmen covered with a wide range of irregular markings on clavus and postmedian section, but four oblique dark bands and eight dark streaks near costal margin in *B. raunoi*, and mottled tegmen in *B. szwedoi*); and 3) detailed wing venation, including extended Pc+CP (Pc+CP submerged to margin only at half of tegmen length in *B. raunoi*, WCFF between last third of free portion of A<sub>1</sub> and tornus, not extending to CuP (WCFF between terminals CuA<sub>2</sub> and Pcu+A<sub>1</sub> in *B. raunoi* and *B. szwedoi*), and hind wing with stem CuA forked slightly basad of ScP+R fork (subequal R and CuA forks in *B.*

*raunoi*, and CuA forked apparently basad of ScP+R fork in *B. szwedoi*).

*Cretodoros* **gen. nov.** belongs to Mimarachnidae based on the following characters: pro- and mesonotum with doubled median carinae, fore- and hind wing with abundant irregular network of veinlets, tegmen with weakened basal cell and narrow costal area, deeply forked stem ScP+R and less deeply forked stem CuA (Shcherbakov, 2007b; Szwedo & Ansorge, 2015). *Cretodoros* most resembles *Burmissus* in body and tegmen sizes, rostrum beyond tip of tegmina, and very simplified venation with most longitudinal veins are straight and parallel to each other. Still, *Cretodoros* bears a peculiar combination of characters: 1) head moderately elongate, central anterior margin of vertex acutely angled, distinctly shorter than pronotum (head strongly produced, longer than pronotum in *Jaculistilus*, anterior margin more obtuse angled in *Burmissus*, *Mimaplax*, and *Ayaimatum*, and head missing in other genera); 2) pronotum protruded anteriorly, with anterior margin slightly gibbous (pronotum sub-hexagonal, transverse, anterior margin without protrusion in *Burmissus*, *Dachibangus*, *Mimaplax*, and *Ayaimatum*, anterior margin inverted V-shaped, arcuately convex in *Mimarachne* and *Jaculistilus*), and two straight lateral carinae parallel to each other (lateral carinae curved, converging anteriorly or absent in other mimarachnids); 3) tegmen with MP unbranched (MP 2-branched in *Saltissus*, *Mimamontsecia*, *Chalicoridulum*, *Burmissus*, and *Ayaimatum*, with 2–3 terminals in *Mimaplax*, and multi-branched, more than 4 terminals in *Mimarachne*, *Dachibangus* and *Jaculistilus*).

Including the current study, ten species ascribed to six genera of Mimarachnidae have been reported from the Burmese (Myanmar) palaeobiota (Shcherbakov, 2017; Zhang *et al.*, 2018; Jiang *et al.*, 2018, 2019; Fu *et al.*, 2019; Luo *et al.*, 2020; this study). They include *Burmissus raunoi* Shcherbakov, 2017, *B. szwedoi* Luo, Jiang, Wang & Xiao, 2020, *B. latimaculatus* **sp. nov.**, *Jaculistilus oligotrichus* Zhang, Ren & Yao, 2018, *Dachibangus trimaculatus* Jiang, Szwedo & Wang, 2018, *D. formosus* Fu, Szwedo, Azar & Huang, 2019, *Mimaplax ekrypsan* Jiang, Szwedo & Wang, 2019, *Ayaimatum Trilobatum* Jiang & Szwedo, 2020, *Cretodoros granulatus* **sp. nov.**, and *C. angustus* **sp. nov.**.

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## References

- Azar, D., Perrichot, V., Neraudeau, D. & Nel, A. (2003) New psychodid flies from the Cretaceous ambers of Lebanon and France, with a discussion about *Eophlebotomus connectens* Cockerell, 1920 (Diptera, Psychodidae). *Annals of the Entomological Society of America*, 96, 117–127. [https://doi.org/10.1603/0013-8746\(2003\)096\[0117:NPFTCA\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2003)096[0117:NPFTCA]2.0.CO;2)
- Bourgoin, T. (2020) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8, updated 2020-05-07. <http://hemiptera-databases.org/flow/>.
- Bourgoin, T. & Szwedo, J. (2008) The ‘cixiid-like’ fossil planthopper families. *Bulletin of Insectology*, 61, 107–108.
- Bourgoin, T., Wang, R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroinski, A., Yap, S. & 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. <https://doi.org/10.1007/s00435-014-0243-6>
- Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 21, 441–455. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- Emeljanov, A.F. (1983) Nosatka iz mela Taïmyra (Insecta, Homoptera). *Paleontologicheskii Zhurnal*, 1983, 79–85. [English translation: Yemel'yanov, A.F. 1984. Dictyopharidae from the Cretaceous deposits on the Taymyr Peninsula (Insecta, Homoptera). *Paleontological Journal*, 17, 77–82.]
- Emeljanov, A.F. & Shcherbakov, D.E. (2018) The longest-nosed Mesozoic Fulgoroidea (Homoptera): a new family from mid-Cretaceous Burmese amber. *Far Eastern Entomologist*, 345, 1–14. <https://doi.org/10.25221/fee.354.1>
- Evans, J.W. (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. <https://doi.org/10.1111/j.1365-2311.1946.tb00442.x>
- Fu, Y.Z., Szwedo, J., Azar, D. & Huang, D.Y. (2019) A second species of *Dachibangus* (Hemiptera: Fulgoromorpha: Mimarachnidae) in mid-Cretaceous amber from northern Myanmar. *Cretaceous Research*, 103, 104170. <https://doi.org/10.1016/j.cretres.2019.06.016>
- Fujiyama, I. (1978) Some fossil insects from the Tedori Group (Upper Jurassic–Lower Cretaceous), Japan. *Bulletin of the National Science Museum, Series C (Geology)*, 4, 181–191.
- Grimaldi, D.A., Engel, M.S. & Nascimbene, P.C. (2002)

- Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361, 1–72.  
[https://doi.org/10.1206/0003-0082\(2002\)361<0001:FCAFMB>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2)
- Hamilton, K.G.A. (1990) Homoptera. In: Grimaldi, D. (Ed.), *Insects from the Santana Formation, Lower Cretaceous of Brazil. Bulletin of the American Museum of Natural History*, 195, 82–122.
- Jiang, T., Szwedo, J., Song, Z.S., Chen, J., Li, Y.L. & Jiang, H. (2020) *Ayaimatum Trilobatum* gen. et sp. nov. of Mimarachnidae (Hemiptera: Fulgoromorpha) from mid-Cretaceous amber of Kachin (northern Myanmar). *Acta Palaeontologica Sinica*, 59, 70–85.  
<https://doi.org/10.19800/j.cnki.aps.2020.01.09>
- Jiang, T., Szwedo, J. & Wang, B. (2018) A giant fossil Mimarachnidae planthopper from the mid-Cretaceous Burmese amber (Hemiptera, Fulgoromorpha). *Cretaceous Research*, 89, 183–190.  
<https://doi.org/10.1016/j.cretres.2018.03.020>
- Jiang, T., Szwedo, J. & Wang, B. (2019) A unique camouflaged mimarachnid planthopper from mid-Cretaceous Burmese amber. *Scientific Reports*, 9, 13112.  
<https://doi.org/10.1038/s41598-019-49414-4>
- Latreille, P.A. (1807) *Genera crustaceorum et insectorum, secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*. Tomus tertius. A. Koenig, Parisiis et Argentorati [= Paris & Strasbourg], 258 pp.  
<https://doi.org/10.5962/bhl.title.11558>
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. L. Salvii, Holmiae [= Stockholm], 824 pp.  
<https://doi.org/10.5962/bhl.title.542>
- Luo, C., Jiang, T., Wang, B. & Xiao, C. (2020) A new species of *Burmissus* (Hemiptera: Fulgoromorpha: Mimarachnidae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 110, 104417.  
<https://doi.org/10.1016/j.cretres.2020.104417>
- Luo, C., Jiang, T., Szwedo, J., Wang, B. & Xiao, C. (2020). A new planthopper family Katlasidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea) from mid-Cretaceous Kachin amber. *Cretaceous Research*.  
<https://doi.org/10.1016/j.cretres.2020.104532>
- Mao, Y.Y., Liang, K., Su, Y.T., Li, J.G., Rao, X., Zhang, H., Xia, F.Y., Fu, Y.Z., Cai, C.Y. & Huang, D.Y. (2018) Various amberground marine animals on Burmese amber with discussions on its age. *Palaeoentomology*, 1, 91–103.  
<https://doi.org/10.11646/palaeoentomology.1.1.11>
- Martynov, A.V. (1935) Permian fossil insects from Arkhangelsk District. Part.5. *Homoptera. Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR*, 4, 1–35.
- Nel, A., Prokop, J., Nel, P., Grandcolas, P., Huang, D.Y., Roques, P., Guilbert, E., Dostál, O. & Szwedo, J. (2012) Traits and evolution of wing venation pattern in paraneopteran insects. *Journal of Morphology*, 273, 480–506.  
<https://doi.org/10.1002/jmor.11036>
- Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D. & Ponomarenko, A.G. (2016) Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). *Cretaceous Research*, 61, 234–255.  
<https://doi.org/10.1016/j.cretres.2015.12.025>
- Ross, A.J. (2019) Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology*, 2, 22–84.  
<https://doi.org/10.11646/palaeoentomology.2.1.5>
- Ross, A.J. (2020) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019. *Palaeoentomology*, 3 (1), 103–118.  
<https://doi.org/10.11646/palaeoentomology.3.1.14>
- Ross, A.J., Mellish, C., York, P. & Crighton, B. (2010) Burmese amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.
- Shcherbakov, D.E. (2000) Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permian-Triassic crisis. *Paleontologicheskii Zhurnal*, 34, 251–267.
- Shcherbakov, D.E. (2007a) An extraordinary new family of Cretaceous planthoppers (Homoptera: Fulgoroidea). *Russian Entomological Journal*, 16, 139–154.
- Shcherbakov, D.E. (2007b) Mesozoic spider mimics — Cretaceous Mimarachnidae fam.n. (Homoptera: Fulgoroidea). *Russian Entomological Journal*, 16, 259–264.
- Shcherbakov, D.E. (2017) First record of Cretaceous family Mimarachnidae (Homoptera: Fulgoroidea) in amber. *Russian Entomological Journal*, 26, 389–392.  
<https://doi.org/10.15298/rusentj.26.4.12>
- Shcherbakov, D.E. & Popov, Y.A. (2002) Superorder Cimicidea Laicharting, 1781 order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc. In: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds), *History of insects*. Kluwer, Dordrecht, pp. 152–155.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research*, 37, 155–163.  
<https://doi.org/10.1016/j.cretres.2012.03.014>
- Sidorchuk, E.A. & Vorontsov, D.D. (2018) Preparation of small-sized 3D amber samples: state of the technique. *Palaeoentomology*, 1, 80–90.  
<https://doi.org/10.11646/palaeoentomology.1.1.10>
- Smith, R.D.A. & Ross, A.J. (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*