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Morphological features of the Upper Cretaceous planthopper *Mimaeurypterus burmiticus* suggest specialization for cryptic camouflage on tree bark

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Abstract

The extinct planthopper family Mimarachnidae is widely known in the Cretaceous of Eurasia. Two new specimens of the monotypic genus *Mimaeurypterus* Fu & Huang, 2021, from the early Upper Cretaceous of northern Myanmar are described. The intraspecific variation is assessed, and the description supplemented morphology of the head, pronotum, legs, and abdomen is provided. The flattened pronotum and broad forewings are interpreted as adaptations for the reduction of shadows at body margins, thus blurring the body outline of the insect and facilitating crypsis.

Keywords: fossil, Mesozoic, *Mimaeurypterus burmiticus*, Myanmar amber, planthopper

Introduction

Plant-insect interaction seems an important driver of evolution, leading to diversification of phytophagous animals of the group Pterygota ("flying insects"). Hemipterans, including true bugs, aphids, planthoppers, cicadas, and their relatives, possess highly specialised mouthparts forming a sucking beak, that many of them use to consume juices from plants. The hemipteran infraorder Fulgoromorpha constitutes a highly diverse group, with approximately 13,900 described species (Bourgoin, 2021), the representatives of which are commonly known as planthoppers. The Cretaceous marks a significant period for the diversification of planthoppers, with eleven families reported, including three extant families and eight extinct families (Bourgoin, 2021; Song *et al.*, 2021). Mimarachnidae Shcherbakov, 2007 is such an extinct lineage displaying high morphological diversity indicative of various ecological strategies (Shcherbakov, 2007; Bourgoin & Szwedo, 2008; Szwedo & Ansorge, 2015; Zhang *et al.*, 2018; Jiang *et al.*, 2019). To date, Mimarachnidae comprises 23 formally described species occurring in the Cretaceous of England, Spain, Russia, Japan, and Myanmar (Jiang *et al.*, 2023).

The early Upper Cretaceous Kachin amber, Myanmar harbours an astonishingly diverse terrestrial palaeobiota (Ross, 2019, 2023). Mimarachnidae is well represented in Kachin amber, with 9 known genera: Burmissus Shcherbakov, 2017, Dachibangus Jiang, Szwedo & Wang, 2018, Jaculistilus Zhang, Ren & Yao, 2018, Mimaplax Jiang, Szwedo & Wang, 2019, Ayaimatum Jiang et Szwedo, 2020, Cretodorus Fu et Huang, 2020, Mimaeurypterus Fu & Huang, 2021, Multistria Zhang, Yao & Pang, 2021, and Tenebricosus He, Jiang & Szwedo, 2022 (Shcherbakov, 2017; Jiang et al., 2018, 2019, 2020; Zhang et al., 2018, 2021; Fu & Huang, 2020, 2021; He et al., 2022). Mimaeurypterus burmiticus is a large sized representatives of Mimarachnidae and is characterised by a distinctive pattern on its mesonotum and tegmina that are subrectangular in shape (Fu & Huang, 2021). Here, we describe two new specimens of Mimaeurypterus burmiticus from the early Upper Cretaceous of northern Myanmar. These specimens provide insights into the previously unknown morphology of the head, pronotum, legs, and abdomen, adding new diagnostic characters to the genus and species.

Material and methods

Two specimens (NIGP203978 and NIGP203979) of Mimarachnidae studied herein were sourced from amber mines near Noije Bum, situated in the Hukawng Valley, Myitkyina District, Kachin State, northern Myanmar. Available data suggest that Myanmar amber is generally assigned an age around the Albian-Cenomanian boundary (Cruickshank & Ko, 2003; Shi *et al.*, 2012; Mao *et al.*, 2018). The specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

The amber piece with inclusion (NIGP203978) was manually cut, polished with different grades of sandpaper of gradually finer grits, and finally with rare earth polishing powder. Photographs were taken using a Zeiss AxioZoom V16 stereoscope and a Keyence VHX-6000 digital microscope. All images were optimized and organized into plates using Adobe Photoshop CC 2019. Morphological measurements were conducted using ImageJ software. Wing venation terminology mainly follows Bourgoin *et al.* (2015).

Systematic palaeontology

Hemiptera Linnaeus, 1758 Fulgoromorpha Evans, 1946 Fulgoroidea Latreille, 1807 Mimarachnidae Shcherbakov, 2007

Mimaeurypterus Fu & Huang, 2021

Type species. *Mimaeurypterus burmiticus* Fu & Huang, 2021; by original designation.

Mimaeurypterus burmiticus Fu & Huang, 2021 (Figs 1, 2)

Material. NIGP203978 and NIGP203979, deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Type locality and horizon. Amber mine near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, northern Myanmar; early Upper Cretaceous.

Supplemental description. Head (Fig. 2C) triangular in dorsal view, wider than long, vertex expanded laterally over eyes, with a shallow median line, lateral margins lightly carinate; compound eyes subequal in length and width and prominently bulging; dorsal ocular ration of about 0.5 (width of head over width of intraocular space); anterior margin of eyes at one third of head length; labium reaching to metacoxa. Pronotum (Fig. 2B) about 3.0 times wider than long; surface wrinkled in texture and with common small tubercles, bearing doubled median carination diverging near posterior margin; anterior margin of pronotum concave, widely U-shaped; anterolateral margin with expanded flattened rectangular lobes (in dorsal view); anterior angle of lobes very sharp, lateral and posterior angles slightly rounded; lobes reach middle of eye level forming a median depression between the expanded lobes; posterior margin of pronotum evenly concave. Mesonotum (Figs 1C, 2B) wider than long medially, roughly hexagonal (in dorsal view), surface with sparse small tubercles each with what appears as a sensory pit; median carination doubled, slightly arcuate, diverging posteriorly and anteriorly, extending to anterior quarter of mesonotum; lateral carinae emerge at center of posterolateral margins of mesonotum and bend mediad converging with anterior apex of median carinae to form a pair of subtrapezoid sections; sparse dark mottled colouration forming concentric rings around a pair of darkly pigmented ovately shaped clusters of enlarged granular protrusions on both sides of median carinae (Fig. 2E); scutellum triangular with transverse wrinkles (Fig. 2B). Mesoscutellar auxillari cord surface with densely packed in small microscopic granules approximately 10 µm in diameter (Fig. 1E). Tegmen (forewing) (Figs 1A, 2D) with variable number and pattern of secondary forking in MP, between two and three total, with one or two terminals for each of MP_{1+2} and MP_{3+4} ; very dense crossveins over tegmen surface, denser near wing base progressively becoming more sparse towards wing apex; microstructure of forewing consisting of faint transverse wrinkles (Fig. 1B). Hind wing dark (Figs 1A, 2D). Legs with procoxa unclear, protibia carinate; mesotibia carinate, subequal to mesofemur in length; metacoxa short, metafemur subequal to metacoxa in length; metatibia (Fig. 1F) carinate, bearing 5 distal teeth; metatarsus (Fig. 1F) with proximal tarsomere nearly three times as long as mid tarsomere, each with 5 distal teeth, distal tarsomere subequal to proximal tarsomere, distal tarsomere very narrow with a pair of claws, pulvilli indistinct; tibia and tarsi with uniform dark pigmentation. Abdomen flattened, not reaching tips of tegmina, segment III broadest (Fig. 1D).

Measurements. NIGP203978 (adult female): Mesonotum: length 3.43 mm, width 7.36 mm. Tegmen: preserved length 17.3 mm, width 7.76 mm. Hind wing: length 14.63 mm and width 7.94 mm. Legs (femur/tibia// tarsomere1/2/3//claws) (in mm): Foreleg lengths (2.60/2. 04//0.97/0.22/0.31//?); midleg lengths (3.79/3.53//?/1.12 /?/?//?); hindleg lengths (2.70/4.25//1.52/0.55/0.63//0.18); metatibial distal teeth about 0.25 mm long, two lateral teeth 0.41 mm long.

NIGP203979: Head length 1.38 mm, width 2.54 mm; compound eyes length 0.96 mm, width 0.88 mm; pronotum length 2.47 mm, width 8.76 mm; mesonotum length 4.54 mm, width 7.55 mm; pronotal lobes length



FIGURE 1. Photographs of *Mimaeurypterus burmiticus*, NIGP203978, under light microscopy. **A**, General habitus, dorsal view. **B**, Closeup of tegmen showing wrinkled microrelief. **C**, Mesonotum. **D**, Thorax and abdomen, ventral view. **E**. Closeup of mesonotal axillary cord, showing granular microrelief. **F**. Hind tarsus. Abbreviations: mac, mesonotal axillary cord; mttb, metatibia; mtt1–3, metatarsomeres 1–3.



FIGURE 2. Photographs of *Mimaeurypterus burmiticus*, NIGP203979, under light microscopy. A, General habitus. B, Head, pronotum, and mesonotum. C, Head. D, Forewing and hind wing. E, Enlargement of a pair of darkly pigmented clusters of tubercles on mesonotum. Abbreviations: ce, compound eye; pn, pronotum; msn, mesonotum.

3.32 mm, width 1.72 mm; maximal intraocular distance 1.36 mm; Tegmen length 19.51 mm, width 8.59 mm.

Remarks. The specimens can be identified as *M*. *burmiticus* based on the following characters: mesonotum

median carinae paired, closely adhering and not reaching anterior margin, median carinae connecting to lateral carinae to form ovoid raised sections, mesonotum with a pair of darkly pigmented ovately shaped clusters of enlarged granular protrusions on both sides of median carinae (surrounded by concentric mottling); tegmen subrectangular in shape, with apical margin truncate, anterobasal angle widely rounded, tegmen length close to 20 mm (17.3–19.6), with length to width ratio of about 2.1–2.3, tegmen venation as in the type specimen (e.g., stem ScP+R+MP distinctly shorter than stem ScP+R, RP unbranched, and stem CuA forked deeply, slightly basad of claval veins Pcu and A1 junction), with extremely fine mesh polygonal cells, tegmen with postcostal cell wider than C1 cell but narrower than radial cell, tegmen colouration consisting of uniform brown near base and progressively increased mottling distally, with three light spots along radial cell (first slightly proximal to initial fork, second past fork, and third distally) and one in center of medial cell.

The morphological characteristics of the head, pronotum, and legs of *M. burmiticus* are supplemented here, based on two new specimens from Myanmar amber as follows: head small, length about half of width; ocular ratio of 0.5, eyes subequal in length and width. Pronotum with anterior margin concave, widely U-shaped, with pointed lateral angles; anterolateral margin expanded into flattened subrectangular lobes; lobes reach middle of eye level; pronotum wider than mesonotum, about 3.5 times wider than head. Metatibio-metatarsal apical teeth formula 5:5:5.

Discussion

The new specimens differ from the already known specimens of Mimaeurypterus burmiticus. These differences are minor and cannot warrant interpreting the new specimens as representing a new species. In consequence these characters are interpreted as representing variability. One such variable character is the number of terminals of MP, which vary between two and three, and their exact positions also differ, with each of MP_{1+2} and MP₂₁₄ having between one and two terminals. The number of MP terminals has been commonly used as a diagnostic character for species and also higher taxonomic units (genera) within Mimarachnidae. However, the variability in the number of MP terminals in M. burmiticus and in the type specimen of Mimaplax ekrypsan calls into question the strict use of this character for species diagnosis (Jiang et al., 2019). Further investigation is necessary, especially in genera with multiple forks on MP such as Dachibangus, Xiaochibangus, and Jaculistilus.

Additionally, the hind wings of the new specimens appear significantly darker compared to the type specimen, which may be a possible taphonomic artefact. The mesonotum colouration additionally presents minor differences in the color pattern. NIGP203978 shows a well-defined pattern of dark concentric rings, whereas the type specimen and NIGP203979 show a strongly reduced contrast in these markings. However, this variation may be attributed to differences in the preservation of the three specimens. with NIGP203978 being the only specimen that preserved a complete body cavity, which subsequently infilled with light-colored calcite crystals resulting in an increased contrast of the markings. Given the consistent body size and proportions, colour pattern (particularly the positioning of light and dark spots on the tegmen), form and distribution of veins and cells, size of the polygonal crossvein mesh, shapes of the pronotum, mesonotum, and tegmen among the specimens, along with the same locality of origin, it is reasonable to interpret these three specimens as representing the same species.

The new specimens of M. burmiticus exhibit a notably small head compared to both the pronotum and mesonotum. The head is twice as wide as it is long, and about 3.50 and 2.75 times shorter than pronotum and mesonotum respectively. This ratio is consistently below 2.20 times for the pronotum and 2.36 times for the mesonotum in all other known representatives of Mimarachnidae, both in Jaculistilus oligotrichus, which possesses a remarkably narrow yet elongated head (Zhang et al., 2018). Additionally, the new fossils display an expanded pronotum, wider than the mesonotum, which is characterized by a widely U-shaped anterior margin with pointed lateral angles, and the anterolateral margin expanded into flattened subrectangular lobes, appearing subrectangular in dorsal view. The shape and dimensions of the pronotum are unique for this species within Mimirachnidae, at least for the species for which the structure is known. Mimaeurypterus burmiticus shares the metatibio-metatarsal formula (distal teeth) of 5:5:5 with Ayaimatum minutum, whereas the ratio in M. ekrypsan is 4:5:5, 6:7:7 in Jaculistilus oligotrichus, and 6:6:7 in J. xixuanae.

Representatives of Mimarachnidae commonly show mottled color patterns or dark and light bands, these were interpreted as cryptic and disruptive coloration to camouflage the insects (Zhang *et al.*, 2021). This adaptation is particularly useful as fulgoromorphans are phytophagous insects feeding on plant fluids, as such they have to stay in place for long periods of times to obtain adequate nutrition exposing them to potential predators (Stevens & Merilaita, 2009). *Mimaeurypterus* presents cryptic mottled coloration on its body, well suited for camouflage on tree bark. Additionally, *M. burmiticus* bears a suite of characters that could represent "flatoidinization syndrome", coined to describe a set of characters including flattened body form, cryptic coloration, and morphology enabling an insect to be mostly invisible on the bark of trees (Szwedo et al., 2017). Two fossil occurrences of planthoppers exhibiting this syndrome have been reported, Gedanotropis sontagae Szwedo et Stroiński, 2017 (Tropiduchidae) from Baltic amber and M. ekrypsan (Mimarachnidae) from Myanmar amber (Szwedo et al., 2017; Jiang et al., 2019). The new fossils of *M. burmiticus* present strongly expanded and flattened pronotum lobes laterally covering the head, a feature newly observed for this species. Additionally, M. burmiticus exhibits the broad and flat forewings with widened costal area, straight posterior, and truncate apical margins allowing for full tegmen closure and tight adherence to the underlying surface at rest. The tight adherence of the insects to the ground surface, along with tight jointing of their body structures, likely facilitated the reduction of profile and edge shadows, thus blurring the body outline and improving tree bark camouflage.

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