Stonymetopus megus gen. et sp. nov. (Hemiptera: Fulgoromorpha), the first Fulgoridiidae genus from mid-Cretaceous Burmese amber

Authors: Poinar, George, Brown, Alex E., and Bourgoin, Thierry

Source: Palaeodiversity, 15(1) : 83-90

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/pale.v15.a6

Stonymetopus megus gen. et sp. nov. (Hemiptera: Fulgoromorpha), the first Fulgoridiidae genus from mid-Cretaceous Burmese amber

George Poinar Jr., Alex E. Brown & Thierry Bourgoin

Abstract

A new genus and species of planthopper, *Stonymetopus megus* gen. et sp. nov. (Hemiptera: Fulgoromorpha: Fulgoridiidae) is described as the first Fulgoridiidae from mid-Cretaceous Burmese amber, a family previously only known from the Jurassic. The new genus has a relatively large size with pointed head and obelliptic eyes (in lateral view). Its short metatibia are not apically dilated, and first metatarsomere exhibits five to six short teeth bearing sarcosetae between two longer lateral ones, while the second metatarsomere seems toothless but with a blunt ventroapical extension. Tegmina are coleopterous-like with long subparallel main veins. A mature, post-parasitic dryinid larva (Hymenoptera: Dryinidae) is adjacent to the fossil planthopper and the ethology of these parasites is briefly discussed.

Key words: Burmese amber, Cenomanian, planthopper, Fulgoridiidae, Dryinidae.

1. Introduction

The Fulgoromorpha or planthoppers, which extend back to the Early Permian, comprise a large mainly tropicopolitan group of very diverse taxa classified into three superfamilies (Szwedo et al. 2004). The superfamily Fulgoroidea presently contains some 34 extant and fossil families (Bourgoin 2022). Basic characters of the Fulgoroidea are tegulae at the base of the forewings, antennae ventral to the eyes, antennal pedicel enlarged and often swollen, bearing "placodea sensilla", and the frons occupying most of the facial part of the head. The 21 extant families and 13 extinct Fulgoroidea families are distinguished mainly by the shape of the head, forewing venation and arrangement of teeth and spines on the metatibia and metatarsi (Dietrich 2009; Fletcher & Carver 1991; Szwedo 2018; Song et al. 2019; Bourgoin 2022).

Planthoppers damage plants by ovipositing in their tissues and feeding on the phloem, sometimes vectoring a variety of plant pathogens. Cixiidae and Delphacidae are the families with the most injurious species. Cixiids are vectors of phytoplasma, mycoplasma and Mollicutes, whereas delphacids are mainly virus vectors. These diseases cause serious damage on a great number of economically important crops (Bourgoin 2022). Planthoppers were considered as one of the significant obstacles to the success of the Green Revolution in tropical Southeast Asia with losses from them estimated in hundreds of millions of dollars. The rice crop in Asia, which feeds 60% of the world population, is particularly damaged by the delphacid *Nilaparvata lugens* (the rice brown planthopper), which is considered as the most important pest of rice in Asia. Some 150 species of planthoppers from various families are currently directly or indirectly recorded as pests of 99 economic plants (O'Brien 2002).

The present study describes a new genus and species of planthopper in Burmese amber. The fossil is the first Cretaceous representative of the Fulgoridiidae, a family only known from the Jurassic. It depicts some unique characters, thus adding to the already extensive morphological variation that occurs in these small, fragile insects. A mature, post-parasitic dryinid larva (Hymenoptera: Dryinidae) is adjacent to the fossil planthopper. The biology and occurrence of adult members of dryinids in Burmese amber are briefly discussed.

2. Material and methods

The fossil planthopper originated from the Noije Bum 2001 Summit Site mine located southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E) in Myanmar. Based on paleontological evidence this site was dated to the Upper Albian of the Early-Mid Cretaceous (Cruickshank & Ko 2003), placing the age at 97 to 110 mya. A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma (Shi et al. 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar et al. 2007).

Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 X. Helicon Focus Pro X64 was used to stack photos for better depth of field.

Tegminal venation and morphological terminologies follow the works of Fletcher & Carver (1991), Fletcher (1999) and Bourgoin et al. (2015).

This specimen was first sampled in 2015, well prior to the onset of challenges regarding amber from Myanmar and therefore is in compliance with all ethical standards for the study of Burmese amber fossils (see also Poinar & Ellenberger 2020).

LSID for publication: urn:lsid:zoobank.org:pub:135AC1AC-0C39-4616-A5C1-602CF7FF(7)D06

3. Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Superfamily Fulgoroidea Latreille, 1807

Family Fulgoridiidae Handlirsch, 1939

Genus *Stonymetopus* nov.

LSID for genus:urn:lsid:zoobank.org:act:97D0AFA3-3D74-499E-A89E-E6C71CBD72AF

Etymology: The generic name is derived from the Greek "stonyx" = sharp point and the Greek "metopon" = forehead, in reference to the pointed head of the fossil.

Type species: *Stonymetopus megus* sp. nov., monotypic.

Diagnosis: *Stonymetopus* gen. nov. is separated from all other mid-Cretaceous taxa by its general flattened conformation, its large size with a pointed head and obelliptic eyes, short metatibia bearing five apical teeth and metatarsomere I exhibiting a median ventral row of teeth bearing strong sarcosetae while metatarsomere II is very short, apparently toothless and with a blunt ventroapical extension. Tegmina are opaque, coleopterous, with a venation pattern similar to the Fulgoridiidae genus *Cixiites* but with R forking much earlier and CuA1 apically forked.

The above characters separate the genus from any other mid-Cretaceous taxa of planthoppers (Table 1), including other members of the family Fulgoridiidae (Szwedo & Zyla 2009) in which it is provisionally classified (see Discussion chapter).

Stonymetopus megus gen. et sp. nov.
Figs. 1–7

LSID for species: urn:lsid:zoobank.org:act:EADD956B-EB42-427F-A6FA-C4998713518D

Etymology: The specific epithet is derived from the Greek "megas" = large in reference to the size of the fossil.

Type material: Holotype female deposited in the Poinar amber collection (accession # B-He- 40) maintained at Oregon State University. The specimen is complete except for the tip of the left forewing. The tarsi are missing except for a single protarsus and single metatarus. A single syninclusion is a dryinid larva adjacent to the abdomen of the fossil planthopper.

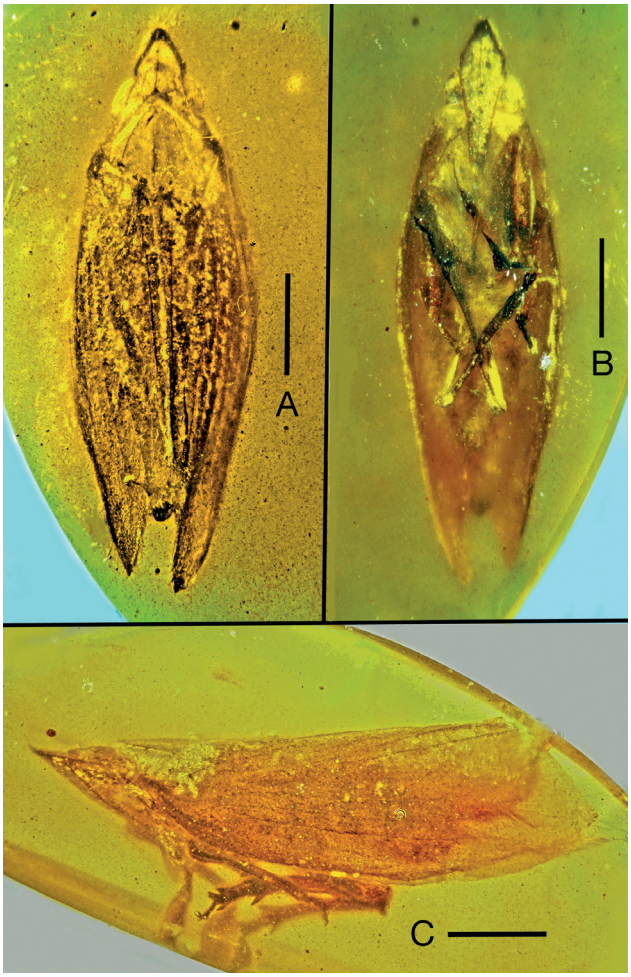

Fig. 1. Holotype of *Stonymetopus megus* gen. et sp. nov. in Burmese amber. **A** – Dorsal view. Scale bar = 2.3 mm. **B** – Ventral view. Scale bar = 2.3 mm. C. Lateral view. Scale bar = 2.5 mm.

Type locality: Hukawng Valley southwest of Maingkhwan in Kachin State (26º20´N, 96º36´E), Myanmar.

Diagnosis: See diagnosis of genus.

Description: Female Holotype. Entire body light brown, speckled with small brown spots.

Head: Laterally flattened, narrowing apically. Vertex slightly declivitous anteriorly, protruding in front of eye level, with medial and lateral carinae. Posterior margin of vertex arcuate, ending laterally slightly before anterior angles of compound eyes from above. Frons much longer than wide, occupying (with clypeus) all of facial part of head, wider before dorsal level of eyes; lateral margins of frons carinated, converging at apex; with single median, unforked carina. Median ocellus absent; postclypeus elongated, slightly declivitous dorsally, with median carina in direct prolongation with frontal one; lateral carinae sharp, in direct prolongation with frontal ones. Eyes relatively small, obelliptic in lateral view, only slightly protruding from surface of head, positioned below top of head; lateral ocelli not observed; rostrum short, three-segmented, extending only to level of mesocoxae, with terminal segment approxi-

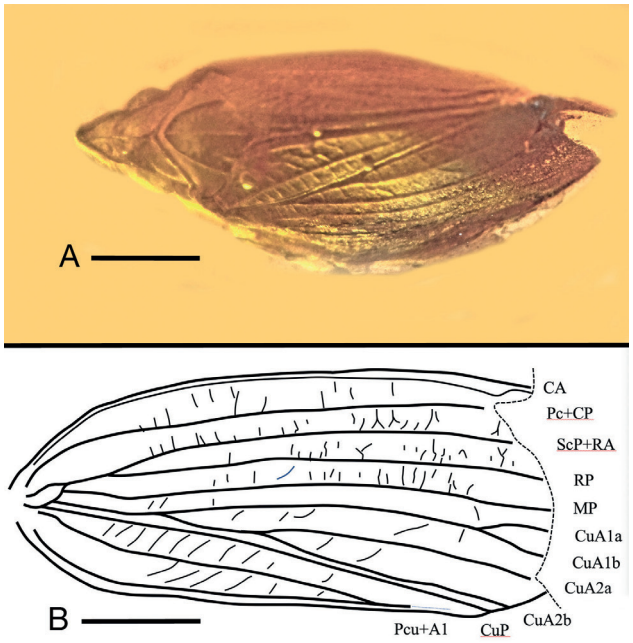

Fig. 2. Wing venation of *Stonymetopus megus* gen. et sp. nov. in Burmese amber. **A** – Dorsal-lateral view of specimen. Scale bar = 1.5 mm. **B** – Wing vein nomenclature. Scale bar = 1.7 mm.

mately four times longer than its basal width. Antenna ventral to eyes, with small short scape, elongated bulbous pedicel bearing sensilla placodea and short flagellum with developed basal swelling. Postclypeus visible between posterior margin of vertex and anterior margin of pronotum.

Thorax: Pronotum with wide and long median disc protruding between the eyes in dorsal view; posterior margin distinctly angulated medially; pronotal area pectoralis twice the length of the eyes and strongly developed lateroventrally in ventral view. Mesonotum with distinct median carina. Disc also marked by strong lateral carinae meeting anteriorly before its anterior margin; lateral slopes of disc declivous. Scutellum triangulate, not separated by transverse carina.

Legs: Protarsus three-segmented. Metatibia relatively short, with a series of five apical teeth with two lateral larger teeth; metatarsomere I as long as metatarsomeres II + III, with a row of five or six shorter teeth bearing sarcosetae between two longer lateral ones; metatarsomere II very short, apparently toothless, perhaps with a ventral unique expansion; metatatarsomere III narrow, twice as long as midmetatarsomere, with a pair of long tarsal claws between a dorsal arolium and long ovoid sclerotised unguitractor plate.

Wings: Tegmina opaque, coleopterous, folded steeply tectiform over abdomen in repose. Distal part not observable: at least 3.1 times as long as wide with bluntly pointed apical margin; all main veins running more or less parallel. Costal margin slightly thickened, widening apically when reaching nodal level; common stem ScP+R almost as long as basal cell, issuing separately from MP, forking before CuA into ScP+RA and RP, both not forked until nodal line; MP not forked before nodal line; CuA forking once early into anterior branch; CuA1 forking again apically at nodal line level into CuA1a and CuA1b and CuA2 forking again early, well before nodal line level into two long single terminals CuA2a and CuA2b. CuA posterior branches running straight close to CuP. Claval vein Pcu + A1 fused late, after half length of the wing in an elongated and thin clavus with apex reaching last third of the wing. Numerous irregular veinlets, particularly well-marked between Pcu and CuP forming subquadrangular cells. Hindwings not observed.

Abdomen: Anterior portion of abdomen mostly hidden from view by wings. Terminalia difficult to observe. Female specimen with short ovipositor protruding from paired gonoplacs.

Measurements: Length body, 13.0 mm; width body 3.8 mm; body L/W ratio, 3.4; width head across eyes, 2.2 mm; length eye (lateral), 1.3 mm; width eye, 0.4 mm; width top of frons, 1.2 mm; length tip of head to pronotum, 1.7 mm; length pronotum, 0.3 mm; width pronotum, 2.5 mm; length mesonotum, 2.3 mm; width mesonotum, 2.2 mm; length rostrum, 1.7 mm; antennae located beneath eyes, length scape, 70 µm; length pedicel, 260 µm; length flagellum, 130 µm; length metatibia, 2.2 mm; length spines in row at base of metatibia, 320 µm; length large lateral spine at base of metatibia, 530 µm; length metatarsomere 1.9 mm; length two lateral spines at apex of metatarsus 1.5 mm and 370 µm; length metatarsomere 2.7 mm; length blunt extension at apex of metatarsomere 2.7 mm; length metatarsomere 3.9 mm; length claws, 320 µm; length empodium, 213 µm; length tegmen, 10.6 mm, width tegmen 3.5 mm; tegmen L/W ratio, 3.0.

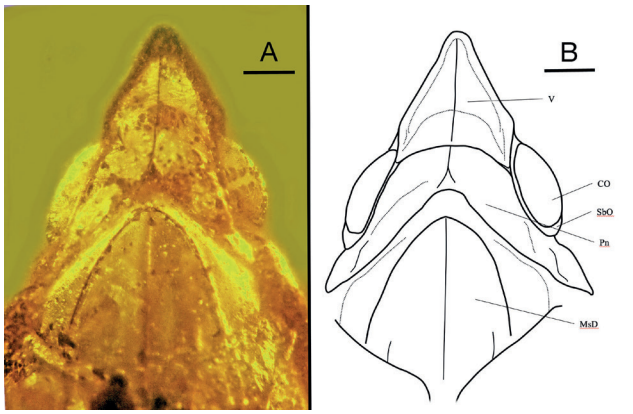

Fig. 3. Dorsal view of head of *Stonymetopus megus* gen. et sp. nov. in Burmese amber. Scale bar = 0.5 mm. B. Major head parts labeled. CO = compound eye; SbO = suborbital plate of compound eye; MsD = mesonotal disk; Pn = pronotum; V = vertex. Scale bar = 0.5 mm.

4. Discussion

The diagnostic characters of *Stonymetopus megus* separate the genus from all other described Burmese amber fossils (Table 1). Several morphological configurations, such as those on the metatibiotarsi or the mesonotum, are unique for planthoppers. The forewing venation places the genus in a group of taxa considered to have evolved either from "primitive" lineages related to fulgoridiids, or from a "pre-cixioid group" (Shcherbakov

2007a). This would include many of the recently described mid-Cretaceous new fossil planthopper families such as the Perforissidae Shcherbakov, 2007, Jubisentidae Zhang, Ren & Yao, 2019, Mimarachnidae Shcherbakov, 2007, Dorytocidae Emeljanov & Shcherbakov, 2018, Neazoniidae Szwedo, 2007, Katlasidae Luo, Jiang & Szwedo, 2020 as well as the recently described Inoderbidae Shcherbakov & Emeljanov, 2021. However, *Stonymetopus* cannot be included within any of these because of its many other characters that depict a unique general habitus within this group of mid-Cretaceous planthoppers.

While previous studies have described new genera from Burmese amber in monotypic families, we decided against this action with *Stonymetopus*. While such a decision emphasizes the great disparity and diversity of the mid-Cretaceous planthopper fauna, on the other hand, it also conceals the evolutionary dimensions of these taxa. Elevating these monotaxic units to family rank avoids considering the question of their evolutionary relationship. Accordingly, and in agreement with its venational pattern being similar to the Fulgoridiidae genus *Cixiites*, we place, at least provisionally, *Stenometopus* in Fulgoridiidae with which it shares a multibranched CuA. Its exact placement within this family, artificially restricted to Jurassic genera relative to other taxa, will be determined in future comparative and phylogenetic analyses.

The discovery of a dryinid larva (Hymenoptera: Dryinidae) (length 2.1 mm: width 0.8 mm) adjacent to *Stonymetopus megus* is quite interesting (Fig. 7). Dryinids are specialized wasps that have evolved a unique method of parasitizing nymphs and adults of leafhoppers (Hemiptera: Cicadellidae), planthoppers (Hemiptera: Fulgoroidea) and treehoppers (Hemiptera: Membracidae). Adult female wasps deposit their eggs in these hemipterans and are also predaceous, so dryinids can be both parasites and predators at the same time, which makes them excellent biological control organisms (Clausen 1962).

Female dryinids oviposit in various locations on their hosts, but two of the most preferred are beneath the wing lobes and between the first two abdominal segments (Clausen 1962). One of these sites was probably where oviposition and larval development occurred on *Stonymetopus megus*.

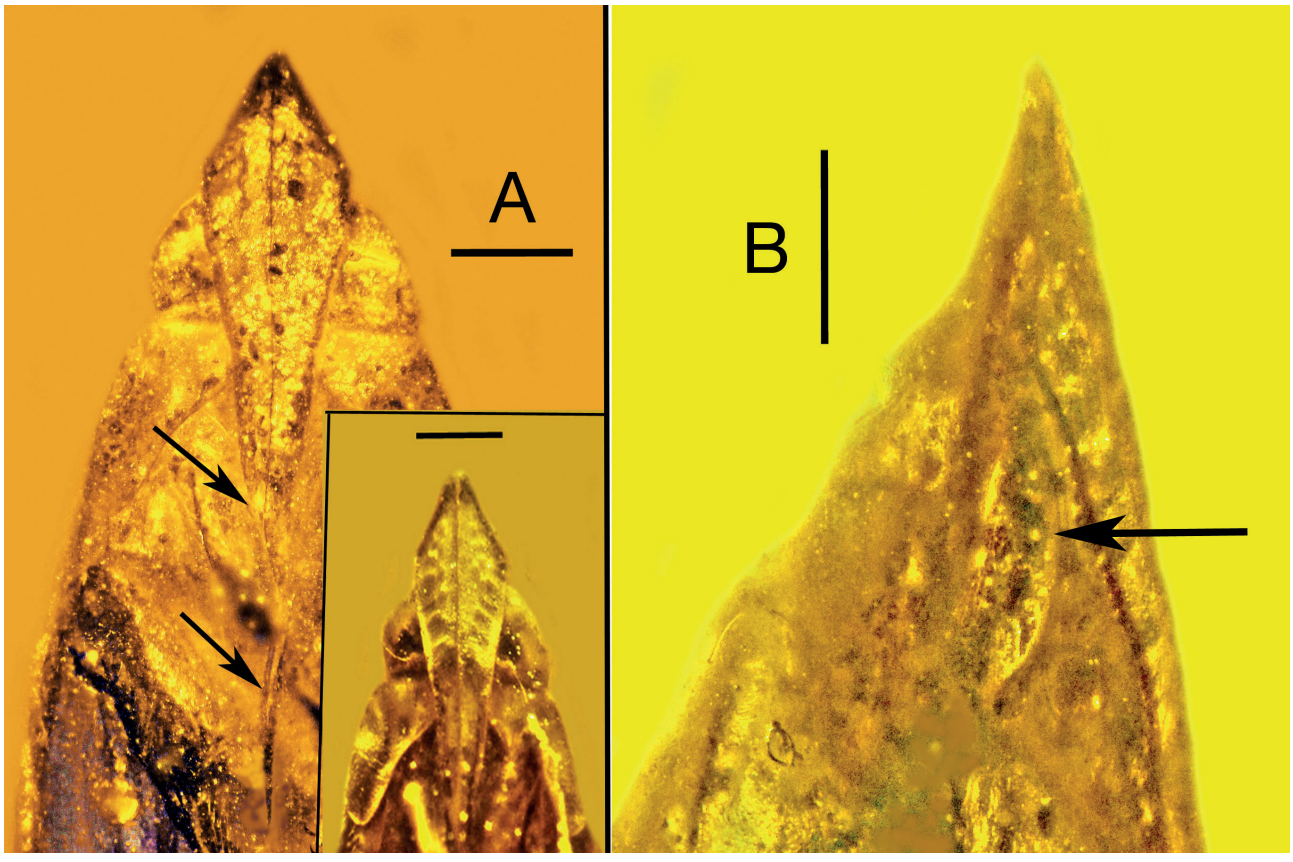

Fig. 4. Holotype of *Stonymetopus megus* gen. et sp. nov. in Burmese amber. **A** – Ventral view of head. Upper arrow shows frontoclypeal suture. Lower arrow shows rostrum. Scale bar = 1.0 mm. Insert shows slanted flutes on front. Scale bar = 1.2 mm. **B** – Lateral view of head. Arrow shows obelliptic eye. Scale bar = 0.3 mm.

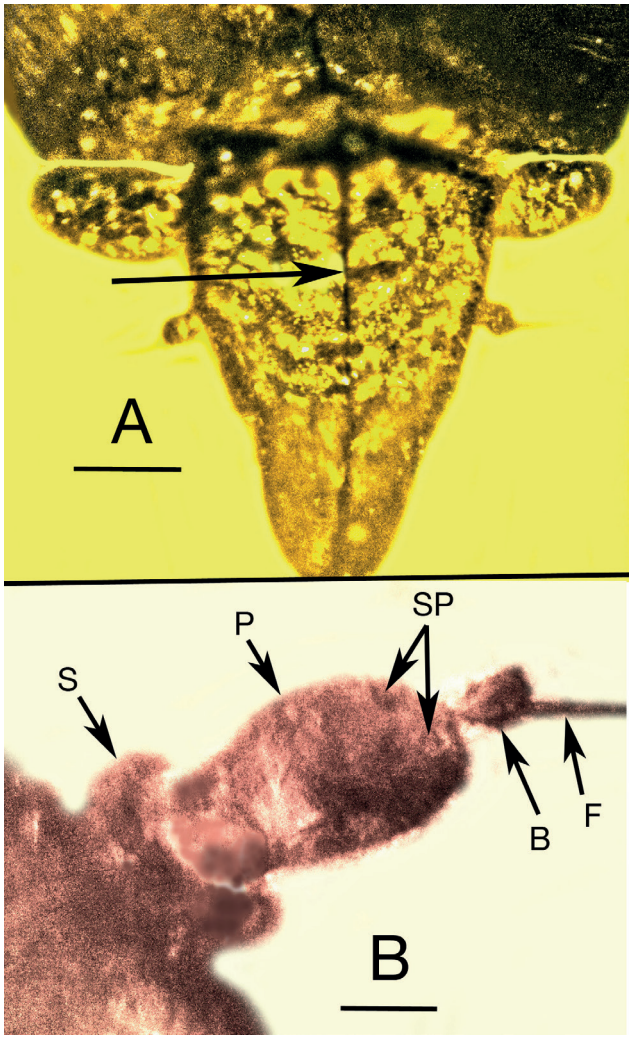

Fig. 5. Holotype of *Stonymetopus megus* gen. et sp. nov. in Burmese amber. **A** – Frontal view of head. Arrow shows medial carina. Scale bar = 0.4 mm. **B** – Antenna. S = Scape; P = pedicel; SP= sensilla placodea; B = basal swelling of flagellum; F = flagellum. Scale bar = 0.8 mm.

As the dryinid larvae develop inside the host, with each successive molt, they rupture the host's body wall and start to emerge from the host, but are always contained in the last larval skin, which protrudes as a sac, or thylacia. When mature, the active white, 5th stage dryinid larva leaves the host and searches for a place to pupate. This is probably what the dryinid larva adjacent to *Stonymetopus megus* was preparing to do when its host landed in resin. The shock of entering the resin probably caused the mature parasite to emerge, similar to the behavior of mature mermithid nematodes that leave their planthopper host when the latter falls in resin (Poinar 2001).

A number of adult dryinid wasps, also known as pincer wasps, have been described from Burmese amber, however, it is not possible to determine if the larva adjacent to *Stonymetopus megus* belongs to any of these described wasp taxa (Olmi et al. 2014, 2020, 2021).

Dryinid parasites are known to alter their host morphology, usually causing a condition known as "parasitic castration" where the reproductive organs are reduced or destroyed (Clausen 1962). While there are no known records of planthopper hosts modified in size or pigmentation due to dryinid parasitism, whether other features are altered, such as wing venation patterns, is unknown.

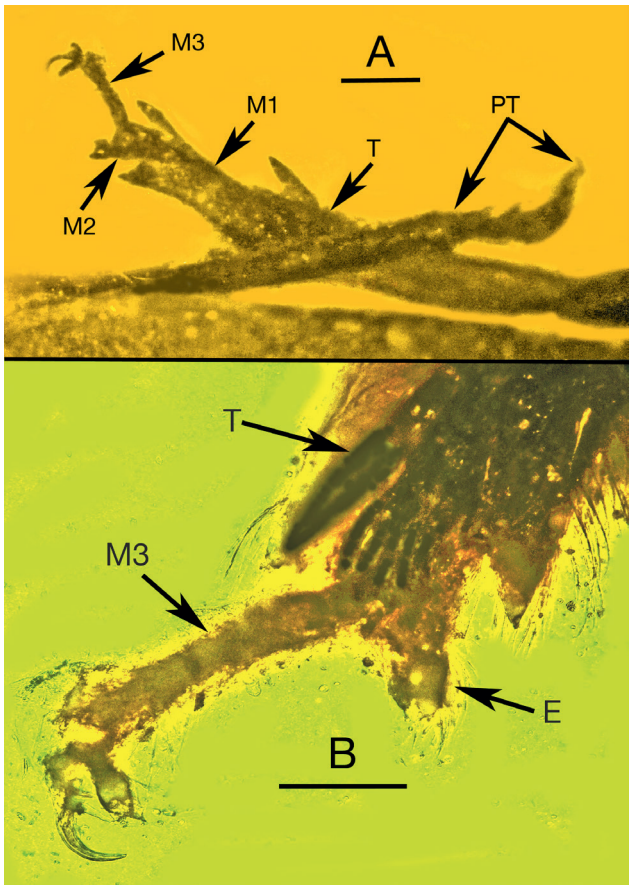

Fig. 6. Holotype of *Stonymetopus megus* gen. et sp. nov. in Burmese amber. **A** – Lateral view of apex of fore and hind legs. T = metatibia with two long lateral spines and five smaller apical spines; M1 = metatarsus 1 with two apical spines; M2 = metatarsus 2 with truncate spine; M3 = metatarsus 3 with claw and arolium; PT = protarsus. Scale bar = 0.2 mm. **B** – Apex of hind leg. M3 = slender metatarsus 3 with claw and arolium; T = metatibia with two long lateral spines and five smaller apical spines; E = truncate spine on metatarsus 2. Scale bar = 0.7 mm.

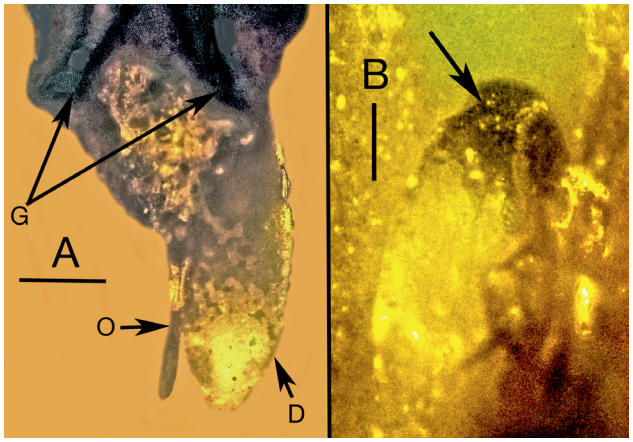

Fig. 7. A – Holotype of *Stonymetopus megus* gen. et sp. nov. in Burmese amber with adjacent dryinid larva (D). O = Ovipositor; G = ventral margins of paired gonoplacs of abdominal segment lX. Scale bar = 0.6 mm. **B** – Anterior portion of dryinid larva. Arrow shows head capsule. Scale bar = 0.2 mm.

5. Conclusions

Here we present yet another fossil planthopper with its own set of unique characters, showing the tremendous diversity of the Fulgoroidea in the mid-Cretaceous, which remains by far underestimated. This high diversity of Cretaceous planthoppers has been repeatedly credited to the rise and diversification of angiosperms (Berendse & Sheffer 2009; Poinar 2018; Bateman 2020; Luo C. et al. 2020, 2021; Luo Y. et al. 2021), which were rapidly branching out into new habitats in competition with the established gymnosperms. While this is probably true for the extant planthopper families, old lineages within the Fulgoridiidae might also have been too specialized to switch from gymnosperm to angiosperm host plants, and became extinct. A clearer understanding of the basal planthopper phylogeny will allow scientists to better estimate the role of angiosperms as key factors in planthopper evolution. Perhaps we can also determine why such a wide diversity

Table 1. Other planthopper families described from Mesozoic deposits with diagnostic features that separate them from *Stonymetopus megus* gen. et sp. nov.

Family	Diagnostic features	References
Acanaloniidae	Under 2.0 L/W tegmen ratio	Zherikhin1978; Bourgoin 2022
Achilidae	Dorsoventrally flattened; wings overlapping at rest	Hamilton 1990; Szwedo 2004; Brysz & Szwedo 2017
Cixiidae	Median ocellus; metatarsomere 2 with row of spines	Botosaneanu 1981
Mimarachnidae	Metatibia with pectens	Shcherbakov 2007b; Szwedo & Ansgorg 2015
Derbidae	Medial head carina absent: apical beak segment short	Emeljanov & Shcherbakov 2020
Dictyopharidae	Small species with elongate head process	Emeljanov 1983; Szwedo 2002
Dorytocidae	Nymphs: long head process, long rostrum	Emeljanov & Shcherbakov 2018
Inoderbidae	Head laterally compressed; pronotum lacking carina	Shcherbakov & Emelijanove 2021; Luo et al. 2022
Jubisentidae	Small, compact, hairy body	Zhang et al. 2019
Katlasidae	Pronotum with elevated disc; CuA 1-branched	Luo et al. 2020
Lalacidae	Median ocellus; pectens on hind legs; claws reduced	Hamilton 1990
Neazoniidae	Nymphal features only	Szwedo 2007; Luo et al. 2021
Perforissidae	Narrow tegman; apical tarsal pectins	Shcherbakov 2007a; Peñalver & Szwedo 2010
Szeiinidae	Under 2.0 L/W tegmen ratio	Zhang et al. 2021
Yetkhatidae	Tegmen membraneous; vertex shorter than pronotum	Song et al. 2019

of planthoppers in the Mid-Cretaceous is not reflected in more recent Cenozoic fossils as well as with extant planthopper families.

A c k n o w l e d g e m e n t s

The authors thank two anonymous reviewers whose comments greatly improved the paper.

6. References

Bateman, R. M. (2020): Hunting the Snark: the flawed search for mythical Jurassic angiosperms. – Journal of Experimental Botany, **71**: 22–35.

Berendse, F. & Scheffer, M. (2009): The angiosperm radiation revisited, an ecological explanation for Darwin's 'abominable mystery'. – Ecology Letters, **12**: 865–872.

Botosaneanu, L. (1981): On a false and a genuine caddis-fly from Burmese amber (Insecta: Trichoptera, Homoptera). – Bulletin Zoölogisch Museum, Universiteit van Amsterdam, **8**: 73–77.

Bourgoin, T. (2022): FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8, updated 20-03-2022. http://hemiptera-databases.org/flow/

Bourgoin, T., Wang, R. R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroiński, A. & Yap, S., Szwedo, J. (2015): From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns of planthoppers (Hemiptera: Fulgoromorpha). – Zoomorphology, **134**: 63–77.

Brysz, A. M. & Szwedo, J. (2017): The fossil record of the planthopper family Achilidae, with particular reference to those in Baltic amber (Hemiptera: Fulgoromorpha). – Earth and Environmental Science, Transactions of the Royal Society of Edinburgh, **107**(2–3): 279–288. https://doi.org/10.1017/S175569101700041X

Clausen, C. P. (1962): Entomophagous Insects. New York (Hefner Publishing Company).

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.

Dietrich, C. H. (2009): Auchenorrhyncha: (Cicadas, Spittlebugs, Leafhoppers, Treehoppers and Planthoppers). In: Resh, V. H. & Cardé, R. T. (eds.): Encyclopedia of Insects (2nd Edition), pp. 56–64; Amsterdam (Elsevier).

Emeljanov, A. F. (1983): Nosatka iz mela Taimyra (Insecta, Homoptera). – Palaeontologicheskii Zhurnal, **17**: 79–85.

Emeljanov, A. F. & Shcherbakov, D. E. (2018): The longest-nosed Mesozoic Fulgoroidea (Homoptera): a new family from mid-Cretaceous Burmese amber. – Far Eastern Entomologist, **354**: 1–14.

Emeljanov, A. F. & Shcherbakov, D. E. (2020): The first Mesozoic Derbidae (Homoptera: Fulgoroidea) from Cretaceous Burmese amber. – Russian Entomological Journal, **29**: 237–246.

Evans, J. W. (1946): A natural classification of leaf-hoppers (Jassoidea, Homoptera). Part. 1. External morphology and systematic position. – Transactions of the Royal Entomological Society of London, **96**(3): 47–60. http://flow.hemiptera.info-syslab.fr/flowpdf/3309.pdf

Fletcher, M. J. (1999): Identification key and checklists for the Planthoppers of Australia and New Zealand (Superfamily: Fulgoroidea). http://www1.dpi.nsw.gov.au/keys/fulgor/index.html

Fletcher, M. J. & Carver, M. (1991): Superfamily Fulgoroidea. In: Neumann, I. D. (ed.): The Insects of Australia, Vol. 1 (2nd Edition), pp. 474–479; Ithaca (Cornell University Press).

Handlirsch, A. (1939): Neue Untersuchungen über die fossilen Insekten, Teil 2. – Annalen des Naturhistorischen Museums in Wien, **49**: 1–240.

Hamilton, K. G. A. (1990): Homoptera. In: Grimaldi, D. A. (ed.): Insects from the Santana Formation, Lower Cretaceous, of Brazil. – Bulletin of the American Museum of Natural History, **195**: 82–121.

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.

Jiang, T., Szwedo, J. & Wang, B. (2019): A unique camouflaged mimarachnid planthopper from mid-Cretaceous Burmese amber. – Scientific Reports, **9**: 13112.

Latreille, P. A. (1807): Sectio secunda. Familia quarta. Cicadariae. Cicadaires. Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata, **3**: 1–258.

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, **115**: 104532 https://doi.org/10.1016/j.cretres.2020.104532

Luo, C., Wang, B. & Jarzembowski, E. A. (2021): A bizarre planthopper nymph (Hemiptera: Fulgoroidea) from mid-Cretaceous Kachin amber. – Insects, **12**: 318. https://doi.org/10.3390/insects12040318

Luo, Y., Bourgoin, T., Szwedo, J. & Feng, J. (2021): Acrotiarini trib. nov., in the Cixiidae (Insecta, Hemiptera, Fulgoromorpha) from mid-Cretaceous amber of northern Myanmar, with new insights in the classification of the family. – Cretaceous Research, **128**: 104959. https://doi.org/10.1016/j.cretres.2021.104959

Luo, C., Song, Z., Liu, X., Jiang, T., Jarzembowski, E. A. & Szwedo, J. (2022): Ingensalinae subfam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea: Inoderbidae), a new planthopper subfamily from mid-Cretaceous Kachin amber from Myanmar. – Fossil Record, **24**: 455–465.

O'Brien, L. B. (2002): The wild wonderful world of Fulgoromorpha. – Denisia, **04**: 83–102.

Olmi, M., Xu, Z. & Guglielmino, A. (2014): A. Descriptions of new fossil taxa of Dryinidae (Hymenoptera: Chrysidoidea) from Burmese amber (Myanmar). – Acta Entomologia Musei Nationalis Pragae, **54**: 703–714.

Olmi, M, Perkovsky, E. E., Martynova, K. V., Contarini, M., Bückle, C. & Gugilielmino, A. (2020): An important intermediate step in the evolution of pincer wasps: an extraordinary new type of chela from mid-Cretaceous Burmese amber (Hymenaea, Dryinidae). – Cretaceous Research, **111**: 104420. https://doi.org/10.1016/j.cretres.2020.104420

Olmi, M., Chen, H-Y., Shih, C., Müller, P., Capradossi, L., Ren, D., Perkovsky, E. E. & Gugilielmino, A. (2021): New species of *Hybristodryinus* Engel (Hymenoptera: Dryinidae) from mid-Cretaceous amber of northern Myanmar, with notes on their possible hosts. – Journal of Hymenopteran Research, **81**: 43–55.

Peñalver, E. & Szwedo, J. (2010): Perforissidae (Hemiptera: Fulgoroidea) from the Lower Cretaceous San Just amber (Eastern Spain). – Alavesia, **3**: 97–103.

Poinar, G. (2018): Mid-Cretaceous Angiosperm flowers in Myanmar amber. In: Welch, B. & Wilkerson, M. (eds.): Recent advances in Plant Research, pp. 187–218; New York (Nova Science Publishers).

Poinar, G. & Ellenberger, S. (2020): Burmese amber fossils, mining, sales and profits. – Geoconservation Research, **3**: 12–16.

Poinar, G. O. Jr. (2001): *Heydenius brownii* sp. n. (Nematoda: Mermithidae) parasitizing a planthopper (Homoptera: Achilidae) in Baltic amber. – Nematology, **3**: 753–757.

Poinar, G. O. Jr., Lambert, G. J. B. & Wu, Y. (2007): Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. – Journal of the Botanical Research Institute of Texas, **1**: 449–455.

Shcherbakov, D. E. (2007a): An extraordinary new family of Cretaceous planthoppers (Homoptra: 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 the Cretaceous family Mimarachnidae (Homoptera: Fulgoroidea) in amber. – Russian Entomological Journal, **26**: 389–392.

Shcherbakov, D. E. & Emeljanov, A. F. (2021): Paradoxical derbid-like planthopper (Homoptera: Fulgoroidea) from Cretaceous Burmese amber. – Russian Entomological Journal, **30**: 135–130.

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.

Song, Z.-S., Xu, G.-H., Liang, A.-P., Szwedo, J. & Bourgoin, T. (2019): Still greater disparity in basal planthopper lineage: A new planthopper family Yetkhatidae (Hemiptera, Fulgoromorpha, Fulgoroidea) from mid-Cretaceous Myanmar amber. – Cretaceous Research, **101**: 47–60.

Szwedo, J. (2002): Amber and amber inclusions of planthoppers, leafhoppers and their relatives (Hemiptera, Archaeorrhyncha et Clypaeorrhyncha). – Denisia, **04**: 37–56.

Szwedo, J. (2004): *Niryasaburnia* gen. nov. for '*Liburnia*' *burmitina* Cockerell, 1917, from Cretaceous Myanmar (Burmese) amber (Hemiptera, Fulgoromorpha: Achilidae). – Journal of Systematic Palaeontology, **2**: 105–107.

Szwedo, J. (2007): Nymphs of a new family Neazoniidae fam. n. (Hemiptera: Fulgoromorpha: Fulgoroidea) from the Lower Cretaceous Lebanese amber. – African Invertebrates, **48**: 127–143.

Szwedo, J. (2008): Distributional and palaeoecological pattern of Lower Cretaceous Mimarachnidae (Hemiptera: Fulgoromorpha). – Entomologia Generalis, **31**: 231–242. doi: 10.1127/entom.gen/31/2008/231

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**: 109–128.

Szwedo, J. & Ansorge, J. (2015): The first Mimarachnidae (Hemiptera: Fulgoromorpha) from Lower Cretaceous lithographic limestones of the Sierra del Montsec in Spain. – Cretaceous Research, **52B**: 390–401. doi: 10.1016/j.cretres.2014.03.001.

Szwedo, J. Bourgoin, T. & Lefebvre, F. (2004): Fossil Fulgoromorpha of the World. An Annotated Catalogue with Notes on Hemiptera Classification. Warsaw (Studio 1).

Szwedo, J. & Zyla, D. (2009): New Fulgoridiidae genus from Upper Jurassic Karatau deposits, Kazakhstan (Hemiptera: Fulgoromorpha: Fulgoroidea). – Zootaxa, **2281**: 40–52.

Zhang, X., Ren, D. & Yao, Y. (2018): A new genus and species of Mimarachnidae (Hemiptera: Fulgoromorpha: Fulgoroidea) from mid-Cretaceous Burmese amber. – Cretaceous Research, **90**: 168–173.

Zhang, X., Ren, D. & Yao, Y. (2019): A new family Jubisentidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea) from the mid-Cretaceous Burmese amber. – Cretaceous Research, **94**: 1–7.

Zhang, X., Jiang, T., Szwedo, J. & Zhang, H. (2021): A new family of Triassic planthoppers (Hemiptera: Fulgoromorpha: Fulgoroidea) from the Shaanxi Province of China. – Alcheringa: an Australasian Journal of Palaeontology, **45**(1): 86–90. https://doi.org/10.1080/03115518.2021.1919206

Zherikhin, V. V. (1978): Razvitie i smena melovykh i kainozoiskikh faunisticheskikh kompleksov (Trakheinyie i Khelicerovye) (In Russian). – Trudy Paleontologicheskogo instituta, Akademia Nauk SSSR, Moskva, **165**: 1–198.

Addresses of the authors

George Poinar Jr., Department of Integrative Biology, Oregon State University, Corvallis, OR 97331 U.S.A.; e-mail: poinarg@science.oregonstate.edu

Alex E. Brown, 629 Euclid Avenue, Berkeley, CA 94708 U.S.A.; e-mail: amberbrownie@icloud.com

Thierry Bourgoin, Institut Systématique Évolution Biodiversité (ISYEB), UMR 7205 MNHN-CNRS-UPMC-EPHE, Muséum National d'Histoire Naturelle, Sorbonne Université, 57 rue Cuvier, CP 50, 75005 Paris, France; e-mail: bourgoin@mnhn.fr

Manuscript received: 11 June 2022, revised version accepted: 4 August 2022.