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Taxonomic additions to the genus †*Megacoxa* Brazidec *et al.*, 2024 (Hymenoptera: Megalyridae) from Kachin amber

CORENTIN JOUAULT[1,*]
[1]*Oxford University Museum of Natural History, University of Oxford, Parks Road, Oxford OX1 3PW, UK*
jouaultc0@gmail.com; *https://orcid.org/0000-0002-3680-5172*
**Corresponding author*

Abstract

The extinct genus *Megacoxa* was recently described from Kachin amber and currently includes six formally recognized species. Despite the recent addition of three new species, additional, yet-undescribed specimens continue to be discovered in both institutional and private collections, awaiting formal description. The vast quantity of material extracted from the Kachin biota provides a practically inexhaustible source of new species. As with many insect families preserved in mid-Cretaceous Kachin amber, the diversity and number of megalyrid wasps remain significantly underestimated. In this study, I illustrate a new specimen of *Megacoxa chandrahrasa* Brazidec *et al.*, 2024. I also describe a new species, *Megacoxa miscea* **sp. nov.**, which exhibits a combination of characters found in *M. janzeni* and *M. synchrotron*. Furthermore, I present an updated identification key for *Megacoxa* species, incorporating this newly described species.

Keywords: Apocrita, long-tailed wasp, new taxon, parasitoid wasp, taxonomy

Introduction

The family Megalyridae, commonly known as long-tailed wasps, comprises a small lineage of parasitoid insects, named for the extremely elongated ovipositor found in some extant species (*e.g.*, *Megalyra shuckardi* Westwood, 1851). Today, Megalyridae are primarily distributed across the Southern Hemisphere, with significant diversity in Australia. However, fossil evidence from the Northern Hemisphere suggests that this restricted distribution is a relictual pattern rather than a historical norm (Vilhelmsen *et al.*, 2010: fig. 1).

The current distribution of Megalyridae is believed to have resulted from climatic and biome shifts during the Cenozoic, which likely led to the contraction or displacement of their range following the Eocene (Shaw, 1990a, b). This hypothesis is particularly supported by the presence of the extant genus *Megalyra* Westwood, 1832 in Eocene Baltic amber (Poinar & Shaw, 2007). Furthermore, the biogeographic histories of other lineages indicate a migration from Europe to Southeast Asia, with analyses revealing affinities between the European Eocene amber fauna and present-day Southeast Asian fauna. These findings suggest a broader pattern of migration or range retraction from Europe to Southeast Asia (Guénard *et al.*, 2015; Aria *et al.*, 2023).

The biogeographic history of Megalyridae has long intrigued entomologists, but the family's phylogenetic placement remains a subject of ongoing debate. Initially, the genus *Megalyra* was classified within Ichneumonidae before being reassigned to its own family (Westwood, 1832; Schletterer, 1889). Despite these taxonomic revisions, the exact position of Megalyridae within Hymenoptera is still unresolved (see Brazidec *et al.*, 2024 and references therein for a comprehensive review). This uncertainty extends to the extinct subfamily Cleistogastrinae, whose placement within Megalyridae remains contentious (Rasnitsyn, 1975; Vilhelmsen *et al.*, 2010).

Fossil evidence suggests that Megalyridae were diverse and widely distributed during the Cretaceous, with specimens documented from Europe (France and Spain; Perrichot, 2009) and Asia (Myanmar, Russia, and Azerbaijan; Brazidec *et al.*, 2024). However, both the extant and fossil diversity of these ectoparasitoid wasps of beetles (Shaw, 1990a; see additional information on the biology of Megalyridae in Brazidec *et al.*, 2024) remains poorly defined, with numerous undescribed species housed in institutional collections. This is particularly evident in the mid-Cretaceous Burmese amber, where the pace of Hymenoptera fossil descriptions has been remarkably rapid, yet the family Megalyridae remains understudied (Ross, 2025). While recent efforts have begun to address

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this gap (Brazidec *et al.*, 2024; Vilhelmsen *et al.*, 2025), a substantial taxonomic effort is still needed to formally describe the numerous specimens from this deposit.

In this study, I contribute to this ongoing effort by illustrating a new specimen of the recently described species *Megacoxa chandrahrasa* Brazidec *et al.*, 2024, and describing a new species of *Megacoxa* from mid-Cretaceous Burmese amber.

Material and methods

The pieces of amber containing the specimens come from the deposits of Noije Bum in the Hukawng Valley (26°29′ N, 96°35′ E), Kachin State, northern Myanmar (see detailed map in Grimaldi & Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi *et al.*, 2012). Some ammonites found in the amber-bearing bed and within amber corroborate a late Albian–early Cenomanian age (Cruickshank & Ko, 2003).

The pieces of amber were polished using thin silicon carbide papers on a Buehler Metaserv 3000 polisher. The new specimen of *M. chandrahrasa* is housed in the Geological Department and Museum of the University of Rennes, France (IGR) under collection number IGR.BU-090, together with the holotype of *Megacoxa miscea* **sp. nov.** (a well-preserved female) under collection number IGR.BU-091. The specimens were examined and photographed with a Zeiss Axio Zoom V16 stereomicroscope with an attached Zeiss AxioCam 512 color camera. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 software. The published work and nomenclatural acts are registered in ZooBank with the following LSID: urn:lsid:zoobank.org:pub:32D60B37-46D4-4F28-9F70-BF177AAB89C4

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Superfamily Megalyroidea Schletterer, 1889
Family Megalyridae Schletterer, 1889
Subfamily Megazarinae Perrichot, 2009
Tribe Megalavini Brazidec *et al.*, 2024
Genus *Megacoxa* Brazidec *et al.*, 2024

Included species. *Megacoxa brazideci* Vilhelmsen *et al.*, 2025; *Megacoxa chandrahrasa* Brazidec *et al.*, 2024; *Megacoxa gungner* Vilhelmsen *et al.*, 2025; *Megacoxa janzeni* Brazidec *et al.*, 2024 (type species); *Megacoxa mjoelner* Vilhelmsen *et al.*, 2025; *Megacoxa synchrotron* Brazidec *et al.*, 2024; and *Megacoxa miscea* **sp. nov.**

***Megacoxa chandrahrasa* Brazidec *et al.*, 2024**
(Figs 1, 2, 5A)

Material. IGR.BU-090 (CJ/MA-12), a slightly damaged female specimen preserved in a trapezoidal piece of amber

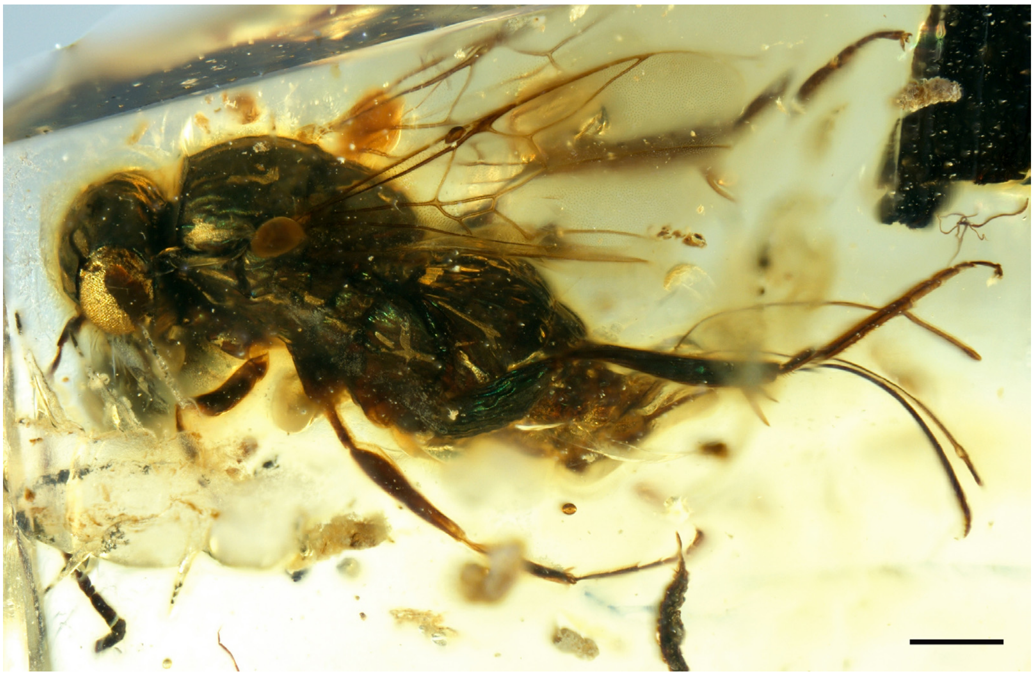

FIGURE 1. *Megacoxa chandrahrasa* Brazidec *et al.*, 2024, specimen IGR.BU-090. Habitus in left lateral view. Scale bar = 0.5 mm.

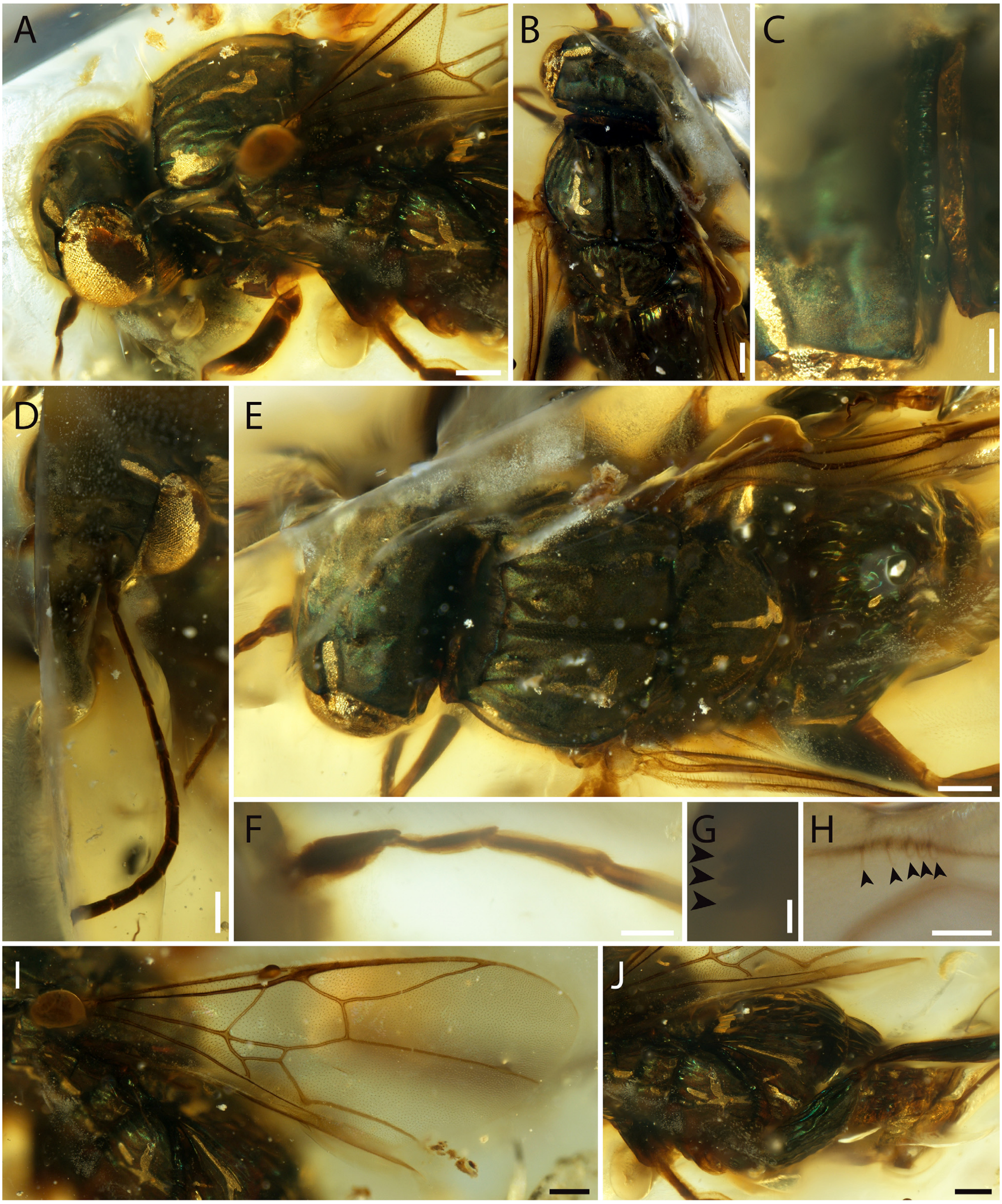

FIGURE 2. *Megacoxa chandrahrasa* Brazidec *et al*., 2024, specimen IGR.BU-090. **A**, Head and mesosoma in left lateral view. **B**, Head and mesosoma in dorsal view. **C**, Detailed view of occipital carina (foveate). **D**, Detailed view of left antenna. **E**, Habitus in dorsal view. **F**, Detailed view of scape, pedicel, and first flagellomeres. **G**, Detailed view of left mandible, with black arrows pointing to each tooth. **H**, Detailed view of hind wing hamuli. **I**, Forewing. **J**, Left lateral view of metasoma. Scale bars = 0.2 mm (**A**, **B**, **D**, **E**, **I**, **J**); 0.1 mm (**C**, **F**, **H**); 0.05 mm (**G**).

measuring 8 × 7 × 3 mm with remains of a Myriapoda, deposited in the amber collection of the Geological Department and Museum of the University of Rennes, France (IGR).

Locality and horizon. The amber specimen was collected from Kachin (Hukawng Valley) of northern Myanmar, which is dated at 98.79 ± 0.62 Ma (Cruickshank & Ko, 2003; Shi *et al*., 2012).

Remarks. The new specimen is readily attributed to a 'group of species' possessing a metasoma at most as long as mesosoma, encompassing: *Megacoxa chandrahrasa* Brazidec *et al*., 2024 and *Megacoxa gungner* Vilhelmsen *et al*., 2025 (Brazidec *et al*., 2024; Vilhelmsen *et al*., 2025). Among these two species, it is affinities with *M. chandrahrasa* are evident due to its hind coxa carinate and foveate (*vs*. without carina and foveae along posterior margin in *M. gungner*); its hind femur and tibia swollen, tibial apical spurs longer than tibial width (*vs*. spurs very short, less than half max. tibial width in *M. gungner*), hind basitarsomere much longer than remaining tarsomeres combined (*vs*. slightly shorter in *M. gungner*); and its ovipositor shorter than body (*vs*. elongate, longer than body in *M. gungner*). In the original description of *M. chandrahrasa*, the photographs of the holotype and paratype primarily depict the habitus, making direct comparison with the new specimen challenging. However, aside from minor size differences, the morphology of the new specimen closely matches that of the type specimens. The only 'exception' is in the original illustration of *M. chandrahrasa* forewing venation: 1) cu-a is depicted (Brazidec *et al*., 2024: fig. 2D) as emerging distally to the origin of Cu's second abscissa; and 2) the marginal is depicted as relatively short. However, these discrepancies appear to result from slight deformations of the wing membrane or natural variability, as it is inconsistent with the venation pattern observed in the second forewing of the holotype (Brazidec *et al*., 2024: fig. 6A). The 'true' venation pattern is therefore nearly identical to that of the new specimen described herein.

Megacoxa miscea sp. nov.

(Figs 3, 4, 5B, C)
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Material. Holotype IGR.BU-091 (CJ/MA-250), a complete and well-preserved female specimen preserved in a trapezoidal piece of amber measuring 6 × 3 × 1.5 mm with plant debris, deposited in the amber collection of the Geological Department and Museum of the University of Rennes, France (IGR).

Etymology. The species name derives from the Latin verb '*misceo*', meaning mix, mingle, and refers to the combination of diagnostic characters of the new species, mixing that of *M. janzeni* and *M. synchrotron*.

Diagnosis. Body slender (compared to *M. chandrahrasa* and *M. gungner*), metasoma longer than mesosoma (shorter in *M. chandrahrasa* and *M. gungner*). Head without transverse striae on frons (Fig. 4D), antennae shorter than combined length of head + mesosoma (longer than combined length of head + mesosoma in *M. brazideci*). Median mesoscutal sulcus smooth (crenulate in *M. synchrotron*), axillae contiguous (*i.e*., abutting medially *vs.* not contiguous in *M. janzeni* and *M. mjoelner*). Hind coxa carinate and foveate (without carina and foveae along posterior margin in *M. mjoelner* and *M. brazideci*), hind tibia triangular, broadest close to apex (*vs*. spindle-shaped, broadest 2/3ds from base in *M. synchrotron*), apical spurs much shorter than maximal width of hind tibia (*vs*. longer than maximal width of hind tibia in *M. chandrahrasa*), hind basitarsus about the same length of remaining tarsomeres combined (approx. 1.5× the length of remaining tarsomeres combined in *M. chandrahrasa*). Ovipositor shorter than body (longer than body in *M. gungner*).

Locality and horizon. Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

Description. Female; body length (without ovipositor) about 2.45 mm, fore wing length 1.75 mm; wasp well preserved except for tip of right ovipositor sheath damaged.

Head about as long as wide, in full face view about 0.55 mm wide (including eyes) and 0.57 mm high, head capsule without prominent sculpture or setation; eyes oval, apparently bare, higher than wide (about 0.47 mm high and 0.28 mm wide, in lateral view), without postocular carina, interocular distance (in full face view) about 0.32 mm; antennal insertions in depressions, frons overhangs them above; occipital carina well developed, crenulate, area around occipital foramen deeply concave; clypeus short and wide, triangular with tip between antennal insertions; antenna about 1.5 mm long, slightly longer than head + mesosoma combined, with short (about 0.15 mm long) and slightly broadening distally scape, pedicel shorter and thinner than scape, flagellum with flagellomeres shortening and widening from base to apex (except 12), flagellomeres 1–3 about twice as long as wide (about 0.13 mm long and 0.05 mm wide), longer than flagellomeres 4–11, flagellomere 12 about twice as long as wide, tapered apically; labrum small narrow flap below clypeus, concealed when mandibles are closed; mandibles broad, with three teeth each, apical tooth the longest.

Mesosoma about 1 mm long, with elongate, extended

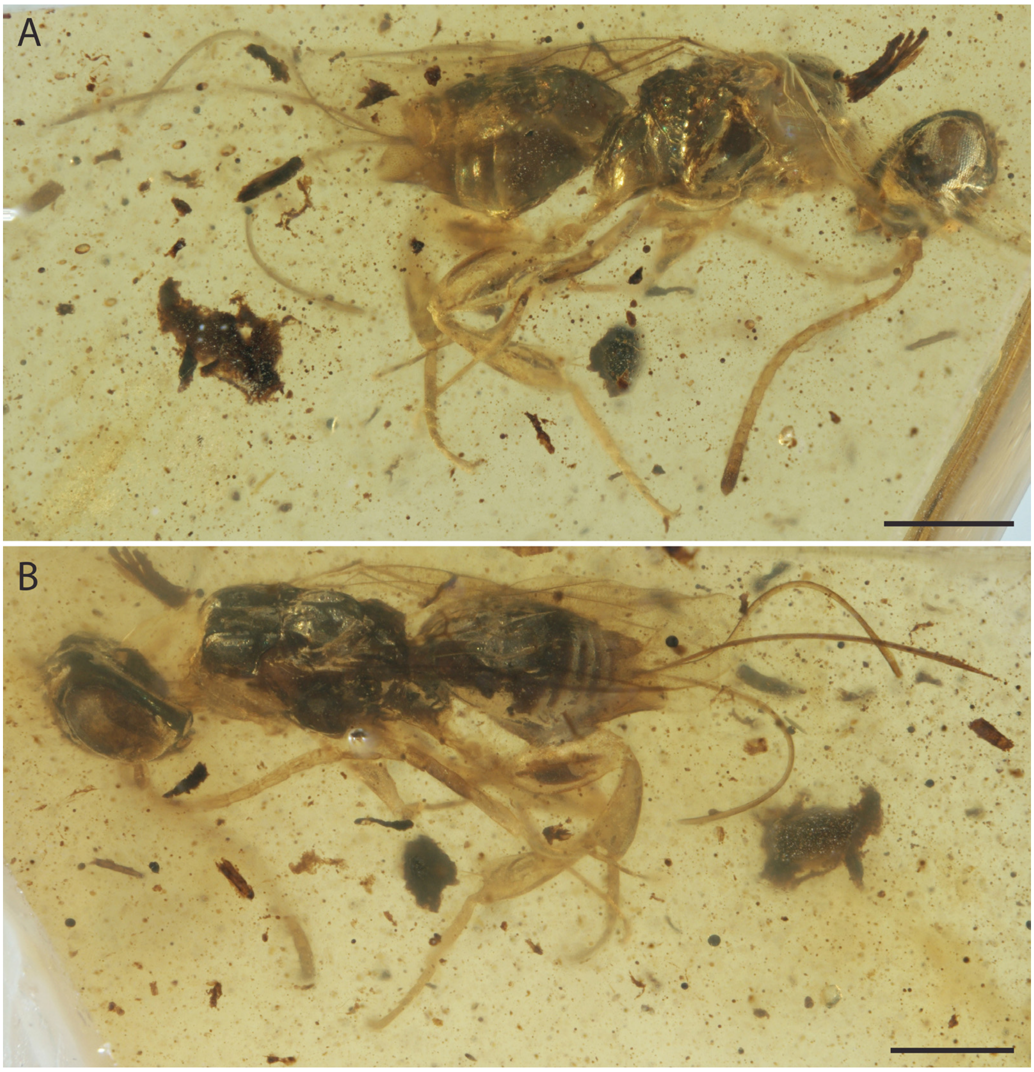

FIGURE 3. *Megacoxa miscea* **sp. nov.**, holotype IGR.BU-091. **A**, Habitus in right lateral view. **B**, Habitus in left lateral view. Scale bars = 0.5 mm.

propectus, without prominent setation; pronotum narrow medially, triangular laterally, with anterior thoracic spiracle in faint notch in upper lateral margin; fore femur spindle-shaped, fore tibia slender, with elongate, curved calcar; mesoscutum strongly arched in lateral view, angled between vertical anterior surface and horizontal surface, anterolateral transverse carina on mesoscutum present; horizontal surface nearly flat, mesoscutellum slightly bulging, not prominently sculptured; median mesoscutal sulcus distinct, deep, smooth, extends to transscutal articulation; axillae distinct, triangular, abutting medially, separated from mesoscutellum by oblique foveate scutoscutellar sulcus; mesoscutellum bulging, smooth, diamond-shaped; mesopleuron smooth, with depression medially, mesopleuro-metapleural sulcus distinct, crenulate; propodeum carinate, carinae delimitating row of large foveae in anterior region and larger foveae in posterior region; mid femur spindle-shaped, mid tibia slender; hind leg much larger than fore and mid legs, hind coxa broad, with carina and foveae along posterior margin, hind femur strongly swollen, hind tibia strongly expanded distally, widest distally, without fringe of setae, with two apical spurs of subequal lengths, spurs shorter than tibial maximum width; hind basitarsomere (about 0.32 mm long) equal in length to remaining tarsomeres (respective length in mm: 0.08, 0.05, 0.05, 0.14); tarsal claws slender, simple.

Forewing hyaline with veins C, R1, Sc+R, M+Cu, A, Rs+M, Rs, M and Cu fully pigmented; Rs+M aligned with M+Cu; medial cell trapezoidal, wide distally, slightly wider along Cu than along 1m-cu; Rs present between Rs+M and r-rs, closing first submarginal cell; marginal cell narrow, closed in straight line by Rs; hind wing could not be observed.

Metasoma about as long as mesosoma, fusiform, without prominent sculpture or setation; sternum 2 tapering anteriorly, broadening posteriorly to broadest point of metasoma, about twice as long as sternum 3;

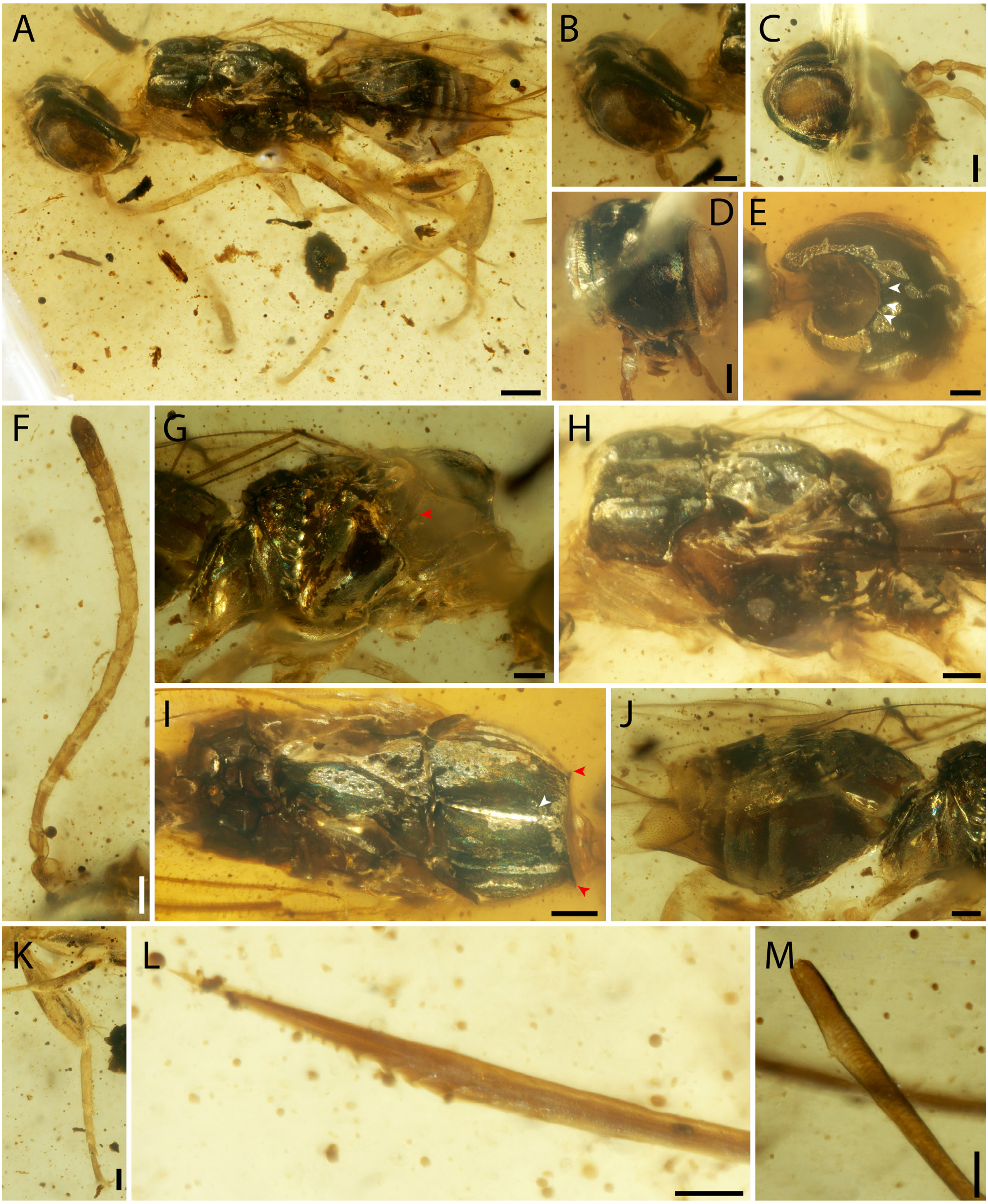

FIGURE 4. *Megacoxa miscea* **sp. nov.**, holotype IGR.BU-091. **A**, Habitus in left lateral view, excluding ovipositor. **B**, Head in left lateral view. **C**, Head in right lateral view. **D**, Head in frontal view. **E**, Head in dorsal view (arrows pointing to large foveae). **F**, Detailed view of antenna. **G**, Mesosoma in right lateral view (red arrow pointing to the anterior thoracic spiracle). **H**, Mesosoma in left dorso-lateral view. **I**, Mesosoma in dorsal view (white arrow pointing to Median mesoscutal sulcus; red arrows pointing to pronotal carina). **J**, Metasoma in right lateral view. **K**, Detailed view of right hind tibia. **L**, Detailed view of ovipositor apex. **M**, Detailed view of ovipositor sheath. Scale bars = 0.2 mm (**A**); 0.1 mm (**B**–**K**); 0.05 mm (**L**, **M**).

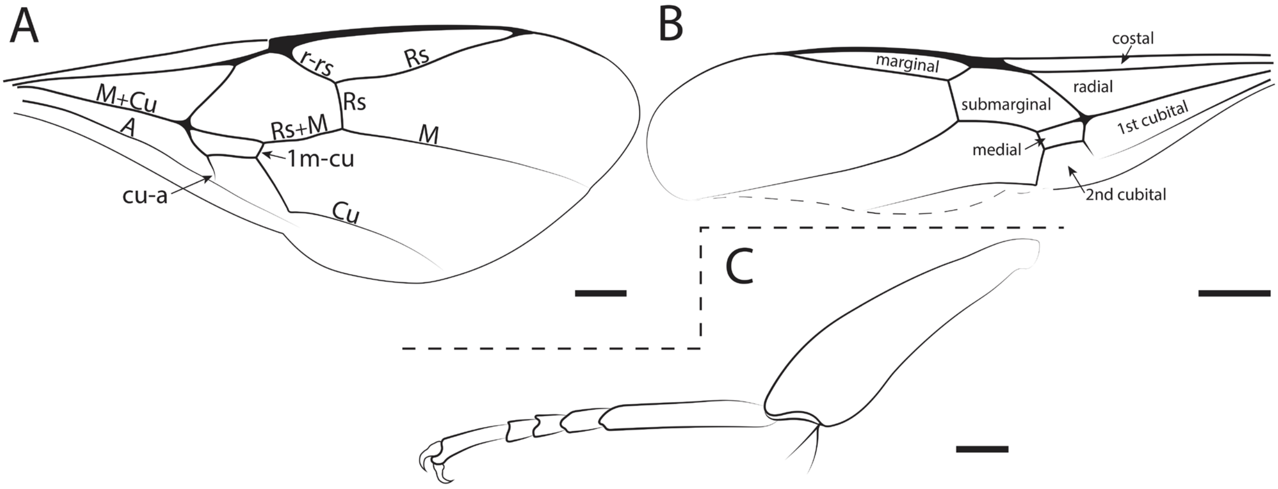

FIGURE 5. Interpretative line drawings. **A**, Forewing venation of *Megacoxa chandrahrasa* Brazidec *et al*., 2024, specimen IGR.BU-090. **B**, Forewing venation of *Megacoxa miscea* **sp. nov.**, holotype IGR.BU-091. **C**, Hind tibia and tarsus of *Megacoxa miscea* **sp. nov.**, holotype IGR.BU-091. Scale bars = 0.2 mm (**A**, **B**) 0.1 mm (**C**).

distal part of the metasoma dislocated; ovipositor at least 1.5 mm long, extending far beyond tips of wings, distally with a series of teeth/serrations; ovipositor sheath with a pre-apical enlargement, tip rounded.

Remarks. Following the key to species of †*Megacoxa* spp. proposed by Vilhelmsen *et al.* (2025), the new specimen keys out close to *M. janzeni* and *M. synchrotron* because of the following couplets: metasoma clearly longer than mesosoma; hind coxal posterior margin with row of large foveae; median mesoscutal sulcus smooth or crenulate. On one hand, it resembles *M. janzeni* in having a median mesoscutal sulcus smooth and hind tibia triangular, broadest close to apex, but differs from the latter in having axillae abutting medially (*vs*. not abutting medially). On the other hand, it resembles *M. synchrotron* in having axillae abutting medially but differs from the latter in having hind tibia triangular, broadest close to apex (*vs*. spindle-shaped, broadest 2/3ds from base) and a median mesoscutal sulcus smooth (*vs*. smooth).

Key to species of *Megacoxa* spp. (modified from Vilhelmsen *et al*., 2025 to integrate the new species)

1. Metasoma at most as long as mesosoma (Vilhelmsen *et al.*, 2025: fig. 3A, B; Brazidec *et al*., 2024: fig. 6B, E).......... 2

\- Metasoma clearly longer than mesosoma (Vilhelmsen *et al.*, 2025: figs 2A, 4A) 3

2. Hind coxal posterior margin strongly carinate and with row of foveae (Brazidec *et al*., 2024: fig. 6C); hind tibial apical spurs longer than maximal width of hind tibia (Brazidec *et al*., 2024: fig. 6B, G); hind basitarsus approx. 1.5× the length of remaining tarsomeres combined (Brazidec *et al.*, 2024: fig. 6B, G); ovipositor shorter than body (Brazidec *et al.*, 2024: fig. 6B, E) .... *M. chandrahrasa* Brazidec *et al*., 2024

\- Hind coxal posterior margin without carina and row of foveae (Vilhelmsen *et al*., 2025: fig. 3B); hind tibial apical spurs much shorter than maximal width of hind tibia (Vilhelmsen *et al*., 2025: fig. 3B); hind basitarsus slightly shorter than combined length of remaining tarsomeres (Vilhelmsen *et al*., 2025: fig. 3A); ovipositor longer than body (Vilhelmsen *et al*., 2025: fig. 3A)............................. ....*M. gungner* Vilhelmsen *et al*., 2025

3. Hind coxal posterior margin with row of large foveae (Brazidec *et al*., 2024: figs 7B, 8C, G); median mesoscutal sulcus smooth or crenulate 4

\- Hind coxal posterior margin without foveae (Vilhelmsen *et al*., 2025: figs 2D, 4C); median mesoscutal sulcus smooth (Vilhelmsen *et al*., 2025: fig. 4B) 6

4. Median mesocutal sulcus smooth (*e.g*., Vilhelmsen *et al.*, 2025: fig. 4B); hind tibia triangular, broadest close to apex (Brazidec *et al*., 2024: fig. 7D).. 5

\- Median mesoscutal sulcus crenulate (Vilhelmsen *et al.*, 2025: fig. 5A; Brazidec *et al*., 2024: fig. 8F); hind tibia spindle-shaped, broadest 2/3ds from base (Vilhelmsen *et al*., 2025: fig. 5C; Brazidec *et al*., 2024: fig. 8A)............... ....*M. synchrotron* Brazidec *et al*., 2024

5. Axillae abutting medially (*e.g*., Vilhelmsen *et al*., 2025: fig. 5A) .... *Megacoxa miscea* **sp. nov.**

\- Axillae not abutting medially (*e.g*., Vilhelmsen *et al*., 2025: fig. 4B)............................ *M. janzeni* Brazidec *et al*., 2024

6. Head with transverse striae on frons (Vilhelmsen *et al*., 2025: fig. 2B); antennae longer than head + mesosoma combined (Vilhelmsen *et al*., 2025: fig. 2A); axillae abutting medially .... *M. brazideci* Vilhelmsen *et al*., 2025

- Head with smooth sculpture on frons; antennae shorter than head + mesosoma combined (Vilhelmsen *et al.*, 2025: fig. 4A); axillae not abutting medially (Vilhelmsen *et al*., 2025: fig. 4B)...................... *M. mjoelner* Vilhelmsen *et al*., 2025

Discussion

The specimens are confidently assigned to the family Megalyridae based on several diagnostic features, including the presence of a subantennal groove, antennal insertions situated below the ventral margin of compound eyes, 14 antennomeres, a distinctly arched mesoscutum divided by a well-developed median mesoscutal sulcus, and large triangular axillae on the mesoscutum (Shaw, 1990b). Additionally, they align with the recently revised diagnosis of the family proposed by Brazidec *et al*. (2024). Furthermore, when using the key to Hymenoptera superfamilies by Goulet & Hubert (1993), the specimens unambiguously key out as Megalyridae based on the following couplets: forewing, when directed backwards, extending far beyond apex of thorax or mesosoma and usually beyond apex of abdomen or metasoma; body with strong and usually conspicuous dorsal and lateral constriction between abdominal segments 1 and 2, thus delimiting the mesosoma and metasoma; head […] without circle of teeth around median ocellus, body shape and size various, often stout or small, ovipositor short, metacoxa usually strongly narrowed at base, the two basal articulations usually very close to one another and arranged obliquely, long axis of metacoxa usually angled away from that of mesosoma; malar space with deep depression for reception of scape (upper margin of depression usually sharply carinate), mesoscutum with large, triangular axilla—usually about as large as scutellum—and almost always with a median groove, antenna with 12 flagellomeres.

Following the key to the genera of Megalyridae proposed by Brazidec *et al*. (2024), the specimens key out into the genus *Megacoxa* Brazidec *et al*., 2024 because of the following couplets: anterior thoracic spiracle not surrounded by pronotal cuticle posteriorly; forewing with M+Cu pigmented; hind legs with comb-like spines along the inner margin; occipital carina foveate; forewing with the medial cell rectangular; mesometapectal sulcus crenulate; mandibles with three teeth; vertex without sulcus (*i.e*., without longitudinal median sulcus); count of tibial spurs different (*i.e.*, different than 'two mesotibial and one metatibial spurs present'); presence of two mesotibial and two metatibial spurs; metacoxa enlarged posteriorly with a row of foveae.

Conclusion

The diversity of the family Megalyridae is expanded with the description of a new species within the genus *Megacoxa*, *Megacoxa miscea* **sp. nov.** With this addition, *Megacoxa* now comprises seven species, all exclusively known from mid-Cretaceous Kachin amber. Further examination of additional material will likely continue to increase both the genus's diversity and, more broadly, that of the Megalyridae family. Similarly, I anticipate that additional *Megacoxa* specimens will be discovered in other Cretaceous amber deposits from Myanmar (*e.g*., Hkamti), extending the genus's temporal range and enhancing our understanding of Megalyridae diversity during the Cretaceous.

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