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A new genus and species of Aulacidae (Hymenoptera: Evanioidea) from mid-Cretaceous Burmese amber

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ABSTRACT

The mid-Cretaceous amber from Kachin State of Myanmar provides a well-diversified fauna of aulacid wasps. Here we describe a new aulacid genus and species *Paleoaulacus minutus*. This discovery highlights the underestimated diversity of aulacid wasps in Burmese Ablian–Cenomanian amber. Interestingly, *Paleoaulacus minutus* gen. et sp. nov. shares wing venation and body characters with the tribes Electrofoenini and Aulacini, challenging a clear placement. Future discoveries of additional specimens are necessary to precise its position or erect a new tribe to accommodate this peculiar genus. This fossil shows a developed wing venation, similar to that of the extant genus *Aulacus* Jurine, 1807.

Keywords. Hymenoptera, Evanioidea, Aulacidae, Cenomanian, fossil record

1. Introduction
The superfamily Evanioidea comprises the families Aulacidae, Evaniidae, Gasteruptiidae, †Praeaulacidae, †Anomopterellidae, †Andreneliidae, †Baissidae, and †Othniodelithidae. These wasps were clearly more diverse during the Mesozoic than in the extant fauna, with records of fossils of all these families. Notice that Engel et al. (2016), Engel (2017), and Turrisi & Ellenberger (2019) considered the praeaulacid subfamily †Nevaniinae as a different family but did not provide a clear phylogenetic argument or synapomorphy justifying such a placement. Thus we prefer to follow Zhang & Rasnitsyn (2007) and Li et al. (2018), keeping the †Nevaniinae as a subfamily of †Praeaulacidae.

Among the Evanioidea, the aulacid wasps are easily recognizable by an anterior margin of metasomal segment 1 distinctly separated from metanotum, and metatibia at most slightly widened toward apex (vs. metasomal segment 1 with anterior margin almost touching metanotum, and metatibia gradually enlarged or markedly swollen toward apex, appearing club-shaped) according to Goulet & Huber (1993). The Aulacidae comprise extant and fossil species, distributed in two subfamilies †Hyptiogastritinae (Engel, 2006, 2017) and Aulacinae (Shuckard, 1841). Furthermore, the monophyly of the family is well-supported (Jennings & Austin, 2000; Smith, 2001; Turrisi, 2006, 2007, 2014; Turrisi et al., 2009; Turrisi & Madl, 2013). Mesozoic Aulacidae are not uncommon but only known from Burmese amber (burmite, Kachin, northern Myanmar) inclusions (Turrisi & Ellenberger, 2019) with 11 described species (Cockerell, 1917a, 1917b; Engel, 2017; Li et al., 2018; Turrisi & Ellenberger, 2019; Jouault et al., 2020). Cockerell (1916a, 1916b, 1917a, 1917b, 1920a, 1920b) provided the first scientific studies on this amber. This resin is now renowned for its plethoric insect inclusions (Ross, 2019, 2020). One more time, it has delivered a new genus and species which is described an illustrated herein.

2. Material and methods

The amber piece containing the specimen studied herein derives from the deposits of Noije Bum in the Hukawng Valley (26° 29′ N, 96° 35′ E), Kachin State, northern Myanmar (Fig. 1). 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 and Ko, 2003; Yu et al., 2019).

The new aulacid specimen is embedded in a piece of clear yellow amber. It is a nearly complete individual but with damaged antennae, with the apical flagellomeres missing on right antenna and left antenna broken. The type specimen is housed in the amber collection of the Geological Department and Museum (IGR) of the University of Rennes, France. The specimen was examined and photographed with a Nikon SMZ25 with an attached Nikon D800 camera. All images were digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 softwares. The wing venation terminology follows Jouault et al. (2020).

Published work and nomenclatural acts are registered in ZooBank (http://www.zoobank.org/, last access: 07/12/2020), with the following LSID (reference): urn:lsid:zoobank.org:pub:478D05C9-6F3D-4395-A7B0-45030873215B

3. Systematic paleontology

Order Hymenoptera Linnaeus, 1758
Suborder Apocrita Gerstaecker, 1867
Superfamily Evanioidea Latreille, 1802
Family Aulacidae Shuckard, 1841
Subfamily Aulacinae Shuckard, 1841
See summary of fossil species in Table 1

Genus *Paleoaulacus* gen. nov.
Type species: *Paleoaulacus minutus* sp. nov.

**Diagnosis.** Head hypognathous; compound eye very large, prominent, ovoid; forewing long and narrow; venation well developed, with veins 1rs-m, 2rs-m present but spectral and 2m-cu tubular; cell 1M narrow with parallel vein 1Rs+M and 1cu; vein 1M short (more than six times shorter than 1Rs); vein 2Rs+M short (twice as short as 2Rs); vein 1cu and M+Cu practically aligned.

*Paleoaulacus minutus* sp. nov.

Material. Holotype IGR.BU-014 (male; preserved in a flat triangular piece of amber measuring 8×5×3 mm with a Psychodidae).

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

**Etymology.** From the Latin word *minutus* meaning ‘small’, referring to the small size of the species.

**Description.** Head globulous, practically hypognathous, higher than wide (in full face view); occipital carina absent; malar space narrow, almost inexistant; gena angled and slightly protruding; compound eye very large, prominent, ovoid, without circum-ocular carina, inner margins slightly angled (maximal distance between eyes near upper margin); ocelli small, arranged in a small triangle on top of vertex above compound eyes and separated by at least their diameter. Antennal toruli broadly separated, situated above head mid-length, distinctly separated from clypeus, near eyes apex; scape robust, 0.13 mm long, longer than wide, more than twice as long as pedicel, enlarged medially, slightly longer than or sub-equal to first flagellomere; pedicel almost as long as wide, 0.06 mm long;
flagellum filiform, with nine preserved flagellomeres, all longer than wide and cylindrical. Mandibles present but closed and not projected forward; palpal formula not clearly visible, at least composed by maxillary palps six-segmented and labial palps bi-segmented.

Mesosoma longer than high; pronotum short, smooth, without defined, raised posterior dorsal surface bordering mesoscutum, posterior border concave; propleuron projected into a conspicuous neck; mesoscutum flat in lateral view, with conspicuous edge along anterior border, with notauli not connected; mesoscelium with slightly developed axilla; tegula visible; mesopleuron short.

Legs long compared to mesosoma, with slender podites; protibial spur clearly curved; tibial spur formula 1-2-2; meso- and metacoxae closer to each other than to procoxa; trochantellus distinct but fused to associated femur; profemur shortest; basitarsus elongate but sub-equal to combined lengths of remaining tarsomeres; pretarsal claws small, simple; arolium minute.

Forewing with moderately wide costal space of comparatively consistent width along its length, slightly narrower than pterostigma; pterostigma longer than wide, expanded in width medially, tapering gradually in width to acute apex; r-rs vein originating at widest part of pterostigma (slightly distad pterostigmatic midlength); cell 1Cu long, separated from cell 2Cu by angled and curved vein 1cu-a; cell R slightly wider than 1Cu; cell 1R1 large compared to other cells, vein 1Rs slightly longer than 2Rs, both slightly curved, vein 2Rs+M short (more than twice as short as 2Rs), vein 1Rs+M straight and parallel to 1Cu, more than twice as long as 2Rs+M and enclosing cell 1M rectangular shaped, conspicuously longer than wide; cell 1M separated from 2M by a small vein 1m-cu sub-parallel to 2Rs and as long as 1M; cell 2Cu wider than long, slightly elongated basally with presence of vein 2cu-a and separated from 2M by vein 2Cu; cell 2M elongated, enclosed by vein 2m-cu and 3Cu; cell 2R1 broad and elongated (twice as long as wide), with greatest width near vein 2rs-m; vein 1rs-m and 2rs-m spectral and subequal, slightly curved; cell 1Rs shorter but as wide as 2Rs. Hind wing hidden under forewing, without visible venation except C+R.

Metasoma elongated in profile, cylindrical, longer than mesosoma; inserted well after metanotum; first metasomal segment long with anterior part modified into a petiole, remaining part cone
shaped; first tergite and sternite longer than remaining ones; tergites and sternites equal to sub-equal in lengths and separated by conspicuous sutures; last segment shorter than preceding ones. Hypopygium divided ventrally to form an elongate, apically rounded lobe on each metasomal side. Apex of gaster projected apically into rounded parameres.

Measurements (in mm). Total length as preserved (excluding antennae) 3.1; head length (excl. mandibles) 0.37; compound eye 0.31 long, 0.24 wide; mesosomal length 1.0, maximum height 0.47; dorsal length of propodeum (between metanotum and petiolar insertion) 0.19; metasomal length 1.35; profemur length 0.46, protibial length 0.43, probasitari length 0.31, combined lengths of remaining tarsomeres 0.23; mesofemur length 0.53, mesotibial length at least 0.5, mesobasitarsus length 0.27, combined lengths of remaining tarsomeres not measurable; metafemur length 0.53, metatibial length 0.62; metabasitarsus length 0.27, combined lengths of remaining tarsomeres 0.35; forewing length 2.1; hind wing length 1.2.

4. Discussion.

*Paleoaulacus* gen. nov. is assigned to the Aulacidae based on the geniculate antenna with a distinct elbow between scape and pedicel, which differentiates it from Baissidae. Also its propleuron is extending forward to form a pronounced ‘neck’ (not present in †Bassidae). However, the current family rank of Baissidae might be challenged since lacking clear apomorphies (Rasnitsyn, 2013) and retaining several plesiomorphies (listed in Engel, 2017). With 11 preserved antennomeres, and a reduced hind wing venation (viz. without 1r cell closed by tubular vein). *Paleoaulacus* gen. nov. vs. †Praeaulacidae that have more than 20 flagellomeres. The family †Praeaulacidae is currently considered as the ‘ancestral’ group of Evanioidea and is characterized by a complete wing venation, except for some species of the subfamily †Cretocleistogastrinae (Rasnitsyn, 1988; Li et al., 2013). Hence, *Paleoaulacus* gen. nov. cannot be assigned to this family since it has not such a wing venation. *Paleoaulacus* gen. nov. has not the typical horn with toruli, the long scape and the high number of antennomeres (20-21) proper to the †Othniodellichtidae. It cannot be
assigned to the †Anomopterellidae because it has only 12(?) antennomeres vs. at least 18 for the latter family.

Following Goulet & Huber (1993), the extant Aulacidae differ from the Gasteruptiidae sensu Engel (2017) (= †Kotujellitinae + Gasteruptiinae + †Hypselogastriinae + Hyptiogastrinae) in having an anterior margin of metasomal segment 1 distinctly separated from metanotum, and metatibia at most slightly widened toward apex (vs. metasomal segment 1 with anterior margin almost touching metanotum, and metatibia gradually enlarged or markedly swollen toward apex, appearing club-shaped in Gasteruptiidae). *Paleoaulacus* gen. nov., thereby, keys out as an aulacid wasp. Following the key to suprageneric groups of Aulaciformes of Engel (2017), *Paleoaulacus* gen. nov. keys out near the tribes Aulcini and Electrofoenini.

Engel (2017) proposed to use the relative positions of the eyes and antennae to separate Gasteruptiidae (see. Engel, 2017: Appendix: ‘toruli never at or bordering ventral tangent of compound eyes’) and Aulacidae (see. Engel, 2017: Appendix: ‘toruli usually at or near ventral tangent of compound eyes’). Following this character *Paleoaulacus* gen. nov. also keys out as an Aulacidae. *Paleoaulacus* gen. nov. has a forewing venation developed as in some other Aulacidae, with the veins 1rs-m, 2rs-m and 2m-cu present (absent in Hyptiogastritinae). In view of all these characters, we assigned *Paleoaulacus* gen. nov. to the subfamily Aulacinae.

Following the key proposed by Engel (2017), *Paleoaulacus* gen. nov. would key out in the Aulacini because of the forewing with 2Rs+M shorter than 1Rs+M, and shorter than 2Rs plus short mandibles. However, *Paleoaulacus* gen. nov. clearly lacks the mesoscutum transversely carinate, challenging a confident placement within the tribe Aulacini. Moreover, *Paleoaulacus* gen. nov. has a metasoma with narrow tube-like petiole, sharply segregated from a cone-like base of the gaster. This character is unknown in Aulacini but occurs in some early diverged Aulacidae (e.g., Archeofoenus Engel, 2017 and some †Electrofoenini).

Similarly, *Paleoaulacus* gen. nov. could fall in the †Electrofoenini because of the mesoscutum not transversely carinate. It also shares with the recently described Electrofoenia jehani Jouault
et al., 2020 (in †Electrofoenini) a forewing with 2Rs+M shorter than 1Rs+M, and similar shape of the metasoma, unlike the remaining †Electrofoenini. Additionally, Paleoaulacus gen. nov. shares with most †Electrofoenini (except Electrofoenia jehani Jouault et al., 2020) subequal veins 2Rs and 1Rs but Paleoaulacus gen. nov. lacks the projected mandibles typical of the †Electrofoenini (see Engel, 2017; Jouault et al., 2020). The complete wing venation with veins 1rs-m, 2rs-m and 2m-cu present is recorded in the Cretaceous tribe †Electrofoenini (e.g. Engel, 2017; Jouault et al., 2020) but also in the tribe Aulacini (e.g. Chen et al., 2016; Ramage and Jouault, 2020).

Based on these comparisons, it appears that Paleoaulacus gen. nov. shares with both tribes Aulacini and †Electrofoenini different wing venation and body characters, challenging a confident placement within one of the two tribes. Therefore, we choose to not place our new genus within the Aulacini nor in the †Electrofoenini until the discovery of additional specimens.

Among Aulacinae, it seems that Paleoaulacus gen. nov., shares with the extant genus Aulacus similar habitus and wing venation (e.g. cell and vein disposition really similar, see Fig. 2C). However, it has a long and cylindrical metasoma while the two extant aulacid genera, Pristaaulacus Kieffer, 1900 and Aulacus, usually have a trapezoidal one (see Goulet and Hubert, 1993; Chen et al., 2016; Ramage and Jouault, 2020). Paleoaulacus gen. nov. shares this putative plesiomorphic character state (see Engel and Wang, 2016) with the Gasteruptiidae from which it can be differentiated in its metasomal insertion clearly separated from metanotum. The Gasteruptiinae can also be distinguished by peculiar connected U-shaped notauli (synapomorphic character) (Grimaldi & Engel, 2005: 419), present since Early Cretaceous (Rasnitsyn, 1991), while the notauli are not connected in Paleoaulacus gen. nov. Basibuyuk and Quicke (1997) proposed to characterize the extant Gasteruptiidae by the presence of three hamuli. Unfortunately this character is not visible in the holotype of Paleoaulacus gen. nov. Moreover, Paleoaulacus gen. nov. does not share the synapomorphies of the aulacid sister group (†Kotujellitinae + Gasteruptiinae), viz. forewing vein 2rs-m spectral or conspicuous (absent or spectral in Paleoaulacus gen. nov.), without any indication of a meeting between Rs and M (while present in Paleoaulacus gen. nov.), and vein 2m-cu absent (pre-
sent in *Paleoaulacus* gen. nov.). *Paleoaulacus* gen. nov. would rather display the ‘groundplan’ ve-
nation features of Evanioidea (Basibuyuk et al., 2002).

Chen et al. (2016) proposed to separate *Aulacus* and *Pristaulacus* on the basis of the follow-
ing characters: occipital carina absent in *Aulacus* vs. present in *Pristaulacus*; forewing with
crossvein 2r-m, with 2Rs+M long in *Aulacus* vs. short in *Pristaulacus*; hind coxa of female without
groove or notch on inner lateral surface in *Aulacus* vs. present in *Pristaulacus*; pretarsal claw not
pectinate, without tooth-like processes along inner margin in *Aulacus* vs. pectinate, with tooth-like
processes along inner margin in *Pristaulacus*. Even if we cannot discern the presence of a ‘groove
or notch on inner lateral surface of hind coxa’, all the others characters allow us to assume that
*Paleoaulacus* gen. nov. shares more characters with *Aulacus* than with *Pristaulacus*. However,
*Paleoaulacus* gen. nov. differs from *Aulacus* in having more developed eyes (completely occupying
the sides of head); cylindrical metasoma; cell 1M narrow with parallel to sub-parallel sides; and
2Rs+M short.

5. Conclusion.

The present description of *Paleoaulacus* gen. nov. suggests that the diversity of aulacid wasps in
mid-Cretaceous Burmese amber is underestimated. *Paleoaulacus* gen. nov. possesses characters of
the †Electrofoenini and of the Aulacini, challenging a clear placement in one of these two tribes.
*Paleoaulacus* gen. nov. could belong to a new tribe, maybe ‘intermediate’ between extant and ex-
tinct tribes. By sharing with the extant genus *Aulacus* a similar wing venation, *Paleoaulacus* gen.
Nov. shows an atypical stability of the wing venation though time; while the evolutionary tendency
in the Aulacidae, and Hymenoptera as a whole, seems to have been towards a reduction and a sim-
plification of the wing venation during geological time.

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https://doi.org/10.1163/187631207788783987

Figure caption

Table 1. List of fossil Aulacidae with their distribution.

Figure 1. *Paleoaulacus minutus* sp. nov. Jouault & Nel, holotype IGR.BU-014 A: Habitus in side view. B: Mesosoma in dorso-lateral view (short arrows pointing bases of notauli and long arrows pointing apices). C: Genitalia. Scale bars: 0.5 mm (A); 0.25 mm (B,C).

Figure 2. *Paleoaulacus minutus* sp. nov. Jouault & Nel, holotype IGR.BU-014. A: Photograph of wings. B: Photograph of antennae basal part. C: Line drawing of forewing venation (cell name in bold). Scale bars 0.5 mm (A,C); 0.125 (B).
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Jouault C: Conceptualization, writing original draft, visualization, analysis, revise manuscript. Nel A: Supervision, writing original draft, revise manuscript.
We declare that we have no conflict of interest

Yours sincerely

Corentin