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Three new species of the long-tailed wasp genus †*Megacoxa* Brazidec *et al.*, 2024 (Hymenoptera: Megalyridae) from Kachin amber

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Abstract. †*Megacoxa* is a recently described extinct genus of Megalyridae Schletterer, 1889 from Kachin amber with three described species until now. Here, we investigate four new fossils and integrate them in a phylogenetic framework. We describe three additional species of †*Megacoxa*: †*M. brazideci* sp. nov., †*M. gungner* sp. nov. and †*M. mjoelner* sp. nov. Furthermore, we describe the previously unknown female of †*M. synchrotron* Brazidec *et al.*, 2024. We provide an emended diagnosis of †*Megacoxa* and a key to all recognized species. The continued expansion of the known Cretaceous diversity of Megalyridae underlines the relictual nature of the Recent fauna.

Keywords. Parasitoid wasps, amber fossils, Cretaceous.

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Introduction

Megalyridae Schletterer, 1889 are a small family of parasitoid wasps currently with approx. 70 recognized extant species (Brazidec *et al.* 2024). Most species for which biological information is available apparently have wood-boring insects, e.g., beetle larvae, as hosts (see Vilhelmsen *et al.* 2010 and references therein). Megalyridae are characterized by having a distinct subantennal groove, 14 antennomeres, an arched mesoscutum with a distinct median mesoscutal sulcus, and large triangular axillae posterior to the transscutal articulation (except most species of *Carminator* Shaw, 1988) (Vilhelmsen *et al.* 2010; Brazidec *et al.* 2024); the exposed anterior thoracic spiracle inside the pronotum

characteristic of all extant species is not observed in the extinct subfamily †Megazarinae Brazidec *et al.*, 2024, and the long ovipositor which has given rise to both the scientific and common name of Megalyridae/long-tailed wasps is actually highly variable in length (see, e.g., Vilhelmsen *et al.* 2010: figs s1–s4).

The Megalyridae are today primarily distributed in the southern hemisphere, the Australasian genus *Megalyra* Westwood, 1832 (27 extant + 1 extinct species; see Shaw 1990a and Poinar & Shaw 2007) and the Afrotropical genus *Dinapsis* Waterston, 1922 (19 species; see Mita & Shaw 2020 and van Noort *et al.* 2022) being the largest. Only the genus *Carminator* extends into the Palaearctic, with nine species distributed across southeast Asia and Japan (Mita & Konishi 2011; Chen *et al.* 2021). The fossil diversity of Megalyridae is substantial, particularly in the Cretaceous, and likely to surpass that of the extant fauna (see Perrichot 2009; Brazidec *et al.* 2024). Megalyrids were also more widely distributed in the northern hemisphere (Vilhelmsen *et al.* 2010), occurring in Cretaceous French, Spanish and Taimyr ambers. Recently, Brazidec *et al.* (2024) described six species in three new genera from Cretaceous Kachin amber, including three species of †*Megacoxa*.

Shaw (1990b), Vilhelmsen *et al.* (2010) and Brazidec *et al.* (2024) explored the evolutionary and biogeographic history of Megalyridae. The last study identified two main clades in the family: the Megalyrinae comprising all eight extant genera as well as four Cretaceous and one Cenozoic genus (†*Prodinapsis* Brues, 1923), and the †Megazarinae comprising five genera restricted to the Cretaceous, including †*Megacoxa*. As the knowledge of fossil megalyrid diversity expands, it seems likely that the family has contracted in diversity as well as in distribution in the past 100+ My. The Megalyridae probably arose in the early Mesozoic as part of what has been termed the Mid-Mesozoic Parasitoid Revolution (Labandeira & Li 2021), which in the Hymenoptera gave rise to a range of parasitoid wasps primarily associated with wood, e.g., stephanoids, megalyroids, early evanioids and ichneumonoids. The Megalyridae, to the extent that they have been included in recent phylogenetic studies of Hymenoptera, most consistently appear as sister to the Trigonalidae Cresson, 1887, another small family of hyperparasitoids in sawfly larvae or lepidopteran caterpillars (Klopfstein *et al.* 2013; Mao *et al.* 2024; Tang *et al.* 2019; Blaimer *et al.* 2023; Song *et al.* 2024).

In the present paper, we examine four new fossils from the Kachin amber and integrate them in the phylogenetic framework provided by Brazidec *et al.* (2024). Based on our investigations, we describe three new species of †*Megacoxa* Brazidec *et al.*, 2024 and describe the female of †*M. synchrotron* Brazidec *et al.*, 2024. We provide an emended diagnosis and a key to the six recognized species of †*Megacoxa*.

Material and methods

The type specimens are preserved in Kachin amber and deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNU; Dong Ren, Curator).

The amber specimens were examined under a Leica M205C dissecting microscope. Measurements were taken with an ocular grid. Mesosomal length was measured from the anterior margin of the pronotum to the posterior margin of the propodeum/wasp waist, ignoring the propectus which is liable to be preserved in varying states of extension; metasomal length was measured from the wasp waist to the tip of the metasoma, ovipositor length from the tip of the metasoma to the tip of the ovipositor.

The images were produced with a Visionary Digital imaging setup with flash lighting and P-51 Camlift Driver ver. 2.6.1 to control the camera. A cylinder of semitransparent plastic and/or a cone of semitransparent paper were placed around the specimen to disperse the light. Images were stored in

Adobe Lightroom 2 and composite images were compiled from stacks with the software Zerene Stacker ver. 1.04 by implementing the Pyramidal Stacking Method (PMax). Images were edited in Photoshop, and image plates were assembled in Adobe Illustrator.

To evaluate the phylogenetic positions of the specimens studied, we scored them for the data set presented in Brazidec *et al.* (2024). The data set was assembled in Mesquite 3.70 (Maddison & Maddison 2021); the matrix is available from MegacoxaMatrix2024 (figshare.com). Cladistic analyses were conducted with TNT ver. 1.5 (Goloboff & Catalano 2016). Characters 8, 18, 25, 38, 39 and 47 were treated as ordered. Space for 1 000 000 trees was reserved in the memory. Traditional searches in equal weights analyses and implied weights analyses with the concavity constant k set in turn to 1–10, 15 and 20 were run. Analyses were run with collapsing rules set to max length = 0. For each weighting scheme, analyses with 1000 replications with 1000 trees saved per replication were conducted. The trees were rooted on *Schlettererius* Ashmead, 1900.

Results

Phylogenetic analyses

Overall, the topologies retrieved here are highly similar to those obtained by TNT analyses in Brazidec *et al.* (2024). Megalyridae were retrieved in all analyses, with *Orthogonalys* Schulz, 1905 + *Pristaulacus* Kieffer, 1900 as a sister group. The equal weights consensus tree has †Megazarinae completely collapsed, all the genera placed in a polytomy with a monophyletic Megalyrinae; both subfamilies are retrieved monophyletic in all implied weights (IW) analyses. A clade comprising the described †*Megacoxa* spp. as well as all the new fossils in this genus is retrieved monophyletic in IW analyses with k = 1–8 (Fig. 1); CNU-HYM-MA-2016208 is in a polytomy with the three already described species and a clade comprising the three additional specimens (CNU-HYM-MA-20162[09-11]) treated here. †*Cretolyra* Brazidec *et al.*, 2024 is sister to †*Megacoxa* in most IW analyses (k = 2–8) and the clade combining them is in a polytomy with †*Genkyhag* Brazidec *et al.*, 2024 and †*Megalava* Perrichot, 2009, with †*Megazar* Perrichot, 2009 being the sister to all other †Megazarinae. In Megalyrinae, there is some variation in the relative positions of *Rigel* Shaw, 1987 and the Cretaceous fossils (except †*Cretodinapsis* Rasnitsyn, 1977) at the base of the subfamily in IW analyses with k = 1–4; with k = 5–8 (Fig. 1), the topology of Megalyrinae is identical to that presented in Brazidec *et al.* (2024: fig. 10).

Potential support for †*Megacoxa*, including the new material, is provided by the following characters: antenna shorter than head and mesosoma combined (char. 6:1; reversed in CNU-HYM-MA-2016210; paralleled in †*Genkyhag* and many Megalyrinae); having the posterior mesopleural margin straight (char. 26:0; paralleled in some Megalyrinae). The sister relationship between †*Megacoxa* and †*Cretolyra* is supported by the presence of an anterolateral transverse carina on the mesoscutum (char. 21:1; unknown for in CNU-HYM-MA-2016209; paralleled in most Megalyrinae) and the presence of two mesotibial apical spurs (char. 25:2).

Systematic palaeontology

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Megalyridae Schletterer, 1889
Subfamily Megazarinae Brazidec *et al.*, 2024

Genus †***Megacoxa*** Brazidec *et al.*, 2024

Type species

†*Megacoxa janzeni* Brazidec *et al.*, 2024.

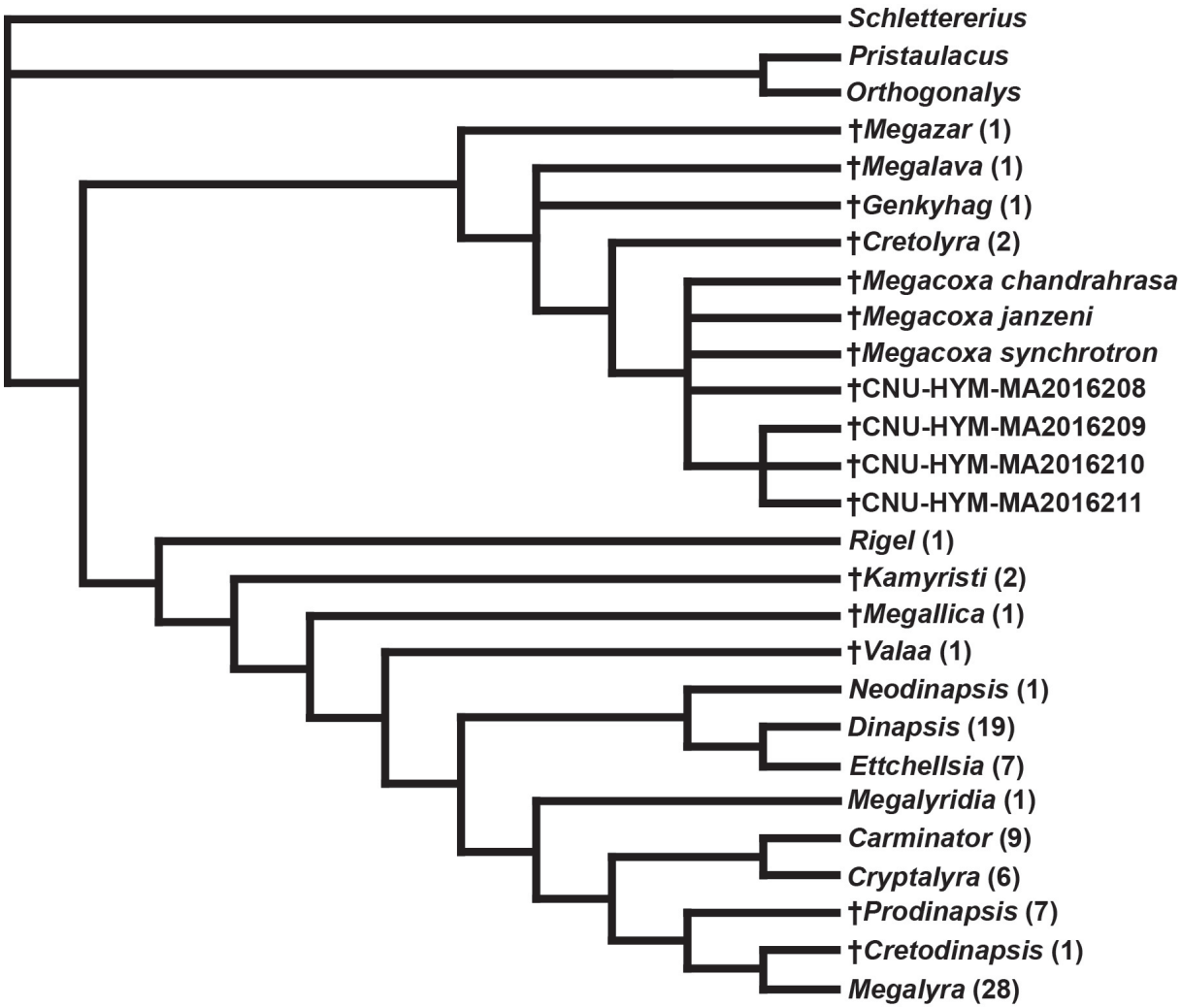

Fig. 1. Phylogeny of Megalyridae. Strict consensus tree of six trees obtained by implied weights analyses with k = 5. All genera except †*Megacoxa* represented by only one terminal, number in brackets indicates total number of recognized species.

Emended diagnosis

Compound eye oval; scape wider than long; low occipital carina slightly crenulate. Mesoscutoscutellar sulcus crenulate. Fore wing venation with veins R1, M+Cu, Sc+R, A and Cu fully pigmented; vein A connected to medial cell with vein cu-a; vein Rs closing marginal cell without bend. Metacoxa much enlarged, with dorsal surface rounded to angular, outer metacoxal surface posteriorly foveate, inner metacoxal surface almost entirely accommodated in anterolateral, shallow concavity of metasoma. Metatibia and metabasitarsus sometimes with ventral row of comb-like setae; two mesotibial and two metatibial spurs. Metasomal length variable.

†***Megacoxa brazideci*** sp. nov.
urn:lsid:zoobank.org:act:5B2A60D5-012F-47C2-8DE0-6D0158F6110C
Fig. 2

Diagnosis

Body comparatively slender (Fig. 2A), metasoma longer than mesosoma (shorter in †*M. chandrahrasa* Brazidec *et al.*, 2024 and †*M. gungner* sp. nov.). Head with transverse striae on frons (Fig. 2B).

Antennae longer than head + mesosoma combined. Median mesoscutal sulcus smooth (crenulate in †*M. synchrotron* Brazidec *et al.*, 2024), axillae contiguous (not contiguous in †*M. janzeni* Bracidec *et al.*, 2024 and †*M. mjoelner* sp. nov.). Hind coxa without carina and foveae along posterior margin (coxa carinate and foveate in †*M. janzeni* and †*M. synchrotron*). Ovipositor elongate, longer than body (Fig. 2A).

Etymology

The new species is named after Manuel Brazidec, the French palaeoentomologist who described †*Megacoxa* as well as a number of other extinct wasp taxa.

Type material

Holotype

MYANMAR • ♀; Kachin State, Myitkyina District, Hukawng Valley; [26°20′ N, 96°36′ E]; unnamed horizon, mid-Cretaceous, upper Albian to lower Cenomanian, 98.79 ± 0.62 Ma (Cruickshank & Ko 2003; Shi *et al.* 2012); CNU-HYM-MA-2016210.

Description

Female

Body. Length (except ovipositor) 3.7 mm, fore wing length 2.6 mm, ovipositor length 4.3 mm. Specimen complete, generally well preserved (left hind femur and tibia somewhat compressed), in clear amber piece with few and small air bubbles, no major occlusions obscuring specimen, anterior part of head covered with thin milky film.

Head. Oval in lateral view, wider than long, eyes oval, occupy most of lateral surface of head (Fig. 2B); ocelli situated on top of head in approx. equilateral triangle; frons with transverse, wavy striation; postocular carina absent; occipital carina well developed, smooth, slightly incurved dorsally, area around occipital foramen deeply concave; antennae slender, elongate, longer than combined length of head + mesosoma, scapus short, expanded distally, short pedicellus inserted subapically on scapus, antennomeres 4 and 5 longest (Fig. 2B), antennomeres gradually shortening until apical antennomere, which is approx. 2 × as long as penultimate antennomere; mandibles with three teeth each; short, slender palps observed.

Mesosoma. With elongate, extended propectus (Fig. 2D); pronotum narrow medially, triangular laterally, with anterior thoracic spiracle in notch in lateral margin; fore femur slender, fore tibia slightly expanded distally, with elongate, curved calcar; mesoscutum strongly arched in lateral view, vertical anterior surface curves smoothly into horizontal surface; horizontal surface flat, level with mesoscutellum, not prominently sculptured; median mesoscutal sulcus distinct, apparently smooth, extends to transscutal articulation; axillae distinct, triangular, continuous medially, separated from mesoscutellum by curved foveate scutoscutellar sulcus (Fig. 2C); mesoscutellum flat, smooth with small punctures, triangular posteriorly; mesopleuron smooth, with depression medially, mesopleuro-metapleural sulcus distinct, crenulate; mid femur slightly spindle-shaped, mid tibia slender, with two short apical spurs; hind coxa broad basally, cone-shaped, without carina or foveae along posterior margin; hind femur spindle-shaped, broadened in middle; hind tibia flattened, expanded distally, without fringe of setae, with two apical spurs of subequal length (Fig. 2A), inner spur approx. to distal tibial width of tibia; hind basitarsus with short erect pegs on inner side, of approx. same length as remaining tarsomeres, tarsal claws simple, slender.

Wings. Fore wing 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 wide distally, rectangular; Rs present between Rs+M and r-rs,

closing first submarginal cell; marginal cell narrow, closed in straight line by Rs; hind wings mostly covered by fore wings, apparently with little venation developed.

Metasoma. 1.12× as long as mesosoma, slender, fusiform, without prominent sculpture or pilosity; metasomal segment 2 largest, metasoma widest there, sternum 2 with concavities for accommodating hind coxae; slender, slightly swollen cerci extend from tip of metasoma (Fig. 2C); sternum 7 tapered apically, folded over medially along longitudinal axis; ovipositor extending posteriorly, elongate, length 1.16× body length (Fig. 2A), ovipositor proper and sheaths slender, tip of 2nd valvula with 6–7 small dorsal teeth.

Male

Unknown.

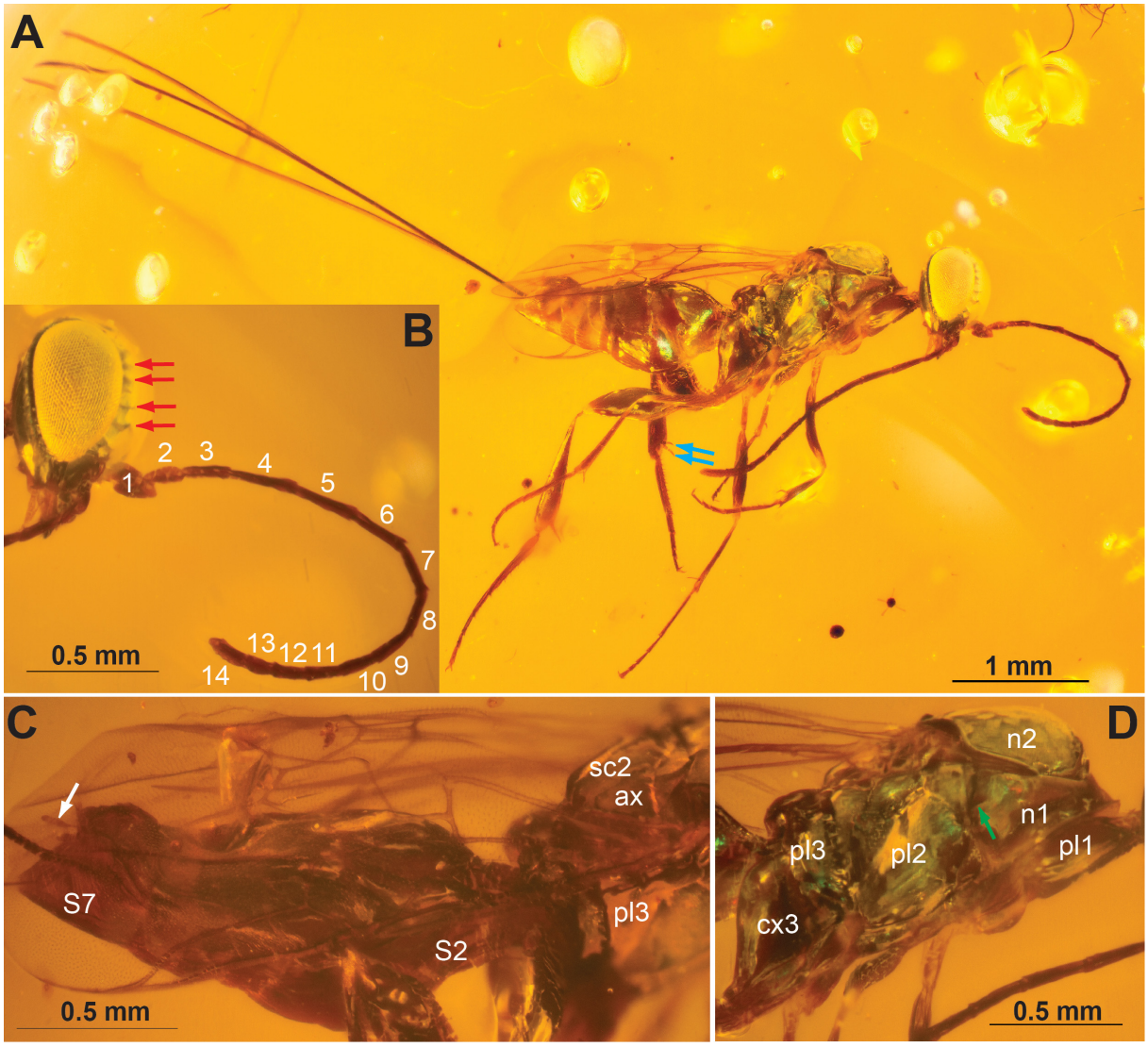

Fig. 2. †*Megacoxa brazideci* sp. nov., ♀, holotype (CNU-HYM-MA-2016210). **A**. Habitus, lateral view. **B**. Head, lateral view, with antennomeres enumerated. **C**. Metasoma, lateral view. **D**. Mesosoma, lateral view. Red arrows = transverse striae on frons; blue arrows = hind tibial apical spurs; white arrow = cercus; green arrow = spiracular notch. Abbreviations: ax = axilla; cx3 = hind coxa; n1 = pronotum; n2 = mesoscutum; pl1 = propleuron; pl2 = mesopleuron; pl3 = metapleuron; S2 = second abdominal sternum; S7 = seventh abdominal sternum; sc2 = mesoscutellum.

Remarks

†*Megacoxa brazideci* sp. nov. can be most easily recognized by the transverse striae on the frons and the elongate antennae; the ovipositor is also longer than in most other species of the genus. The frontal sculpture might help facilitate eclosion from a pupal chamber in wood; many other wood-living wasps have prominent sculpture on the head or mesosoma for this purpose (Turrisi & Vilhelmsen 2010; Vilhelmsen & Turrisi 2011). The species resembles †*M. mjoelner* sp. nov. in having the median sulcus smooth and the hind coxa without carina and foveae posteriorly, but differs in having the axillae contiguous.

†***Megacoxa gungner*** sp. nov.
urn:lsid:zoobank.org:act:15AEDADB-4F15-4903-A7C3-A633A786FEF0
Fig. 3

Diagnosis

Compact body, metasoma of approx. same length as mesosoma (Fig. 3A–B). Antennae shorter than head + mesosoma. Median mesoscutal sulcus smooth, axillae contiguous. Hind coxa without carina and foveae along posterior margin (coxa carinate and foveate in †*M. chandrahrasa*). Hind femur and tibia swollen, tibial apical spurs very short, less than half max. tibial width (spurs longer than tibial width in †*M. chandrahrasa*), hind basitarsomere slightly shorter than remaining tarsomeres combined (much longer in †*M. chandrahrasa*). Ovipositor elongate, longer than body (Fig. 3A; ovipositor shorter than body in †*M. chandrahrasa*).

Etymology

The species epithet is after Gungner, the never-missing spear of Odin, king of the Norse gods. It refers to the long ovipositor of this species.

Type material

Holotype

MYANMAR • ♀; Kachin State, Myitkyina District, Hukawng Valley; [26°20′ N, 96°36′ E]; unnamed horizon, mid-Cretaceous, upper Albian to lower Cenomanian, 98.79±0.62 Ma (Cruickshank & Ko 2003; Shi *et al*. 2012); CNU-HYM-MA-2016211.

Description

Female

Body. Length (except ovipositor) 5.1 mm, fore wing length 3.2 mm, ovipositor length 6.9 mm. Specimen complete, generally well preserved in clear piece of amber with moderate amount of grit, no major occlusions around specimen but several diffraction planes, particularly in lower part of specimen; lower part of head obscured by frothy mass of bubbles with hair-like extensions. Small to minute air bubbles on surface of parts of specimen, especially around antennae, making observations difficult. Syninclusion: remains of spider exuvium.

Head (Fig. 3B). Held closely appressed to mesosoma, globular, without prominent sculpture or setation, eyes oval; ocelli situated on anterodorsal part of head in approx. equilateral triangle; postocular carina absent; occipital carina well developed, finely crenulate, slightly incurved dorsally; antennae shorter than head and mesosoma combined, basal antennomeres difficult to observe, distal antennomeres not much longer than wide except apical antennomere, approx. twice as long as wide and tapering; mouthparts difficult to observe, short palps observed.

Mesosoma. With propectus concealed; pronotum narrow medially, triangular laterally, with anterior thoracic spiracle in notch in upper lateral margin; fore femur spindle-shaped, thickened, fore tibia slender, slightly widening distally, calcar not observed; mesoscutum strongly arched in lateral view, vertical anterior surface curves smoothly into horizontal surface; horizontal surface flat, level with mesoscutellum, not prominently sculptured, with short, evenly spaced hairs; median mesoscutal sulcus distinct (Fig. 3B), apparently smooth, extends to transscutal articulation; axillae narrow, continuous medially, separated from mesoscutellum by angled foveate scutoscutellar sulcus; mesoscutellum flat, smooth with small hairs, rounded posteriorly; mesopleuron smooth with small, evenly spaced hairs, with slight depression in middle, mesopleuro-metapleural sulcus straight, distinct, crenulate; mid femur thickened, spindle-shaped, mid tibia slender, slightly expanded distally, with two short apical spurs of approx. same length as distal tibial width; hind coxa broad basally, cone-shaped, without carina or foveae along posterior margin; hind femur very thickened, broadened in middle (Fig. 3B); hind tibia very thickened, expanded distally, with dense mat of setae on inner side, two minute apical spurs of subequal length present, spur length less than half distal tibial width; hind basitarsus with short erect pegs on inner side, slightly shorter than remaining tarsomeres, tarsal claws simple, slender.

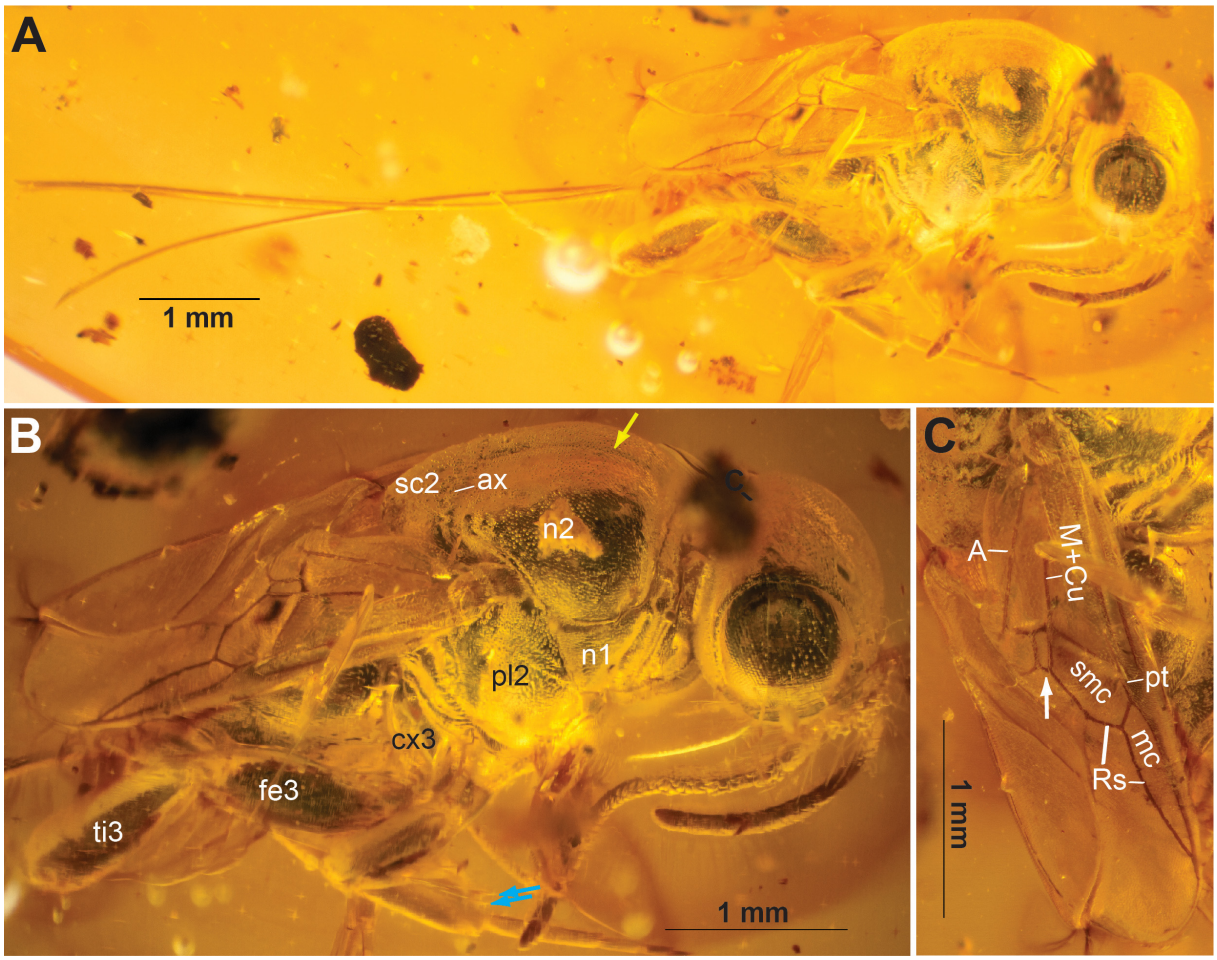

Fig. 3. †*Megacoxa gungner* sp. nov., ♀, holotype (CNU-HYM-MA-2016211). **A**. Habitus, lateral view. **B**. Body, lateral view. **C**. Fore wing. Yellow arrow = median mesoscutal sulcus; blue arrows = hind tibial apical spurs; white arrow = medial cell. Abbreviations: ax = axilla; cx3 = hind coxa; fe3 = hind femur; mc = marginal cell; n1 = pronotum; n2 = mesonotum; pl2 = mesopleuron; pt = pterostigma; sc2 = mesoscutellum; smc = submarginal cell; ti3 = hind tibia. Remaining abbreviations (A, M+Cu, Rs) refer to wing veins; see main text.

Wings. Fore wing (Fig. 3C) 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 wide distally, rectangular; Rs present between Rs+M and r-rs, closing first submarginal cell; marginal cell narrow, closed in straight line by Rs; hind wings covered by fore wings.

Metasoma (Fig. 3B). 1.09× as long as mesosoma, compact, turnip-shaped, hardly separated from mesosoma, without prominent sculpture but with short, evenly spaced hairs; metasomal segment 2 largest, metasoma widest there; sternum 7 tapered apically, folded over medially along longitudinal axis; ovipositor (Fig. 3A) extending posteriorly, elongate, length 1.35× body length; ovipositor proper and sheaths slender, teeth on tip of 2nd valvula not observed.

Male

Unknown.

Remarks

†*Megacoxa gungner* sp. nov. mostly resembles †*M. chandrahrasa* among the other species in the genus, but differs from the latter in having the hind coxa without prominent carina or foveae, the apical hind tibial spurs and hind barsitarsus shorter, and the ovipositor longer.

†***Megacoxa mjoelner*** sp. nov.

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Fig. 4

Diagnosis

Body comparatively slender (Fig. 4A), metasoma longer than mesosoma (shorter in †*M. chandrahrasa* and †*M. gungner* sp. nov.). Antennae shorter than head + mesosoma (longer in †*M. brazideci* sp. nov.). Median mesoscutal sulcus smooth (crenulate in †*M. synchrotron*), axillae not contiguous (contiguous in †*M. brazideci*). Hind coxa without carina or foveae along posterior margin (coxa carinate and foveate in †*M. janzeni* and †*M. synchrotron*).

Etymology

The new species takes its name after Mjølner (or Mjolnir), the magic hammer that was the chief weapon and primary attribute of Thor, the thunder god in Norse mythology. Like the ovipositor in †*M. mjoelner* sp. nov. (see below), the shaft of the hammer was shorter than it was originally supposed to be, due to the interference of the trickster god Loke in the form of a fly; he viciously stung the dwarven smith Brokk as Mjølner was being finalized, thus confirming the timeless malevolence of Diptera.

Type material

Holotype

MYANMAR • ♀; Kachin State, Myitkyina District, Hukawng Valley; [26°20′ N, 96°36′ E]; unnamed horizon, mid-Cretaceous, upper Albian to lower Cenomanian, 98.79±0.62 Ma (Cruickshank & Ko 2003; Shi *et al*. 2012); CNU-HYM-MA-2016209.

Description

Female

Body. Length (except ovipositor) 4.3 mm, fore wing length 3.3 mm, ovipositor length 1 mm as preserved (Fig. 4A), probably broken (see below). Specimen in mostly clear amber piece, with small midge (Diptera) syninclusion. Exudate covers lower part of head and a few diffraction planes extend from dorsal part of mesosoma.

Head (Fig. 4D). Globular, slightly wider than long, without prominent sculpture or setation; eyes oval, cover most of lateral surface of head; ocelli situated on top of head in approx. equilateral triangle; postocular carina absent; occipital carina well developed (Fig. 4D), smooth, area around occipital foramen deeply concave; antenna clearly shorter than head + mesosoma combined, scapus curved, pedicellus short, antennomeres 3–13 cylindrical (Fig. 4D), slightly longer than wide, decreasing in length distally, antennomere 14 approx. twice as long as wide, tapering distally; mouthparts difficult to observe, mandible apparently broad, teeth not visible; short palps can be observed.

Mesosoma. With elongate, extended propectus; pronotum narrow medially, triangular laterally, with anterior thoracic spiracle in notch in lateral margin (Fig. 4C); fore femur spindle-shaped, fore tibia

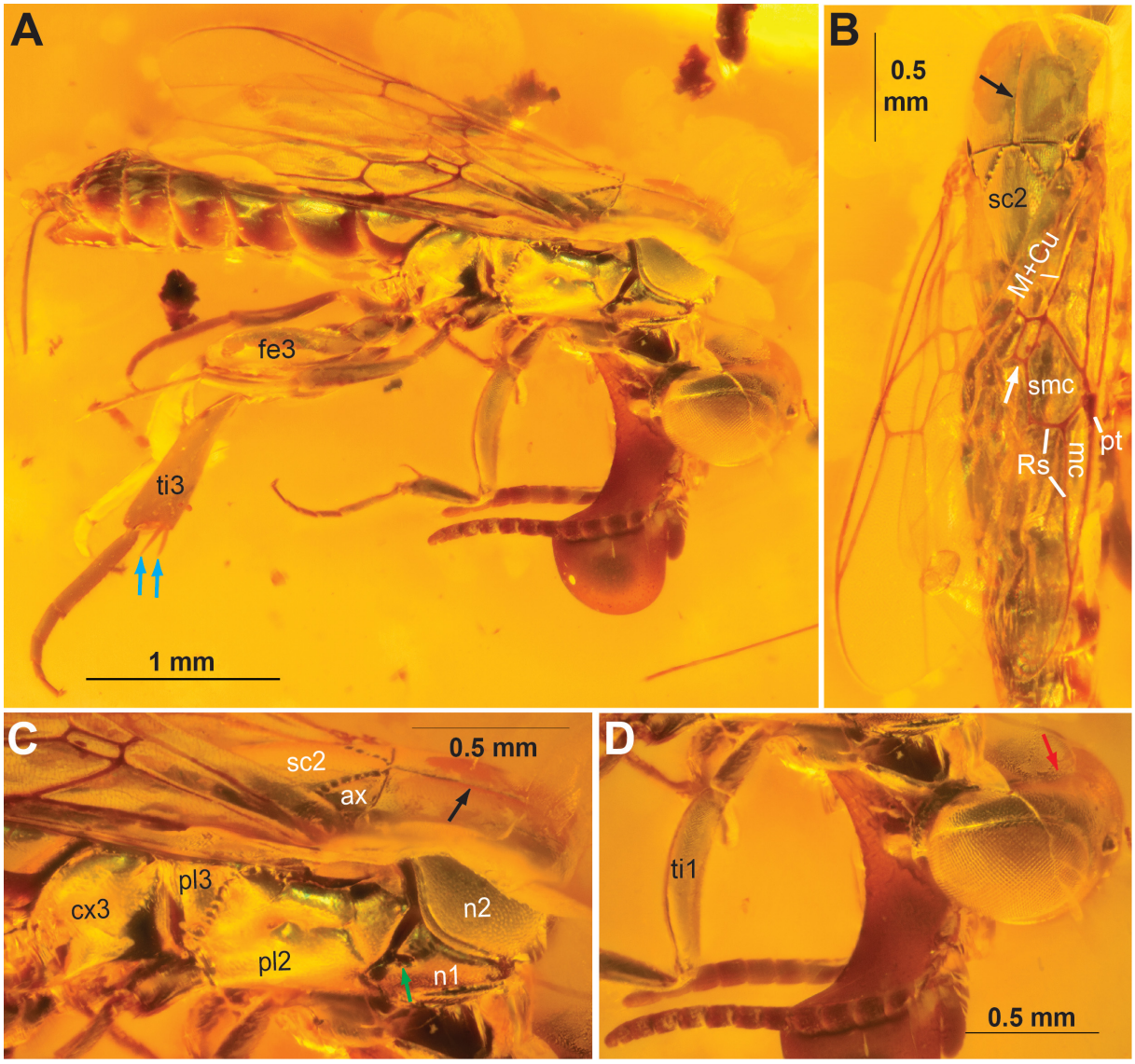

Fig. 4. †*Megacoxa mjoelner* sp. nov., ♀, holotype (CNU-HYM-MA-2016209). **A**. Habitus, lateral view. **B**. Fore wings. **C**. Mesosoma, lateral view. **D**. Head, lateral view. Blue arrows = hind tibial apical spurs; black arrow = median mesoscutal sulcus; white arrow = medial cell; green arrow = spiracular notch; red arrow = occipital carina. Abbreviations: ax = axilla; cx3 = hind coxa; fe3 = hind femur; mc = marginal cell; n1 = pronotum; n2 = mesoscutum; pl2 = mesopleuron; pl3 = metapleuron; pt = pterostigma; sc2 = mesoscutellum; smc = submarginal cell; ti1 = fore tibia; ti3 = hind tibia. Remaining abbreviations (Rs, M+Cu) refer to wing veins; see main text.

slightly expanded distally (Fig. 4D), with elongate, curved calcar; mesoscutum strongly arched in lateral view, angled between vertical anterior surface and horizontal surface; horizontal surface flat, level with mesoscutellum, not prominently sculptured; median mesoscutal sulcus distinct (Fig. 4B–C), smooth, extends to transscutal articulation; axillae distinct, triangular, not abutting medially, separated from mesoscutellum by oblique foveate scutoscutellar sulcus; mesoscutellum flat, smooth with small punctures, diamond-shaped; mesopleuron smooth, with depression medially, mesopleuro-metapleural sulcus distinct, crenulate (Fig. 4C); mid femur spindle-shaped, mid tibia slender, with two short apical spurs; hind coxa broad, with carina along posterior margin but without foveae; hind femur spindle-shaped; hind tibia (Fig. 4A) flattened, expanded distally, without fringe of setae, with two apical spurs of subequal length, inner spur shorter than distal tibial width; hind basitarsus slightly longer than remaining tarsomeres, tarsal claws simple, slender.

Wings. Fore wing (Fig. 4B) 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 wide distally; 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 (Fig. 4A). 1.27× as long as mesosoma, slender, fusiform, without prominent sculpture or pilosity; metasomal segment 2 largest, metasoma widest there; sternum 7 tapered apically, folded over medially along longitudinal axis; ovipositor (Fig. 4A) bent ventrally, apparently broken, 1st and 2nd valvulae separated at tip and no teeth observed on tip of 2nd valvula.

Male

Unknown.

Remarks

†*Megacoxa mjoelner* sp. nov. mostly resembles †*M. brazideci* sp. nov., from which it differs in having a smooth frons, shorter antennae and the axillae not being contiguous.

†***Megacoxa synchrotron*** Brazidec *et al.*, 2024

Fig. 5

Diagnosis

See Brazidec *et al.* (2024).

Material examined

MYANMAR • ♀; Kachin State, Myitkyina District, Hukawng Valley; [26°20′ N, 96°36′ E]; unnamed horizon, mid-Cretaceous, upper Albian to lower Cenomanian, 98.79 ± 0.62 Ma (Cruickshank & Ko 2003; Shi *et al*. 2012); CNU-HYM-MA-2016208.

Description

Female

Body. Length (except ovipositor) 5.4 mm, fore wing length 3.4 mm. Specimen in slightly gritty amber piece together with small beetle (Coleoptera) and midge (Diptera); wasp well preserved except for right foreleg cut off at base of tibia and ovipositor (Fig. 5A) cut off approx. 0.5 mm from tip of abdomen.

Head. Wider than long, head capsule without prominent sculpture or setation; eyes oval (Fig. 5B), higher than long, without postocular carina; antennal insertions in depressions, frons overhangs them above; occipital carina well developed (Fig. 5A), crenulate, area around occipital foramen deeply

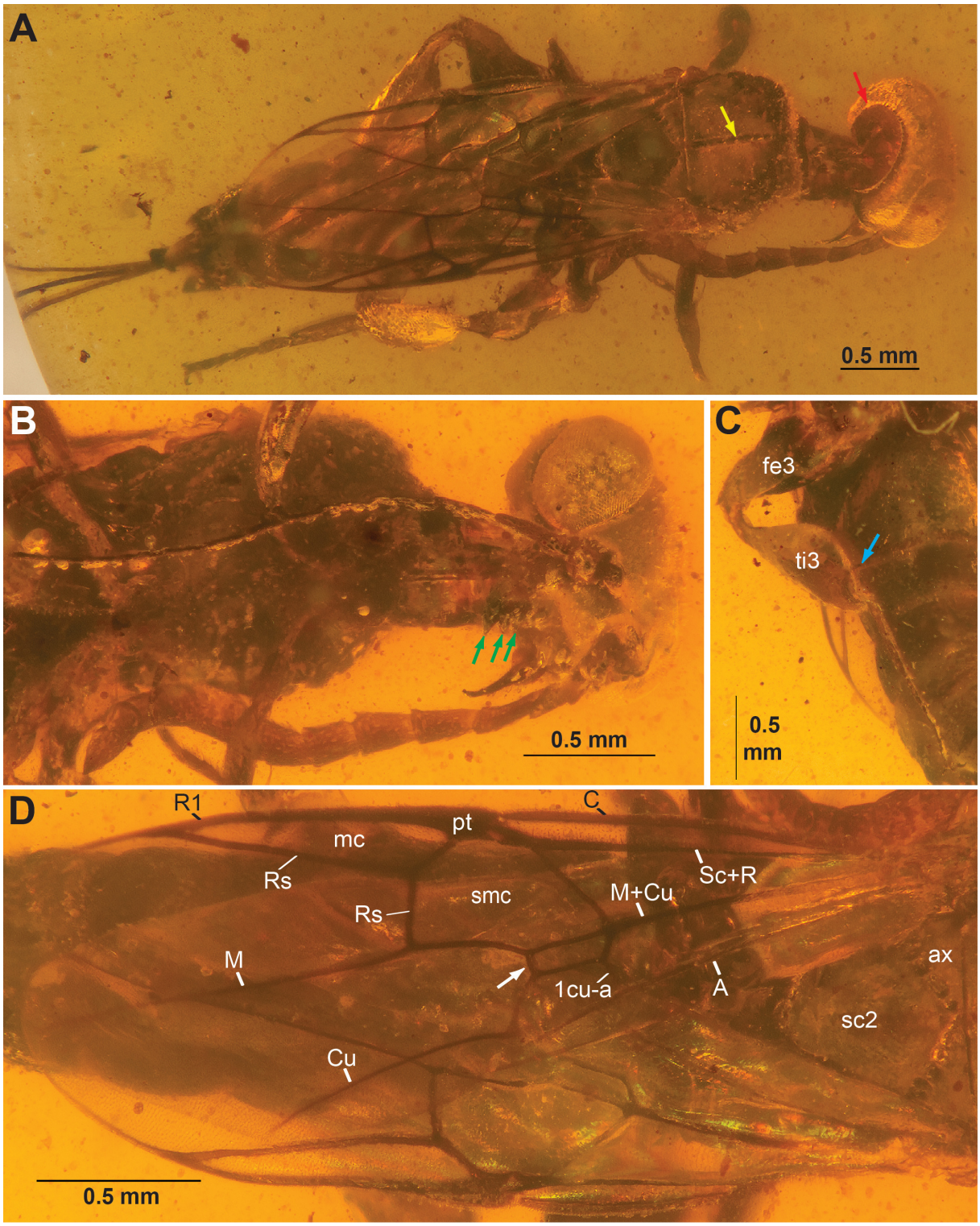

Fig. 5. †*Megacoxa synchrotron* Brazidec *et al.*, 2024, ♀ (CNU-HYM-MA-2016208). **A**. Habitus, dorsal view. **B**. Head and mesosoma, ventral view. **C**. Hind leg, ventral view. **D**. Fore wings. Yellow arrow = median mesoscutal sulcus; red arrow = occipital carina; green arrows = mandibular teeth; blue arrow = hind tibial apical spur; white arrow = medial cell. Abbreviations: ax = axilla; fe3 = hind femur; mc = marginal cell; pt = pterostigma; sc2 = mesoscutellum; smc = submarginal cell; ti3 = hind tibia. Remaining abbreviations (A, Cu, M, 1cu-a etc.) refer to wing veins; see main text.

concave; clypeus short and wide, triangular with tip between antennal insertions; antenna (Fig. 5B) slightly shorter than head + mesosoma combined, with short globular scapus and short flat pedicellus, antennomeres 3–14 flattened (probably an artefact), antennomeres 3–6 longer than 7–13, antennomere 14 approx. twice as long as wide, strongly tapered apically; labrum a small narrow flap below clypeus, concealed when mandibles are closed; mandibles broad, with three teeth (Fig. 5B) each, apical tooth longest.

Mesosoma. With elongate, extended propectus (Fig. 5A–B); pronotum narrow medially, triangular laterally; 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; horizontal surface flat, level with mesoscutellum, not prominently sculptured; median mesoscutal sulcus (Fig. 5A) distinct, crenulate, extends to transscutal articulation; axillae distinct, triangular, abut medially, separated from mesoscutellum by oblique foveate scutoscutellar sulcus; mesoscutellum flat, smooth, pointed anteriorly, rounded posteriorly; mesosoma difficult to observe laterally because of position of legs and curvature of amber piece; mid femur spindle-shaped, mid tibia slender; hind leg much larger than fore and mid legs, hind femur strongly swollen, hind tibia (Fig. 5C) strongly expanded distally, widest at approx. two-thirds from proximal end, with distinct fringe of setae distally on median ventral margin, two apical tibial spurs inserted just distally of fringe, inner spur longer than outer; hind basitarsomere approx. equal in length to remaining tarsomeres; tarsal claws slender, simple.

Wings. Fore wing (Fig. 5D) 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 wide distally; 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. 1.68× as long as mesosoma, fusiform, with weak sculpture and setation in ventral view; sternum 2 tapering anteriorly, broadening posteriorly to broadest point of metasoma, approx. twice as long as sternum 3; sternum 7 strongly tapered apically, folded over medially along longitudinal axis; base of ovipositor (Fig. 5A) extends straight from dorsal part of metasomal tip and beyond tips of wings.

Male

See Brazidec *et al.* 2024.

Remarks

†*Megacoxa synchrotron* was described from a male and the holotype was deposited in Phyletisches Museum Jena, Germany (CASENT0753237; Brazidec *et al.* 2024: figs 2f, 8). The female we describe here resembles the holotype in a number of features: the antennal configuration, the crenulate median mesoscutal sulcus, the medially abutting axillae, the uniquely enlarged hind tibia (Fig. 5C; Brazidec *et al.* 2024: fig. 8a). The wing venation is virtually identical in the holotype and the present female (compare Fig. 5D with fig. 2f in Brazidec *et al.* 2024). The main difference between the two specimens is in their size, the female being almost twice as long as the holotype. However, such sexual dimorphism is not unusual in wood-living wasps (L. Vilhelmsen, pers. obs.). In most of the phylogenetic analyses (Fig. 1), the female specimen CNU-HYM-MA-2016208 comes out in a polytomy with the three previously described species of †*Megacoxa*, including †*M. synchrotron*.

Key to species of †*Megacoxa* spp.

1. Metasoma at most as long as mesosoma (Fig. 3A–B; Brazidec *et al.* 2024: fig. 6b, e) 2
– Metasoma clearly longer than mesosoma (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 max. width of hind tibia (Brazidec *et al.* 2024: fig. 6b, g); hind basitarsus approx. 1.5× as long as remaining tarsomeres combined (Brazidec *et al.* 2024: fig. 6b, g); ovipositor shorter than body (Brazidec *et al.* 2024: fig. 6b, e) ..... †*Megacoxa chandrahrasa* Brazidec *et al.*, 2024
– Hind coxal posterior margin without carina or row of foveae (Fig. 3B); hind tibial apical spurs much shorter than max. width of hind tibia (Fig. 3B); hind basitarsus slightly shorter than combined length of remaining tarsomeres (Fig. 3A); ovipositor longer than body (Fig. 3A) ..... †*Megacoxa gungner* sp. nov.

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 (Figs 2D, 4C); median mesoscutal sulcus smooth (Fig. 4B) 5

4. Median mesosocutal sulcus smooth (e.g., Fig. 4B); axillae not abutting medially (e.g., Fig. 4B); hind tibia triangular, broadest close to apex (Brazidec *et al.* 2024: fig. 7d) .... †*Megacoxa janzeni* Brazidec *et al.*, 2024
– Median mesoscutal sulcus crenulate (Fig. 5A; Brazidec *et al.* 2024: fig. 8f); axillae abutting medially (Brazidec *et al.* 2024: fig. 8f); hind tibia spindle-shaped, broadest at two-thirds from base (Fig. 5C; Brazidec *et al.* 2024: fig. 8a) .....†*Megacoxa synchrotron* Brazidec *et al.*, 2024

5. Head with transverse striae on frons (Fig. 2B); antennae longer than head + mesosoma combined (Fig. 2A); axillae abutting medially .....†*Megacoxa brazideci* sp. nov.
– Frons smooth; antennae shorter than head + mesosoma combined (Fig. 4A); axillae not abutting medially (Fig. 4B) ..... †*Megacoxa mjoelner* sp. nov.

Discussion

We retrieved all the new species described in the present paper within a monophylum also comprising the three previously described species of †*Megacoxa*. With the inclusion of the new species, there is more variation in the hind coxal configuration that is the namesake of the genus, but the genus can still be clearly diagnosed compared to other megazarine genera; see emended diagnosis above. Variation in ovipositor length (as observed in specimens with the ovipositor preserved intact) is substantial across the genus (compare †*M. chandrahrasa* and †*M. janzeni* in Brazidec *et al.* 2024 with †*M. brazideci* sp. nov. and †*M. gungner* sp. nov. in the present paper).

In this paper, we have expanded the known diversity of Cretaceous Megalyridae, in particular the genus †*Megacoxa*, where we have doubled the number of recognized species to six. Given that the exploration of Cretaceous insect faunas is still ongoing, it is likely that more taxa will be discovered, corroborating that the current diversity and distribution of Megalyridae is just a remnant of what it was in the Mesozoic.

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Competing interests

The authors declare that they have no competing interests.

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