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A new species of the family Praeaulacidae (Hymenoptera: Evanioidea) from mid-Cretaceous Kachin amber

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Abstract

A new praeaulacid species, *Habraulacus splendidus* **sp. nov.**, is described and illustrated based on a male specimen from mid-Cretaceous Kachin amber. This newly discovered taxon is, *inter alia*, characterised by its relatively low number of antennomeres (about 28) and its complex forewing venation (*i.e.*, with both 2rs-m and 3rs-m present). Together with the recent discoveries of praeaulacid wasps from Kachin amber, this new species lets us assume that the family Praeaulacidae was well-diversified in Cretaceous forests. The subsequent decline of this family likely occurred either in the Late Cretaceous or, in a more optimistic scenario, during the Cenozoic era.

Keywords: Apocrita, new taxon, parasitoid wasp, taxonomy

Introduction

The Praeaulacidae represent the earliest radiation of evanioid wasps and retain 'ancestral' features in their fore- and hind wing venations (*i.e.*, with numerous crossveins) and a high number of antennomeres (Li *et al.*, 2018; Jouault *et al.*, 2022). Time-calibrated phylogenies indicate a Late Triassic to Early Jurassic origin for this family, a result consistent with the well-diversified middle-late Jurassic faunas of praeaulacids found in Russia, China, and Kazakhstan (Jouault *et al.*, 2022). Interestingly, praeaulacid wasps can be readily distinguished from members of the Othniodellithidae family, another lineage within the Protoevanioides clade, by their lack of a cephalic horn and the distinct presence of distinct Cu and cu-a veins in their hind wings (Li *et al.*, 2015, 2023). However, the recent discovery of a praeaulacid species in mid-Cretaceous Kachin amber, featuring a shelf above the insertions of antennae, lends support to the hypothesis that Othniodellithidae may indeed represent a clade within Praeaulacidae (Jouault & Nel, 2024). This hypothesis finds further support in phylogenetic analyses that placed Othniodellithidae within the Praeaulacidae family (Jouault *et al.*, 2022).

The Praeaulacidae family is speciose in Jurassic rock formations across Asia and shows a broader distribution during the Cretaceous period, with records extending beyond Asia, notably into Australia (*e.g.*, Rasnitsyn & Zhang, 2010; Oberprieler *et al.*, 2012). It is anticipated that forthcoming discoveries will expand the geographical range of this clade, although to date, no fossils belonging to this family have been unearthed in the Cretaceous Lagerstätten of Crato or Orapa. The family has also been documented in Cretaceous amber deposits in France (Nel *et al.*, 2023) and Myanmar (*e.g.*, Li *et al.*, 2015). However, in the latter ecosystem, the diversity of the family in terms of species count is significantly underestimated. In this study, we contribute to the knowledge of praeaulacid wasps found in mid-Cretaceous Kachin amber by introducing a new species based on a well-preserved specimen.

Material and methods

The piece of amber containing the specimen derives from the deposits of Noije Bum in the Hukawng Valley

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(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 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 NIGP204259.

The piece of amber was polished with a grinding polisher (Ameritool), with 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, obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2018 and Photoshop CC2018. The wing venation follows Jouault & Rosse-Guillevic (2023), the terminology is adapted from Goulet & Huber (1993), and the surface sculpturing follows Harris (1979). The published work and nomenclatural acts are registered in ZooBank with the following LSID: urn:lsid:zoobank.org:pub:7B650A94-2A3B-431F-87C9-821780997FEE.

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Suborder Apocrita Gerstaecker, 1867
Superfamily Evanioidea Latreille, 1802
Clade Protoevanioides Jouault *et al.*, 2022
Family Praeaulacidae Rasnitsyn, 1972
Subfamily Praeaulacinae Rasnitsyn, 1972
Genus *Habraulacus* Li *et al.*, 2015

Included species. *Habraulacus zhaoi* Li *et al*., 2015 (type species) and *Habraulacus splendidus* **sp. nov.**

***Habraulacus splendidus* sp. nov.**
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(Figs 1–3)

Material. Holotype NIGP204259, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science, China (NIGPAS) (in a circular piece of amber measuring 8.5 × 3mm, with an undetermined larva as syninclusion, maybe a Scraptiidae according to A. Prokin).

Etymology. From the Latin *splendidus* referring to the great preservation of the specimen.

Diagnosis. Antennae with 28(?) antennomeres; forewing with 2m-cu reaching M well-distad 2rs-m; hindwing with M+Cu fork distad the meeting point of cu-a and A.

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

Description. Head ovoid, longer than wide, in lateral view 1.08 mm high (from base of mandibles to vertex) and about 0.75 mm wide; occipital carina well marked; eyes massive, slightly bulging from cephalic capsule, 0.77 mm high and 0.45 wide (in lateral view); distance between eyes (measured below toruli) about 0.5 mm; distance between anterior ocellus about 0.25 mm; vertex bulging between ocelli, long; space between mandible and eyes shorter than mandible base; antennae at least 4.5 mm long, filiform and polymerous; scape thin and about 0.25 mm long, widening medially, twice as long as pedicel; pedicel widening distally, about 0.12 mm long; 28 antennomeres (maybe one more but deformed due to the coprolite) reducing in length towards apex, apical one acute and tapering toward apex; mandibles stout, left mandible with at least three teeth, right mandible with four teeth, about 0.45 mm long (measure from apex of apical tooth to ‘external’ base), 0.25 mm wide (measure at base); maxillary palps long, four palpomeres visible, lengths from apex to base (in mm): 0.3 mm; 0.3 mm; 0.34 mm; labial palpi at least three-segmented.

Mesosoma thin and longer than high, about 2.2 mm long and about 1 mm high (measured perpendicularly to dorsal surface between procoxae and midcoxae); propleura projected anteriorly and forming a neck; pronotum about 0.4 mm long, slightly projecting anteriorly above neck; median mesoscutal sulcus and notauli well-impressed converging and meeting posteriorly; mesopleura deformed; metapleura somewhat trapezoidal; propodeum coarsely aerolate under petiolar insertion; tarsomeres with plantulae; arolium present; forelegs (lengths in mm): femur *ca.* 0.70, tibia 0.76, respective length of tarsomeres from base to apex: 0.45, 0.25, 0.18, 0.10, 0.12; midlegs (lengths in mm): femur about 0.80, tibia 1.19, respective length of tarsomeres from base to apex: 0.72, 0.30, 0.23, 0.12, 0.21; hind legs (lengths in mm): coxa conical *ca*. 0.75, trochanter *ca*. 0.38, femur 1.79, tibia slightly clavate 2.05, respective length of tarsomeres from base to apex: 0.82, 0.35, 0.25, 0.12, 0.22; tibial spurs formula 1-2-2; tarsal claws with one small preapical tooth.

Forewing about 3.6 mm long, 1.25 mm wide; costal space wider than pterostigma; pterostigma long and thin; 1-Rs 1.25× length of 1-M, as long as its distance to pterostigma, strongly inclined; 1-M slightly arched; cell 1rm triangular, longer than wide; Rs+M longer than combined lengths of 1-Rs and 1-M; 1cu-a interstitial to 1-M; cell 1+2r about 2.7× longer than wide, shorter than cell 3r; 2r-rs slightly curved and subequal to 4-Rs, reaching Rs

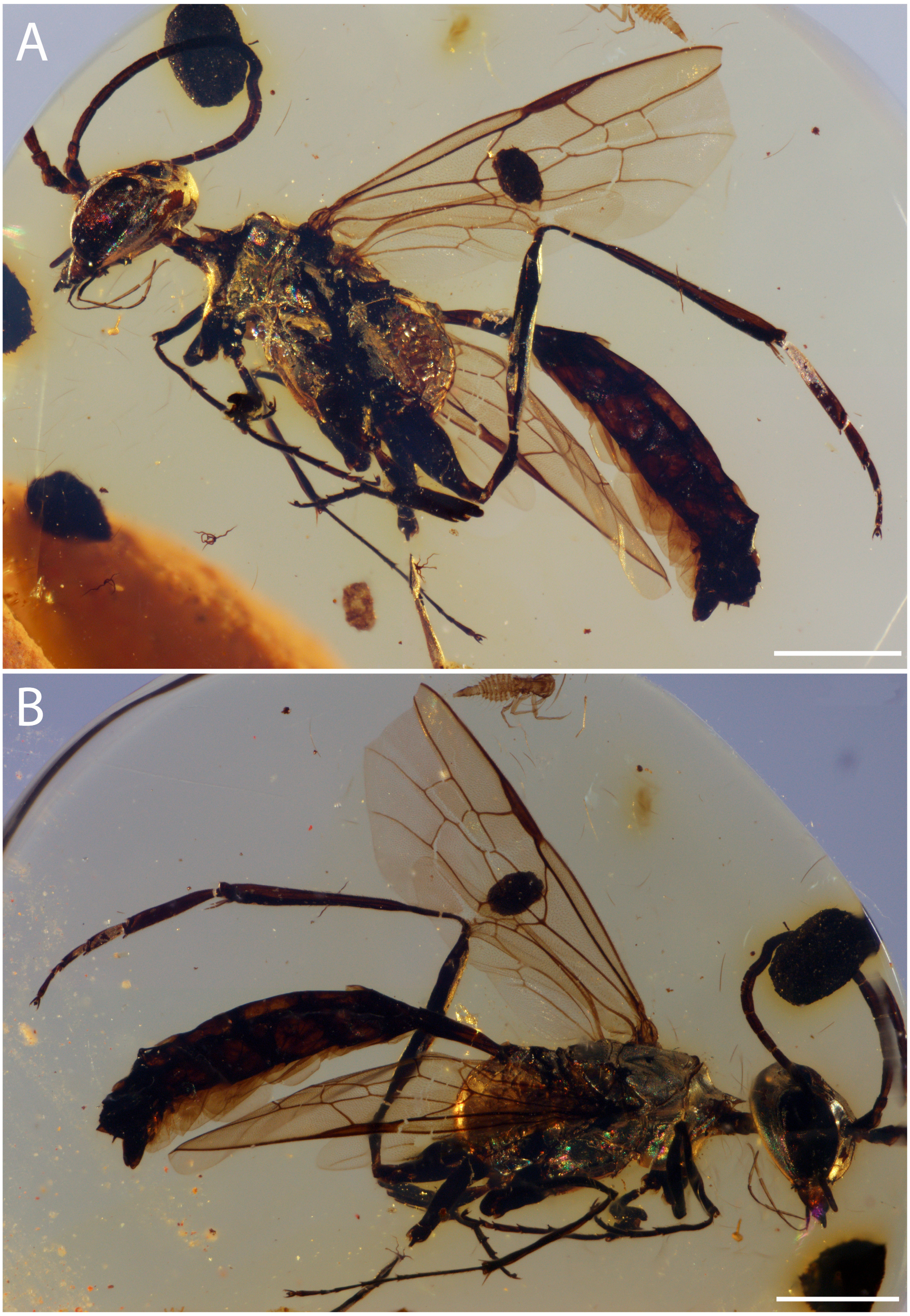

FIGURE. 1. *Habraulacus splendidus* **sp. nov.**, holotype NIGP204259. Habitus **A**, Left lateral view. **B**, Right lateral view. Scale bars = 1 mm.

anteriad 2rs-m, originating near middle of pterostigma; 4-Rs about 5.5× as long as 3-Rs; cell 3r closed; 1-Cu slightly longer than 1m-cu, longer than 2-Cu; 1m-cu longer than 2m-cu; cell 1mcu pentagonal, more than 3× longer than wide in contact with 2rm by well-developed 2-M; 2m-cu reaching M distad 2rs-m (*i.e.*, in cell 3rm); 2-M shorter than 2-Cu; 3-M slightly shorter than 2-Rs; cell 2rm trapezoidal, about 1.9× longer than wide and widening toward 2rs-m; 2rs-m curved, about 0.62× as long as 2r-rs; cell 3rm as long as cell 2rm but wider, with parallel sides; cell 1cua longer than wide, rectangular; 1cu-a strongly arched near 1A (maybe exemplified during fossilisation

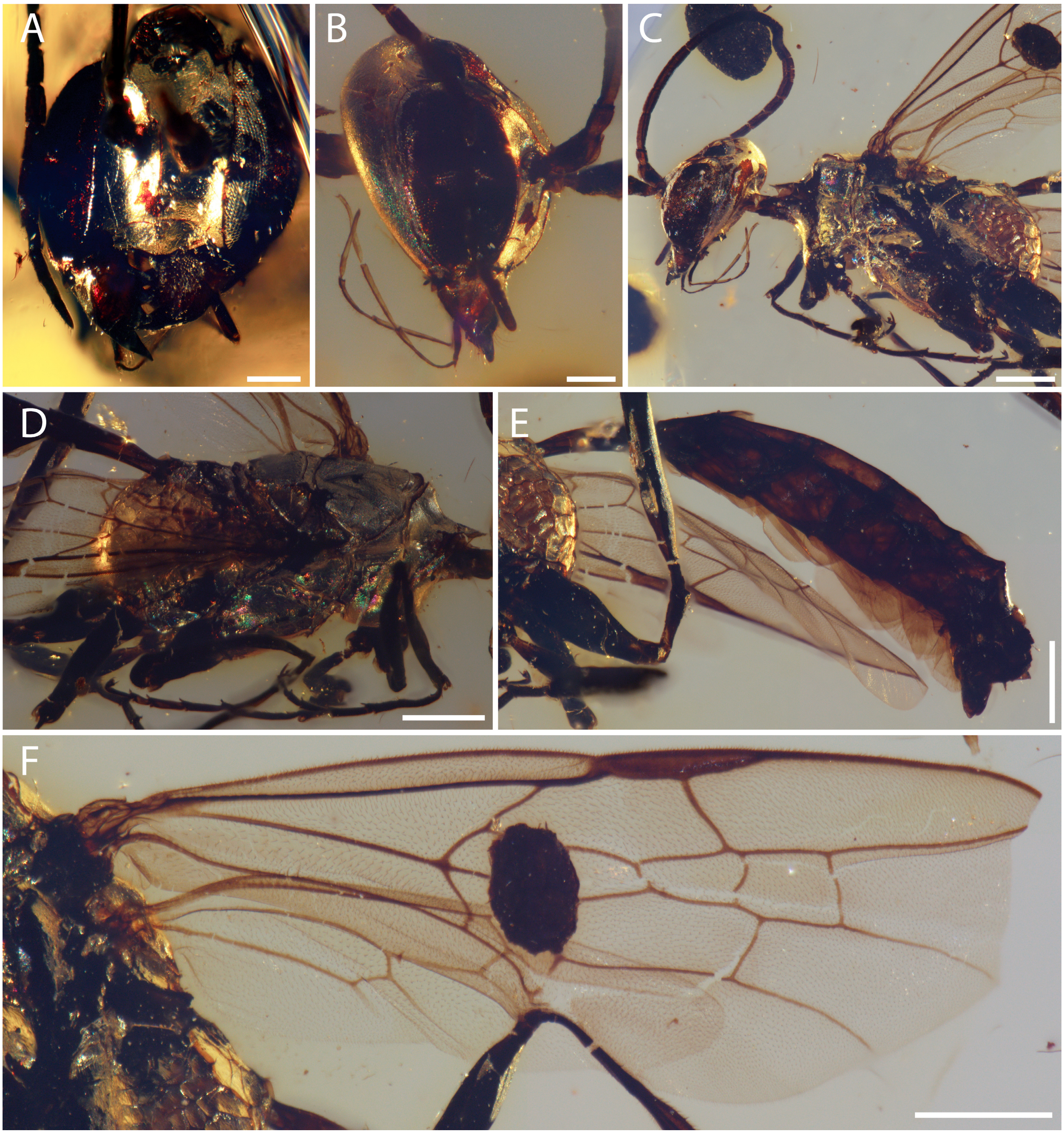

FIGURE 2. *Habraulacus splendidus* **sp. nov.**, holotype NIGP204259. **A**, Head in frontal view. **B**, Head in right lateral view. **C**, Head and mesosoma in left lateral view. **D**, Mesosoma, in right dorsolateral view. **E**, Metasoma, in left lateral view. **F**, Left wings. Scale bars = 0.2 mm (**A**, **B**); 0.5 mm (**C**–**F**).

process); cell 2cua longer than wide, pentagonal; 3-Cu shorter than cell 1+2r; cell 2mcu elongate, slightly less than twice as long as 2rm, and about 2.7× longer than wide; 2m-cu reaching M closer to 2rs-m than to 3rs-m; free abscissae of M and Cu present distad 3rs-m and 2m-cu crossveins.

Hind wing about 2.2 mm long (slightly folded); at least three distal hamuli present along C; 1-Rs straight, as long as 1rs-m; 1-M nearly straight, long (more than twice 1-Rs length); cu-a reaching Cu distad M+Cu fork; 1-Cu shorter than cu-a; free abscissae of M, Cu, and A present distad rs-m and cu-a crossveins; A clearly overpassing cu-a.

Metasoma elongate, longer than mesosoma, about 3.45 mm long, tubular; first segment petiole-like (*i.e.*, long and thin), tubular (*i.e.*, not ventrally inflated in its distal half) about 0.75 mm long and 0.18 mm wide (measured in its distally), second segment conical *ca.* 0.62 mm long, much shorter than petiole; cerci short, male genitalia elongate and narrow in side view, paramere triangular apically rounded.

Sex. Male.

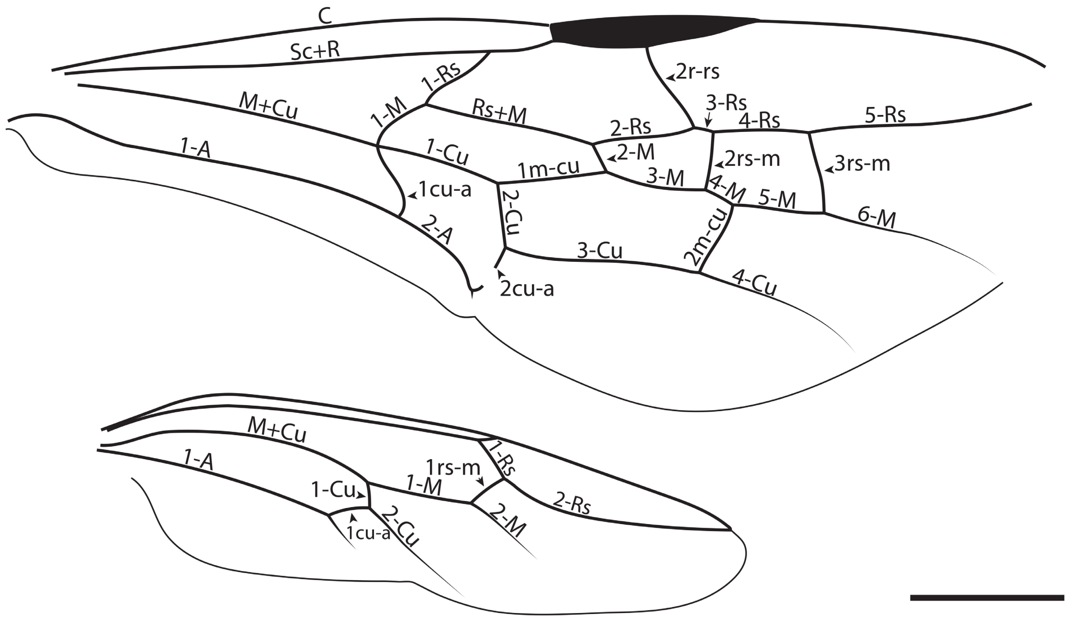

FIGURE 3. *Habraulacus splendidus* **sp. nov.**, holotype NIGP204259. Interpretative line drawings of fore- and hind wing venations with names of veins labelled. Scale bar = 0.5 mm.

Discussion

Systematic placement

The new specimen is confidently assigned to the superfamily Evanioidea due to its metasoma attached high on the mesosoma (*e.g.*, Goulet & Hubert, 1993). The superfamily Evanioidea encompasses eight extant and extinct families, with the clade Protoevanioides (Praeaulacidae + Othniodellithidae) representing their earliest radiation. Protoevanioides exhibit plesiomorphic features in fore and hind wing venations, characterised by numerous crossveins and the presence of all main veins, as well as a high number of antennomeres (*e.g.*, Li *et al*., 2018; Jouault *et al*., 2022).

The new specimen can be placed into the latter lineage due to its numerous antennomeres (ruling out affinities with all other non-Protoevanioides families: Jouault, 2023), complete forewing venation with two rs-m and two m-cu crossveins, and because of its hind wing with Rs, rs-m, and cu-a present (*e.g.*, Jouault *et al*., 2022). Notably, the specific hind wing venation pattern, coupled with the absence of a cephalic horn (an apomorphy of the family Othniodellithidae), facilitates differentiation between Othniodellithidae and Praeaulacidae (Engel, 2017; Engel *et al*., 2016; Jouault *et al.*, 2022). Within the Praeaulacidae, the specimen cannot be assigned to the Nevaniinae due to its one-segmented petiole (*vs*. two-segmented) and its forewing with M+Cu longer than the combined length of the veins 1Rs and 1M (*vs*. shorter) (Zhang & Rasnitsyn, 2007; Li *et al*., 2014; Jouault *et al*., 2020). We rule out affinities between the new specimen and the subfamily Cretocleistogastrinae because of its forewing with a thin pterostigma (*vs*. wide in Cretocleistogastrinae), the presence of a complete 3rs-m (*vs*. completely lost), and the vein 2-M well developed (*vs*. absent: Rasnitsyn, 1990; Zhang & Zheng, 2000). Following these comparisons, the new specimen is conclusively attributed to the subfamily Praeaulacinae.

Currently, seven praeaulacine genera are known from mid-Cretaceous Kachin amber: *Archeogastrinus* Jouault & Rosse-Guillevic, 2023, *Azygdellitha* Yang *et al*., 2024, *Habraulacus* Li *et al*., 2015, *Hadraulacus* Li *et al*., 2023, *Mesevania* Basibuyuk & Rasnitsyn, 2000, *Paleosyncrasis* Poinar, 2019, and *Praegastrinus* Jouault & Nel, 2024 are documented from mid-Cretaceous Kachin amber (Basibuyuk *et al*., 2000; Jouault & Nel, 2024; Jouault & Rosse-Guillevic, 2023; Li *et al*., 2015, 2023; Poinar, 2019; Yang *et al*., 2024). Among them, the new specimens can be easily differentiated from the genera *Mesevania*, *Paleosyncrasis*, and *Praegastrinus* because of the pear-shape of their cell 3rm (*vs*. squared in the new specimen) (Basibuyuk *et al*., 2000; Poinar, 2019; Jouault & Nel, 2024).

The new specimen cannot be attributed to the genus *Archeogastrinus* because of its forewing with 1-M shorter than 1-Rs (*vs*. the opposite), 1cu-a interstitial with 1-M (*vs*. postfurcal), 2r-rs reaching Rs distinctly anteriad 2rs-m (*vs*. aligned or nearly aligned with 2rs-m); hind wing with 1-Rs short (*vs*. extremely long, much longer than 1rs-m), and A distinctly continuing after cu-a (*vs*. not clearly overpassing cu-a) (Jouault & Rosse-Guillevic, 2023). Based on this comparison, we consider that the new specimen cannot be attributed to the genus *Archeogastrinus.*

The new specimen is smaller than *Azygdellitha* (forewing about 3.6 mm long *vs*. 5.6 mm long in *Azygdellitha*); it has a forewing with 1-M shorter than 1-Rs (*vs*. 1-M longer than 1-Rs), 2r-rs reaching Rs before 2rs-m (*vs*. at the level of 2rs-m); 2rs-m originating from the middle of pterostigma (*vs*. in apical third); a hind wing with 1-Rs about the same length as 1rs-m (*vs*. 1-Rs much longer than 1rs-m), and 1-Cu shorter than cu-a (*vs*. the opposite); a tibial spurs formula of 1-2-2 (*vs*. 2-2-1) (Yang *et al*., 2024). These differences prevent the placement of the specimen in this genus.

Both the new specimen and *Habraulacus zhaoi* are male specimens but they differ due to their different number of antennomeres (about 28 *vs*. at least 30 in *Habraulacus*). The new specimen also differs from *Habraulacus zhaoi* owing to its forewing with 2m-cu reaching M well-distad 2rs-m (*vs*. 2m-cu interstitial with 2rs-m in *Habraulacus*). Additionally, they both differ due to their hindwing venation with the new species having M+Cu fork distad the meeting point of cu-a and A (Li *et al*., 2015).

The new specimen can be readily differentiated from the genus *Hadraulacus* because of its forewing with a well-developed crossvein 2rs-m (*vs*. absent), its first metasomal segment (*i.e*., petiole) less elongated, and its tibial formula 1-2-2 (*vs*. 1-1-2) (Li *et al*., 2023). It is worth mentioning that the type specimen of *Hadraulacus* is poorly preserved which complicates comparison with new material. For instance, one key character of this genus (*i.e*., the absence of 2rs-m) is difficult to confirm based on the illustration provided with the description of the taxon.

Comment on the limits of praeaulacid genera trapped in amber

At present, establishing the diagnostic significance of characters for praeaulacid specimens found in Kachin amber, such as the number of antennomeres and the placement of veins, proves challenging. Differences in the illustration of specimens (*e.g*., poor contrast, limited access to details), influenced by advancements in imaging techniques, obscure the boundaries between genera described nearly a decade ago and those described in more recent studies (*e.g*., Li *et al*., 2015). In the case at hand, the new specimen resembles the species *Habraulacus zhaoi*, yet it can be distinguished from the latter by a combination of characters proposed in the diagnosis of the new species. For instance, some may consider variations in the number of antennomeres (although variable when numerous) and the position of crossveins as characters supporting the differentiation of two genera. We contend that given the current significance of these characters (*i.e*., stability in the treatment of recently discovered species), they only suffice to justify the description of a distinct species (*e.g*., Li *et al*., 2015, 2023; Jouault *et al*., 2020; Jouault & Rosse-Guillevic, 2023; Jouault & Nel, 2024). We anticipate that future discoveries in Kachin amber will refine the boundaries of praeaulacine genera.

Conclusion

Based on a single, well-preserved specimen of Praeaulacidae discovered in mid-Cretaceous Kachin amber, we described a new species, *Habraulacus splendidus* **sp. nov.** This novel taxon prompts a re-evaluation of the diagnostic significance of certain morphological traits traditionally employed to differentiate praeaulacid genera found in Burmese amber, especially considering the limited availability of specimens. For instance, while characteristics such as the number of antennomeres or the arrangement of crossveins in the forewing currently serve as useful discriminators between genera, their reliability may diminish with further examination. We anticipate that future discoveries will contribute to a deeper understanding of the evolutionary history of Evanioidea and refine our understanding of the boundaries delineating their lineages.

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