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A new species of *Hadraulacus* Li, Shih & Ren, 2023 (Hymenoptera: Praeaulacidae) from mid-Cretaceous Kachin amber

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Abstract

A new praeaulacid species, *Hadraulacus liae* **sp. nov.**, is described and illustrated based on a female specimen from mid-Cretaceous Kachin amber. This new species reinforces the validity of key diagnostic characters used to define the genus *Hadraulacus* Li, Shih & Ren, 2023, such as the absence of the 2rs-m crossvein in the forewing. However, it also demonstrates that some traits previously considered diagnostic for the genus, like the tibial spur formula (1-1-2), represent mere interspecific variation and have limited taxonomic value. While the discovery of this species adds to the known diversity of Praeaulacidae in the mid-Cretaceous Kachin amber, it also highlights that the diversity of the subfamily Praeaulacinae within this biota remains significantly underestimated.

Keywords: Cenomanian, Evanioidea, new taxon, taxonomy

Introduction

The extinct Mesozoic wasp family Praeaulacidae represents one of the earliest diverging lineages of Evanioidea, belonging to the Protoevanioides group. They retain several 'ancestral' traits, such as numerous crossveins in the forewing and hind wing venations and a high number of antennomeres (Li *et al.*, 2018; Jouault *et al.*, 2022). Recent phylogenetic analyses suggested that Othniodellithidae may be a subclade of Praeaulacidae, characterized by the presence of a cephalic horn and distinct Cu and cu-a veins in the hind wings (*e.g.*, Yang

et al., 2024). This hypothesis is further supported by the discovery of a praeaulacid species in mid-Cretaceous Kachin amber that features a shelf above the antennae insertions (Jouault & Nel, 2024). It is possible that Othniodellithidae represents a radiation of praeaulacid wasps endemic to the Burmese amber biota. However, our understanding of the morphological diversity and variation within Protoevanioides remains hampered by the scarcity of their fossil record in amber.

The family Praeaulacidae is well documented as adpressions from the Jurassic and Cretaceous of Asia and to a lesser extent, Australia (e.g., Rasnitsyn & Zhang, 2010; Oberprieler et al., 2012). However, the praeaulacid amber record is more restricted. Most of our knowledge of the family comes from Cretaceous deposits is Myanmar (i.e., Kachin and Hkamti), and only one taxon described from Albo-Cenomanian Charentese amber (Nel et al., 2023). In contrast, the family Evaniidae, also part of the superfamily Evanioidea, appears to have been more geographically widespread during the same period, with records in Africa, Asia, Europe, North America, the Near and Middle East (e.g., Bouju & Perrichot, 2020; Rosse-Guillevic & Jouault, 2023). We believe and expect that future taxonomic studies will reveal a broader geographical range for Praeaulacidae, shedding light on its diversity and distribution.

Here, we describe a new species, *Hadraulacus liae* **sp. nov.**, which adds to our understanding of the diversity of praeaulacid wasps in the mid-Cretaceous Kachin amber biota. This new species also helps refine the diagnostic

276 Submitted: 11 Sept. 2024; accepted by Z.Feng: 19 Sept. 2024; published: 26 Sept. 2024 Licensed under Creative Commons Attribution-N.C. 4.0 International https://creativecommons.org/licenses/by-nc/4.0/ value of certain characters previously used to define the genus.

wing venation follows Jouault & Rosse-Guillevic (2023), the terminology is adapted from Goulet & Huber (1993), and the surface sculpturing follows Harris (1979).

Material and methods

The piece of amber containing the specimen derives from the deposits of Noije Bum in the Hukawng Valley ($26^{\circ}29'$ N, $96^{\circ}35'$ 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 Mya) 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 of these sediments (Cruickshank & Ko, 2003; Yu *et al.*, 2019). The specimen is housed in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (NIGPAS), China, under collection number NIGP205567.

The piece amber was polished using a grinding polisher (Ameritool), then a thin silicon carbide sanding paper. The specimen was examined with a Zeiss Axio Zoom V16 stereomicroscope with an attached Zeiss Axiocam 512 colour 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 CC2018 and Photoshop CC2018. The

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758 Superfamily Evanioidea Latreille, 1802 Clade Protoevanioides Jouault *et al.*, 2022 Family Praeaulacidae Rasnitsyn, 1972 Subfamily Praeaulacinae Rasnitsyn, 1972

Genus Hadraulacus Li, Shih & Ren, 2023 (in Li et al., 2023)

Included species. *Hadraulacus perrarus* Li, Shih & Ren, 2023 (type species; *in* Li *et al.*, 2023), and *Hadraulacus liae* **sp. nov.**

Hadraulacus liae sp. nov.

(Figs 1–3)

Material. Holotype NIGP205567, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (NIGPAS).

Etymology. The specific epithet honours Juan Li a friend of DH who sadly passed away during field work in Tibet, July 2023.



FIGURE 1. *Hadraulacus liae* **sp. nov.**, holotype NIGP205567, habitus. **A**, Right lateral view. **B**, Left lateral view. Scale bars = 2 mm.



FIGURE 2. *Hadraulacus liae* sp. nov., holotype NIGP205567. A, Head and mesosoma in left anteroventral view. B, Left antenna. C, Left lateral view of metasoma. D, Right wings. E, Left hind wing. Scale bars = 0.5 mm (A-D), 0.2 mm (E).



FIGURE 3. *Hadraulacus liae* **sp. nov.**, holotype NIGP205567. Interpretative line drawings of fore and hindwing venations. Scale bars = 0.5 mm.

Diagnosis. Forewing with 1-Rs sub-equal to 1-M (*vs.* 1-Rs much shorter than 1-M in *H. perrarus*); 1mcu longer (about $1.5\times$) than 1-M (*vs.* shorter than 1-M); 2m-cu reaching 2+3rm cell before mid-length (*vs.* well distad); 2r-rs originating close to pterostigma mid length (*vs.* basal one-third of pterostigma). Tibial spur formula 1-2-2 (*vs.* 1-1-2).

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

Description. Female. Head ovoid, longer than wide, in lateral view about 1.15 mm high (from the base of mandibles to vertex); occipital carina well marked; eyes massive, bulging from cephalic capsule, about 0.45 mm wide; ocellar triangle isosceles, with ocelli in crater-like recesses, anterior ocellus closer to posterior ocelli than the latter with each other, distance between posterior ocelli about 0.15 mm; vertex bulging behind posterior ocelli, about 0.35 mm long; space between mandible and eyes shorter than mandible base; antennae about 7.2 mm long, filiform and polymerous; scape thin and about 0.4 mm long, widening medially, about twice as long as pedicel; pedicel widening distally; 30 antennomeres, flagellomeres reducing in length towards apex, first flagellomere subequal in length to scape, apical one acute and tapering toward apex; mandibles stout (teeth obscured by a whitish veil); maxillary palps long, four palpomeres visible; labial palps at least three-segmented.

Mesosoma thin and longer than high, about 2.6 mm long and about 1 mm high (measured perpendicularly to

dorsal surface between procoxae and midcoxae); propleura projected anteriorly and forming a neck; pronotum projecting anteriorly above neck; median mesoscutal sulcus and notauli well-impressed, notauli converging and meeting posteriorly; mesopleura and metapleura somewhat trapezoidal; propodeum coarsely areolate under petiolar insertion; tarsomeres with plantulae; arolium present; forelegs (lengths in mm): femur about 1.3, tibia 1.17, respective length of tarsomeres from base to apex: 1.06, 0.48, 0.34, 0.14, 0.18; midlegs (lengths in mm): femur about 1, tibia 1.82, respective length of tarsomeres from base to apex: 1, 0.30, 0.17, 0.09, 0.17; hind legs (lengths in mm): coxa conical about 1, trochanter *plus* femur 2.7, tibia slightly clavate about 2.5, tarsus not preserved; tarsal claws with one small preapical tooth.

Forewing about 4.2 mm long, 1.45 mm wide; costal space wider than pterostigma; pterostigma long and thin; 1-Rs longer than its distance to pterostigma, strongly inclined; 1-M slightly arched; cell 1rm triangular, longer than wide, apex (i.e., along Sc+R) aligned with apex of cell 2cua; Rs+M equal to combined lengths of 1-Rs and 1-M; 1cu-a postfurcal to M+Cu fork; cell 1+2r about $1.9 \times$ longer than wide, shorter than cell 3r; 2r-rs slightly sigmoidal and longer than 1-Rs; cell 3r closed, about 3.2× longer than wide; 1-Cu about 0.8× 1m-cu length, much longer than 2-Cu; 1m-cu longer than 2m-cu; cell 1mcu pentagonal, about 3.6× longer than wide in contact with 2rm by well-developed 2-M; 2m-cu reaching M nearly aligned with 2rs-m (i.e., in cell 2+3rm); 2-M shorter than 2-Cu, 2-Cu about 3× longer than 2-M; 3-M slightly shorter than 2-Rs; cell 2+3rm triangular, about 2.9× longer than

wide and widening toward 3rs-m; 3rs-m curved, about $0.6 \times 2r$ -rs length; cell 1cua much longer than wide; 1cu-a arched near 1A; cell 2cua about $1.45 \times$ longer than wide, pentagonal; 3-Cu shorter than cell 1+2r, about $1.3 \times$ longer than 1m-cu; cell 2mcu elongate, about $0.8 \times$ 1mcu length, and about $2.6 \times$ longer than wide; 2m-cu reaching M closer to 2-M than to 3rs-m; free abscissae of M and Cu present distad 3rs-m and 2m- cu crossveins.

Hind wing about 2.9 mm long; ten distal hamuli present along C; 1-Rs straight, sub-equal to 1rs-m; 1-M nearly straight, long (more than twice 1-Rs length); cu-a reaching Cu distad M+Cu fork; 1-Cu longer than cu-a; free abscissae of Rs, M, Cu, and A present distad rs-m and cu-a crossveins; A clearly overpassing cu-a.

Metasoma ovoid (partially preserved, likely slightly longer than mesosoma), about 3.45 mm long as preserved; first segment petiole-like (*i.e.*, long and thin), tubular (*i.e.*, ventrally inflated in its distal half) about 1 mm long and 0.28 mm wide (maximal with), second segment conical dislocated, much shorter than petiole; ovipositor longer than mesosomal length (apically damaged).

Remarks. Based on the illustrations and photographs provided in the original description of *H. perrarus* (Li *et al.*, 2023: fig. 2E), the type species appears to have 31 antennomeres, whereas our newly described species has 30. Since the type species was described from a male specimen and our new species is based on a female specimen, this difference may reflect sexual dimorphism rather than interspecific variation. Likewise, the differing shapes of the mesosoma (elongate in *H. perrarus vs.* more rounded in the new species) could also be a result of sexual dimorphism, with the more rounded shape possibly being an adaptation for retracting and storing the ovipositor.

In the original description of *H. perrarus*, no details were provided about the hindwing. However, the new specimen allows us to confirm that the hindwing venation of the genus is generally similar to that of other praeaulacid wasps, with the exception that vein 2-Rs, although well developed, does not close the marginal cell.

Discussion

The morphology and wing venation of the new specimen allow for its rapid systematic placement. Within evanioid wasps, only the family Praeaulacidae displays the combination of characters observed: a sub-complete forewing venation with one rs-m and two m-cu crossveins; a hindwing venation with Cu, rs-m, and cu-a present; a fused metasomal segment 1 (unlike the separated metasomal segment 1 in Baissidae); a metasomal segment 1 distinctly separated from the metanotum (as opposed to nearly touching the metanotum in Gasteruptiidae); a head without a cephalic horn and hind wings with Cu and cu-a present (*vs.* a cephalic horn and hindwing venation lacking distinct Cu and cu-a in Othniodellithidae, Engel *et al.*, 2016); and antennae with 30 antennomeres (*vs.* fewer than 20 in other Evanioidea).

Although the forewing of the new specimen lacks the 2rs-m crossvein (which is also absent in Anomopterellidae), it has a short 1-Rs (about as long as 1-M, compared to much longer in Anomopterellidae), a 2r-rs meeting the pterostigma near its middle (*vs.* near the apex), and a long ovipositor (*vs.* short), thus ruling out its attribution to the Anomopterellidae family (Li *et al.*, 2013). Additionally, the specimen differs from Andreneliidae in having a thin, elongated pterostigma (Rasnitsyn & Martínez-Delclòs, 2000) and cannot be placed in Nevaniinae due to its one-segmented petiole (Zhang & Rasnitsyn, 2007; Jouault *et al.*, 2020a). It further differs from Nevaniinae by having a forewing with vein M + Cu longer than the combined lengths of 1-Rs and 1-M (Zhang & Rasnitsyn, 2007).

The specimen's affinities with Cretocleistogastrinae are also excluded, as it has a thin pterostigma (vs. wide in Cretocleistogastrinae), a fully preserved 3rs-m crossvein (vs. completely lost), and a short abscissa between Rs+M and 2-M (vs. absent) (Rasnitsyn, 1990). Based on these characteristics, we place the new fossil within the subfamily Praeaulacinae.

Within this family, the specimen can be attributed to the recently described genus *Hadraulacus* (Li *et al.*, 2023), as it lacks the 2r-m crossvein, resulting in a long cell 2+3rm. Its narrow, conical first metasomal segment further distinguishes this genus from other Praeaulacidae genera, along with its relatively short forewing (around 4 mm long, compared to 6 mm or longer in genera like Evanigaster and Evaniops) (Li *et al.*, 2023). The specimen also differs from the genera *Mesevania* Basibuyuk & Rasnitsyn, 2000, *Paleosyncrasis* Poinar, 2019, and *Praegastrinus* due to the absence of a pear-shaped 3rm cell (Basibuyuk *et al.*, 2000; Poinar, 2019; Jouault & Nel, 2024; Yang *et al.*, 2024).

This new specimen perfectly illustrates a point we recently made regarding the challenges in determining the diagnostic value of certain characters used to define praeaulacid genera and their boundaries. As we noted, there are inherent difficulties in 'establishing the diagnostic significance of characters for praeaulacid specimens found in Kachin amber' (Jouault & Huang, 2024). The description of this new species aligns with this observation, as the tibial spur formula of the type species (1-1-2) was initially considered diagnostic for the genus *Hadraulacus* (Li *et al.*, 2023). However, the new species, with a different tibial spur formula, shows that this character reflects interspecific variation rather than a reliable diagnostic trait. In light of the variability in forewing venation observed both across and within praeaulacid genera, it is possible that *Hadraulacus* may be a junior synonym of another genus, such as *Habraulacus* Li *et al.*, 2015. This hypothesis, along with the broader issue of defining the limits of praeaulacid genera, will be further refined when more material becomes available for study, notably from other deposits from Myanmar (Hkamti: Jouault *et al.* 2020b).

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