



Three new species of *Multistria* from mid-Cretaceous amber of northern Myanmar (Hemiptera: Fulgoromorpha: Mimarachnidae)

DOLEV FABRIKANT¹, DI-YING HUANG² & YAN-ZHE FU^{1,2,*}

¹Ludwig-Maximilians-Universität München, Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

²State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

✉ dolev.fabrikant@campus.lmu.de; <https://orcid.org/0009-0004-4388-4026>

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

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

*Corresponding author

Abstract

The extinct planthopper family Mimarachnidae is well represented in mid-Cretaceous Kachin amber of northern Myanmar. In this study, three new species of mimarachnid planthoppers are described and illustrated from Kachin amber, all belonging to the genus *Multistria* Zhang, Yao & Pang, 2021. The new species, *Multistria irregularis* sp. nov., *M. juanae* sp. nov., and *M. fionae* sp. nov., are primarily distinguished from each other mostly by tegminal characters, such as the branching pattern of the secondary veinlet meshwork, venation, and the colour patterns, as well as differences in head. The tegminal diagnostic characters of *Multistria* are briefly examined.

Keywords: Myanmar amber, planthopper, taxonomy, new taxa, Mesozoic

Introduction

Fulgoromorpha, commonly known as planthoppers, represent a highly diverse group of Phytophagous hemipterans. The Cretaceous period was a crucial time for the diversification of planthoppers. The mid-Cretaceous Kachin amber from northern Myanmar preserves one of the most diverse Cretaceous terrestrial palaeobiota, particularly abundant in fossil insects (Ross, 2019, 2023, 2024), offering a window of significant insight into the diversity of insect lineages during the mid-Cretaceous. To date, four extant families of planthoppers (*i.e.*, Achilidae, Cixiidae, Derbidae, and Nogodinidae) and eight extinct families (*i.e.*, Dorytocidae, Fulgoridiidae, Inoderbidae, Jubisentidae, Katlasidae, Mimarachnidae, Perforissidae,

and Yetkhatidae) have been recorded in Kachin amber (Song *et al.*, 2021; Bourgoïn, 2024; Ross, 2024).

Mimarachnidae Shcherbakov, 2007, is an extinct lineage of planthoppers restricted to the Cretaceous of Eurasia. Currently, ten genera and eighteen species of Mimarachnidae have been documented in Kachin amber (Jiang H *et al.*, 2023; Liu *et al.*, 2024). Those taxa exhibit a high degree of morphological diversity including: large differences in size with the largest species *Dachibangus trimaculatus* about 6 times longer than the smallest species *Chaloricridulum montsecensis*, appreciable differences in colour patterns ranging from fine mottled colouration to broad colour bands and complex eyespots along with body shape modifications for the purpose of crypsis as part of the “flatoidinisation syndrome” (Shcherbakov, 2007; Zhang *et al.*, 2018, 2021; Jiang T *et al.*, 2019; Jiang H *et al.*, 2023; Fabrikant *et al.*, 2024), suggesting this planthopper lineage employed a variety of potential ecological strategies in mid-Cretaceous.

In this study, we describe three new species of the genus *Multistria* Zhang, Yao & Pang, 2021 from Kachin amber, the new fossils showcase well preserved wing venation and colour patterns, thereby enhancing our understanding of the morphological disparity within this group. The type species, *Multistria orthotropa* Zhang, Yao & Pang, 2021, was described based on a single adult male specimen from Kachin amber, which is similar to the newly described species exhibiting distinctive broad colour bands on the tegmina (Zhang *et al.*, 2021). These colour bands have irregular edges and are divided into numerous small polygonal cells, disrupting their uniform appearance. This type of pattern is believed to have aided the insect in avoiding predation via effectively breaking up the body outline.

Material and methods

The specimens studied herein originated from amber mines near Noiye Bum, Hukawng Valley, Kachin State, northern Myanmar. The specimens NIGP205757 and NIGP205758 are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The specimen PED4415 deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany.

The amber pieces with inclusions (NIGP205757 and PED4415) were polished using different grades of sandpaper and finished with rare earth polishing powder. Photographs were taken using a Zeiss AxioZoom V16 stereoscope and a Keyence VHX-6000 digital microscope. Images were further processed in Adobe Photoshop CC 2019 to adjust brightness and contrast. Line drawings were drafted with Procreate 5.3.9. Morphological measurements were conducted using ImageJ software. Wing venation terminology mainly follows Bourgoin *et al.* (2015).

Systematic palaeontology

Hemiptera Linnaeus, 1758

Fulgoromorpha Evans, 1946

Mimarachnidae Shcherbakov, 2007

Multistria Zhang, Yao & Pang, 2021

Type species. *Multistria orthotropa* Zhang, Yao & Pang, 2021

Diagnosis (revised after Zhang *et al.*, 2021). The combination of the following characters: pronotum about 1/4 as long as wide; tegmen with costal area narrow, distinct reaching anteroapical angle, veins ScP+RA and RP close and subparallel, with apices nearly parallel to wing margin; MP with 3–4 terminals; anteroapical angle rounded; stem ScP+R very short, approaching or shorter than width of postcostal cell; postcostal cell about twice as wide as C1 cell (between ScP+RA and RP) at midpoint of wing; posterior of radial cell concave or straight; Pcu nearly straight basally and then curved anteriorly at claval veins junction, free part of Pcu distinctly shorter than common stem of Pcu+A1.

Remarks. The specimens described in this study can be assigned to Mimarachnidae owing to the following characters: mesonotum with doubled median carinae, simplified wing venation with prominent irregular network of secondary veinlets, basal cell weak.

The genus *Multistria* can be distinguished from all genera of Mimarachnidae except from *Dachibangus*, *Xiaochibangus*, and *Jaculistilus* by the following: costal

area narrow but distinct reaching anteroapical angle; ScP+RA and RP close and subparallel, with apices nearly parallel to the wing margin; base of CuA₁ subparallel to stem CuA (oblique in *Dachibangus*); RP simple (as in *Burmissus* and *Cretodorus*); MP with 3–4 terminals. It can further be differentiated by the following characters: frons wide, about equal width to eyes (very narrow in *Jaculistilus*); pronotum about 4 times as wide as long (about 1/2 as long as wide in *Jaculistilus*); anteroapical angle rounded (more pronounced in *Dachibangus*); stem ScP+R shorter than the width of postcostal cell (stem ScP+R longer in *Dachibangus* and *Xiaochibangus*); postcostal cell about twice as wide as C1 cell at tegmen midline (subequal in *Dachibangus*); posterior of radial cell nearly straight or concave (pronounced convexity in *Xiaochibangus*); Pcu curved anteriorly at claval veins junction (straight in *Dachibangus*, *Xiaochibangus*, and *Jaculistilus*); and transverse dark bands along tegmen with light network of secondary veinlets (uniform pigmentation in *Jaculistilus*). The rugulose pronotum described by Zhang *et al.* (2021) was not observed in any of the presently described specimens and thus was excluded from the revised genus diagnosis. This character may be unique to *Multistria orthotropa* or represent a taphonomic artefact.

Key to species of *Multistria* from Kachin amber

1. Tegmen with eyespots in radial cell; veinlet meshwork dominated by veinlets perpendicular to the main veins *Multistria juanae* **sp. nov.**
- Tegmen lacking eyespots in radial cell; veinlet meshwork with rare perpendicular veins **2**
2. Tegmen with costal and posterior margins subparallel; veinlet meshwork fine; pigmented bands with lighter interior and darkened margins ... *Multistria fionae* **sp. nov.**
- Tegmen with costal and posterior margins not parallel; coarser veinlet meshwork, main veins occasionally separated by one or two polygonal cells; pigmented bands uniform in colour **3**
3. Tegmen with eyespot near base of postcostal cell; meshwork of veinlets forming polygonal cells of widely varying size, large cells adjacent to very small cells *Multistria irregularis* **sp. nov.**
- Tegmen lacking eyespot near base of postcostal cell; meshwork of veinlets forming polygonal cells of relatively uniform size *Multistria orthotropa*

Multistria irregularis **sp. nov.**

(Figs 1, 4A)

Material. Holotype, NIGP205757, male.

Etymology. The species name refers to the irregular meshwork of veinlets on the forewing, with sizes that vary widely.

Diagnosis. Compound eyes taking up to 2/3 of head width (up to 1/2 for *M. juanae* and 4/5 for *M. orthotropa*);

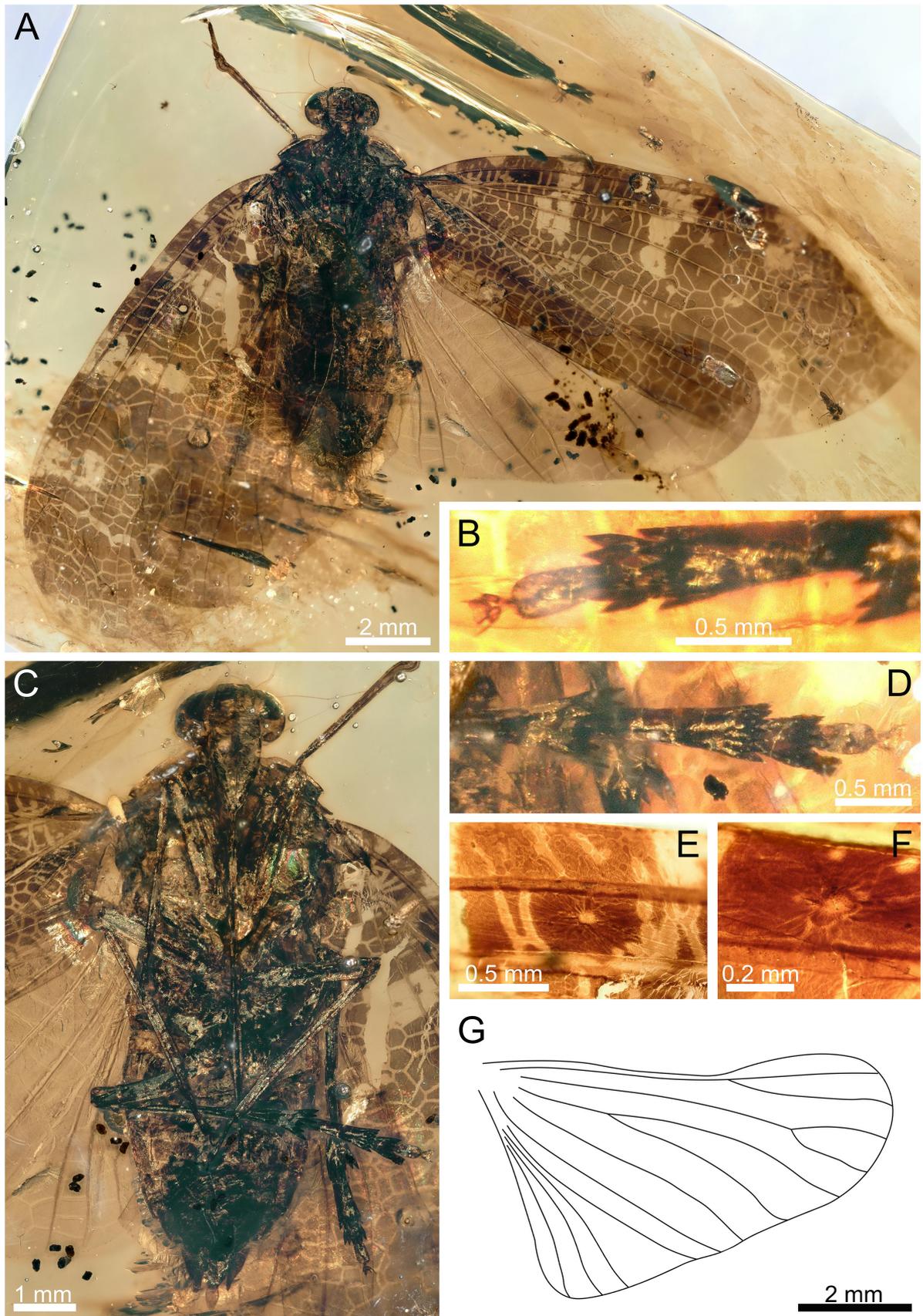


FIGURE 1. Photographs of *Multistria irregularis* sp. nov., NIGP205757, under light microscopy. **A**, General habitus, dorsal view. **B**, General habitus, ventral view. **C**, Right metatarsi. **D**, Left metatarsi. **E**, Eyespot on the left tegmen. **F**, Eyespot on the right tegmen. **G**, Line drawing of hind wing.

basal part of stem MP straight (arched posteriad in *M. orthotropa* and *M. juanae*); MP with 4 terminals (3 terminals in *M. orthotropa*, *M. juanae*, and *M. fionae*); CuA forked basad of claval veins junction (apicad in *M. orthotropa*); Pcu and A1 fused at about 1/4 of tegmen length (1/3 in *M. orthotropa* and *M. juanae*); and veinlets sizes irregular with small cells adjacent to large cells (fairly regular adjacent cell size in *M. orthotropa*, *M. fionae*, and *M. juanae*).

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

Description. Adult male, body about 9.4 mm long, 3.6 mm wide.

Head with compound eyes about 1.7 mm wide; posterior margin of eyes in line with head, compound eyes taking up to 2/3 of head width; vertex with median and lateral carinae at margin; frons about twice longer than wide, about equal in width to eyes, with a median carina; clypeus triangular in shape with lateral and median carinae; lateral margins slightly convex; antenna with scape stout, flagellum filiform; rostrum long and narrow, extending to middle of abdomen.

Pronotum about 2.9 mm wide, 4 times wider than long; anterior margin sinuate, medially slightly convex, lateral margins keeled with row of setae, posterior margin slightly concave medially; posterolateral angle sharp; median carinae paired, lateral carinae indistinct. Colouration consists of two transverse dark stripes. Mesonotum poorly preserved, with fine scaly texture and uniformly distributed granules; about 2.9 mm wide, about as wide as long, 3 times longer than pronotum; median carinae paired, reaching mesonotum; lateral carinae converging anteriorly; scutellum indistinct; tegula distinct.

Tegmen length 12.1 mm, and width 5.5 mm, about 2.2 times longer than wide; venation distinct and connected by veinlets arranged in a polygonal network, veinlets hardly ever perpendicular to main veins, cell sizes very irregular; tegmen slightly broadening towards apex; costal margin slightly arched, tornus weak, posterior margin straight; anteroapical and posteroapical angles broadly rounded; costal area narrow, tapering towards and extending to apical margin; stem ScP+R shorter than stem ScP+R+MP and width of postcostal cell; veins ScP+RA and RP simple, subparallel to costal margin; distal part of ScP+RA slightly arched anteriorly; apex of ScP+RA curved posteriad, running subparallel to apical margin and almost fusing; stem MP nearly straight, slightly arched anteriorly, forked at distal half of wing; MP with 4 terminals; MP₁₊₂ forking distally with 2 terminals; MP₃₊₄ forking proximally with 2 terminals; CuA forked slightly basad of Pcu and A1 junction; CuA₁ and CuA₂ nearly straight; CuP straight; Pcu and A1 fused at about 1/4 of wing length; Pcu curved anteriorly at Pcu and A1 junction. Colouration

consists of 4 transverse brown bands with irregular edges crossed by mesh of light veinlets, joined at posterior half; band width subequal; small eyespot about 0.7 mm long and 0.3 mm wide, near base of postcostal cell. Hind wing about 8.9 mm long and 5.5 mm wide; ScP+R with two terminals; ScP+RA straight; RP curved posteriad distally; MP forked laterally, with two terminals; CuA forked at about 1/3 of wing length; CuA₁ bowed anteriorly basally; CuA₂ curved anteriorly distally; CuP slightly sinuous; Pcu slightly bowed posteriad; A1 simple; anal veins with at least 3 terminals. Colouration: dark at distal part of wing, with two light spots.

Procoxa subequal in length to profemur, protibia carinate slightly longer than profemur; mesocoxa subequal to mesofemur in length; mesotibia carinate about 1/3 longer than mesofemur; metaocoxa subequal to metafemur in length; metatibia carinate twice as long as metafemur, bearing 6 distal teeth; metatarsus with proximal tarsomere nearly three times as long as mid tarsomere, each with 6 distal teeth (with exception for left proximal tarsomere with 7 distal teeth), proximal tarsomere subequal to distal tarsomere in length; distal tarsomere very narrow with a pair of claws, pulvilli indistinct; tibia and tarsi with uniform dark pigmentation.

Legs measurements: (coxa/femur/tibia/tarsomere1/2/3/claw): Foreleg lengths (2.07//2.3/2.9//0.6/?/?/?); midleg lengths (2.22//2.15/3.47//0.21/0.18/0.19//0.06); hindleg lengths (1.455//1.91/3.49//1.22/0.56/0.53//0.06); metatibial distal teeth about 0.25 mm long, two lateral distal teeth 0.41 mm long.

Abdomen flattened, not reaching tips of tegmina with segment III broadest. Male terminalia laterally flanked by symmetrical triangular lobes with external surfaces pigmented; subgenital plate darkly pigmented; anal stylet forming an apically pointed oval flap.

Remarks. *Multistria irregularis* is the first known member of Mimarachnidae with a forked hindwing MP, contrary to the previous assumption that a simple MP is characteristic of the family. This finding is not surprising in the context of the variable venation common within the clade and may result from undersampling, as hindwings are described in few Mimarachnidae.

***Multistria juanae* sp. nov.**

(Figs 2, 4B)

Material. Holotype, NIGP205758. Gender unknown.

Etymology. The specific name is dedicated to Dr. Juan Li, who tragically passed away during a scientific expedition on the Tibetan Plateau in 2023, honouring her outstanding contributions and passion for geological sciences.

Diagnosis. Head with irregular mottled pigmentation in dorsal view (uniform colouration in other species); pronotum medially marked with a light transverse stripe;



FIGURE 2. Photographs of *Multistria juanae* sp. nov., NIGP205758, under light microscopy. **A**, General habitus, dorsal view. **B**, General habitus, ventral view. **C**, Head, pronotum and part of mesonotum, dorsal view. **D**, Eyespot on right tegmen. **E**, Metatarsi.

mesonotum with dark mottled bands (uniform colouration in other species); compound eyes taking up to 1/2 of head width (up to 2/3 in *M. irregularis* and 4/5 in *M. orthotropa*); MP with 3 terminals and MP₁₊₂ forking midway (*M. irregularis* with 4 terminals and MP₁₊₂ forked distally in *M. fionae*); Pcu and A1 fused at about 1/3 of tegmen

length from base (1/4 in *M. fionae* and *M. irregularis*); CuA forked basad of Pcu and A1 junction (apicad in *M. orthotropa*); meshwork of secondary veinlets perpendicular to the main veins, resulting in a rectangular blocky appearance to the cells (rare perpendicular crossveins in other species); two eyespots situated on radial cell (radial

cell without eyespots in other species); and all bands fully separated (some bands joined in other species).

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

Description. Adult, ventral side not visible; body length about 12.5 mm.

Head with compound eyes about 2.8 mm wide; posterior margin of eyes in line with head; compound eyes taking up to 1/2 of head width; vertex with median and lateral carinae at margin; frons about 2 times longer than wide, about 1.5 times wider than eyes, with median carina; head with irregular mottled colouration.

Pronotum about 4.5 mm wide, 4 times wider than long; anterior margin sinuate, and medially slightly convex, posterior margin slightly concave medially; posterolateral angle sharp; median carina paired diverging anteriorly, lateral carinae indistinct, lateral margins keeled with row of setae. Colouration consists of two transverse dark stripes, anterior stripe reaching anterior margin. Mesonotum with fine scaly texture and uniformly distributed granules; about 4.3 mm wide, about as wide as long, 3 times longer than pronotum; median carinae paired reaching mesonotum, lateral carinae converging anteriorly; scutellum small with transverse wrinkles; tegula distinct. Colouration consists of 3 transverse wavy lines of dark irregular mottling and a rectangular median spot near the anterior margin lacking significant mottling.

Tegmen length 11.8 mm, and width 5.3 mm, about 2.2 times longer than wide; venation distinct and connected by veinlets arranged in a polygonal network; secondary veinlet network with abundant veinlets perpendicular to main veins; tegmen slightly broadening towards apex; anteroapical and posteroapical angles broadly rounded; tornus weak; costal area narrow, tapering and almost reaching tegmen apex; stem ScP+R shorter than stem ScP+R+MP and width of postcostal cell; veins ScP+RA and RP simple, subparallel to costal margin; stem MP arched posteriad at base then slightly curved anteriorly, forked at 1/3 from tegmen apex; MP with 3 terminals, MP₁₊₂ forking midway with 2 terminals, MP₃₊₄ simple; CuA with two terminals forked slightly basal of Pcu and A1 vein junction; CuA₁ arched anteriorly, CuA₂ apical half arched posteriorly, CuP simple and straight; Pcu and A1 fused at about 1/3 from tegmen base; Pcu curved anteriorly at junction with A1. Tegmen colouration consists of 4 transverse dark colour bands with irregular jagged edges crossed by mesh of light secondary veinlets; bands narrowly and fully separated; band width progressively increasing apically; two eyespots present on radial cell, the first 0.8 mm wide situated about 2/3 from tegmen base and the second 0.6 mm wide situated next to second fork of mp; eyespot disc of similar colour as pigmented bands. Hindwing mostly missing, colouration dark with at least one light spot near wing margin.

Profemur slightly shorter than protibia; protibia carinate; mesotibia carinate, slightly longer than mesofemur; metatibia carinate, about 1/2 longer than metafemur, bearing 6 distal teeth; metatarsus with proximal tarsomere about three times as long as mid tarsomere, each bearing 6 distal teeth; legs with uniform pigmentation.

Legs measurements (coxa/femur/tibia/tarsomere_{1/2/3}/claws): Foreleg lengths (?/3.15/3.45/?/?/?); midleg lengths (?/2.9/3.3/0.8/?/?/?); hindleg lengths (?/3.1/4.51/1.57/0.61/?/?/?); metatibial distal teeth up to 0.41 mm long.

***Multistria fionae* sp. nov.**

(Figs 3, 4C)

Material. Holotype, PED4415, Gender unknown.

Etymology. The species name is dedicated to Fiona, the beloved cat of Dolev Fabrikant (first author).

Diagnosis. Tegmen narrow, length to width ratio 2.8 (length to width ratio about 2.2 in *M. orthotropa*, *M. juanae* and *M. irregularis*); costal and posterior margins subparallel (tapering proximally in *M. orthotropa*, *M. juanae* and *M. irregularis*); MP with 3 terminals (4 terminals in *M. irregularis*); MP₁₊₂ forking very late (forking close to midway in *M. orthotropa* and *M. juanae*); Pcu and A1 fused at about 1/4 of tegmen length from base (1/3 for *M. orthotropa* and *M. juanae*); CuA forked basal of Pcu and A1 junction (apical in *M. orthotropa*); veinlet mesh very fine (mesh with larger cells in other species); tegmen without eyespots (eyesspots present in *M. irregularis* and *M. juanae*); transverse pigmented bands with darker margins (uniform colour bands in other species), two basal bands fully separated (all bands joined in *M. irregularis*); and distal tarsomere of metatarsus widen, subequal in width to distal portion of basal tarsomere (distal tarsomere narrower in *M. orthotropa*, *M. juanae*, and *M. irregularis*).

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

Description. Adult, body length about 12.8 mm.

Pronotum about 4.5 mm wide, 4 times wider than long, anterior margin sinuate, and medially slightly convex, lateral margins keeled; posterolateral angle sharp; carinae obscured. Mesonotum poorly preserved, with fine scaly texture and uniformly distributed granules; about 4.5 mm wide, 3 times longer than pronotum; median carinae paired reaching mesonotum; lateral carinae converging anteriorly; scutellum obscured; tegula distinct.

Tegmen length 14.7 mm, and width 5.3 mm, about 2.8 times longer than wide; venation distinct and connected by veinlets arranged in a fine polygonal network; tegmen slightly broadening towards apex; costal margin nearly straight, apex rounded, anteroapical and posteroapical

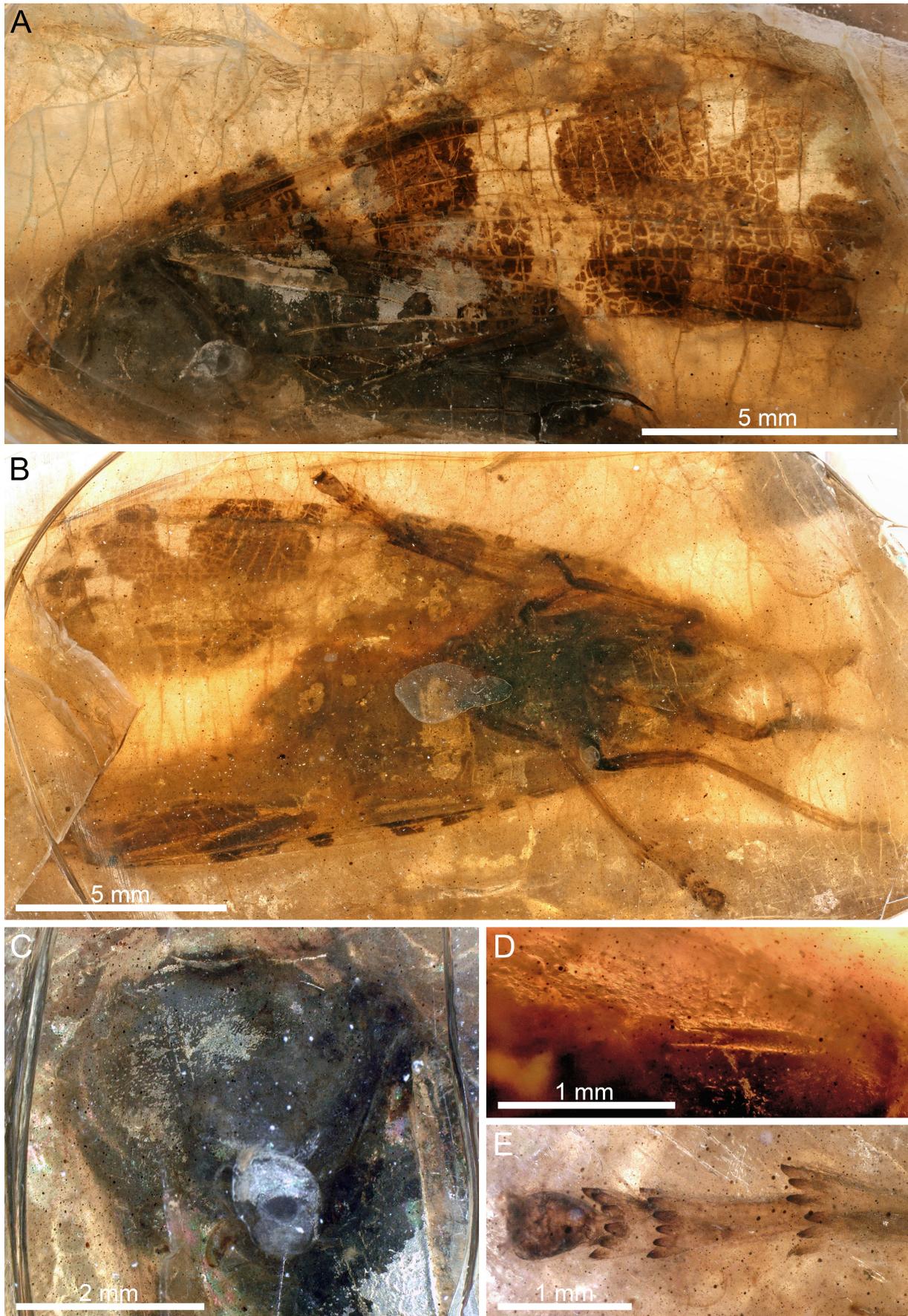


FIGURE 3. Photographs of *Multistria fionae* sp. nov., PED4415, under light microscopy. **A**, Forewing. **B**, General habitus, ventral view. **C**, Mesonotum. **D**, Details of mesonotum median carinae. **E**, Details of left hind tarsus.

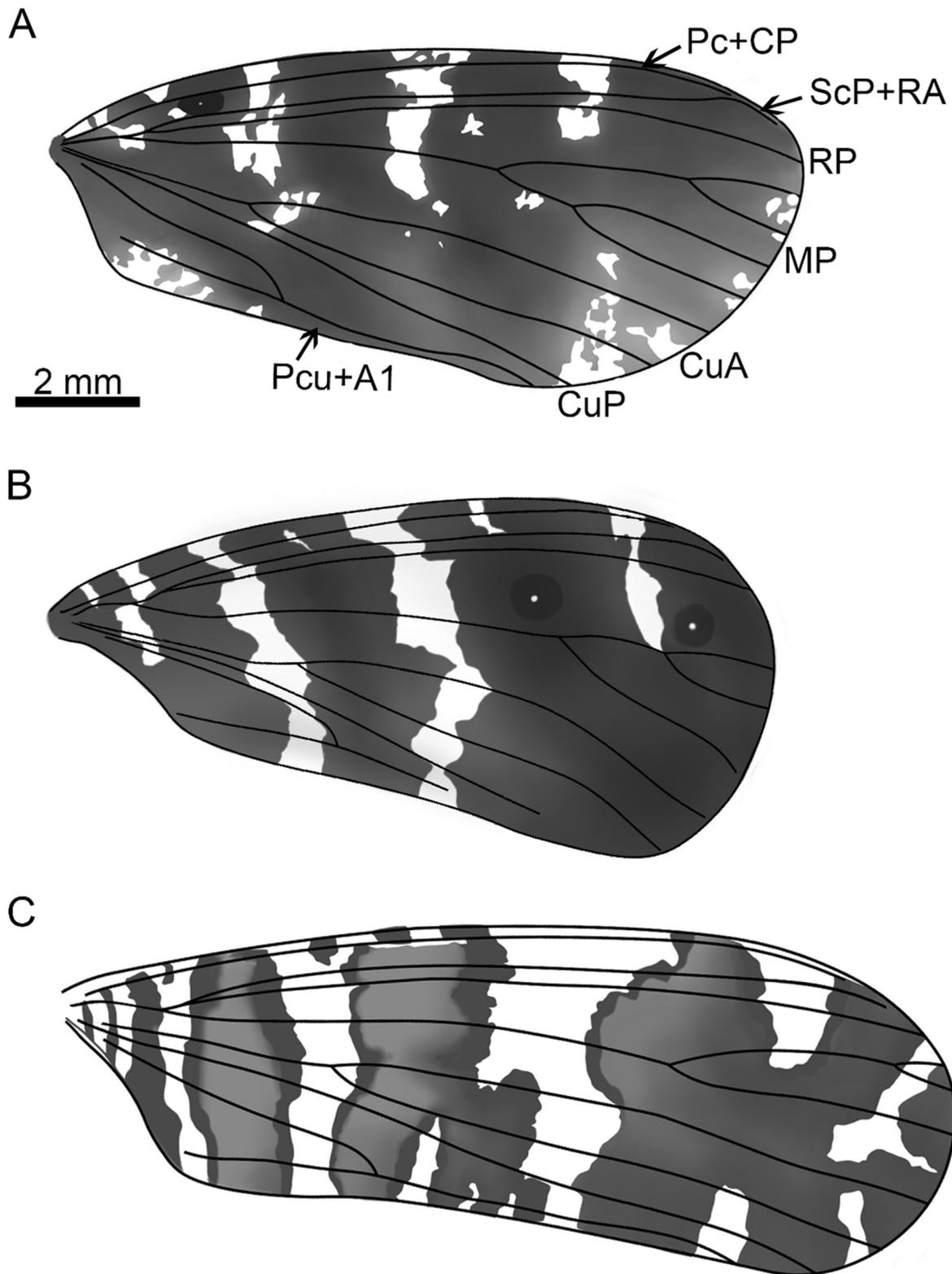


FIGURE 4. Reconstructions of forewings. **A**, *Multistria irregularis* sp. nov. **B**, *Multistria juanae* sp. nov. **C**, *Multistria fionae* sp. nov.

angles broadly rounded, tornus weak, posterior margin straight. Costal area narrow, tapering towards and reaching apical margin; stem ScP+R shorter than stem ScP+R+MP

and width of postcostal cell; veins ScP+RA and RP simple, subparallel to costal margin; apex of ScP+RA slightly arched anteriorly; stem MP nearly straight, slightly arched

anteriad, forked at 1/3 from tegmen apex; MP with 3 terminals; MP₁₊₂ forking very late with 2 terminals; MP₃₊₄ simple; CuA with two terminals forked slightly basal of Pcu and A1 vein junction; CuA₁ and CuA₂ nearly straight, CuP straight and simple; Pcu and A1 fused at about 1/4 of tegmen length from base; Pcu curved anteriad at junction with A1. Tegmen colouration consists of 4 transverse pigmented bands with irregular wavy edges, crossed by fine mesh of light secondary veinlets; two basal bands fully separated; band width roughly subequal; band margins with darker outlines; wing apex with several irregular dark spots.

Profemur slightly shorter than protibia; protibia carinate; mesotibia carinate, about 1/3 longer than mesofemur; metatibia carinate, about 1/3 longer than metafemur, bearing 6 short distal teeth; metatarsus with proximal tarsomere three times as long as mid tarsomere, each bearing 6 distal teeth, distal tarsomere slightly longer than proximal tarsomere; tarsomeres of equal width, claws and pulvilli indistinct; tibia and tarsi with uniform pigmentation. Legs measurements (coxa//femur/tibia//tarsomere1/2/3//claws): Foreleg lengths (2.85/3.2//0.82/?/?/?); midleg lengths (2.37/3.83//1.04/?/?/?); hindleg lengths (2.08/3.19//1.41/0.65/0.733/?); metatibial distal teeth up to 0.24 mm long.

Discussion

With the diversity of Mimarachnidae gradually uncovered, the variability within different characters becomes increasingly clear. The tegmina of mimarachnids contain a large number of measurable characters and represent some of the most commonly preserved diagnostic remains attributable to this lineage. As a result, previous studies on Mimarachnidae emphasized the tegminal venation in the diagnosis of species and genera, particularly the number of MP terminals. However, it appears that this character has high intraspecific variability, and consequently cannot be relied upon for generic diagnoses. This is well illustrated in *Mimaerypterus* and *Mimaplax*, which exhibit varying numbers of MP terminals between the left and right tegmina and among specimens (Jiang T *et al.*, 2019; Fu & Huang, 2021; Fabrikant *et al.*, 2024). Moreover, closely related species belonging to the same genus may show large differences in the branching pattern within MP (unpublished material from *Xiaochibangus* and *Dachibangus*). Additionally, the metatibio-metatarsal spine number appears to be polymorphic in *Multistria*, as illustrated by *Multistria irregularis* sp. nov., which exhibits different counts on the left and right legs (Fig. 1C, D). This variability prompted the revision of the

diagnoses for the genus *Multistria* with a more diagnostic combination of characters that are consistent within species of the genus.

The present discovery enriches the known morphological diversity of Mimarachnidae and highlights the variability and polymorphism of some characters within this clade, which may complicate the diagnosis of taxa with a limited sample size. Future investigation is necessary to define more robust diagnostic criteria for genera in this clade, particularly the addition of body characters, and for uncovering its phylogenetic interrelationships.

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