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Corentin Jouault, André Nel. A new genus and species of Aulacidae (Hymenoptera: Evanioidea) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 2021, 124, pp.104799. 10.1016/j.cretres.2021.104799 . insu-03161875

HAL Id: insu-03161875

<https://insu.hal.science/insu-03161875v1>

Submitted on 8 Mar 2021

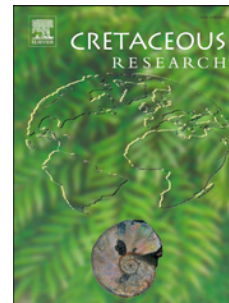
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Journal Pre-proof

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PII: S0195-6671(21)00046-X

DOI: <https://doi.org/10.1016/j.cretres.2021.104799>

Reference: YCRES 104799

To appear in: *Cretaceous Research*

Received Date: 10 July 2020

Revised Date: 8 December 2020

Accepted Date: 23 February 2021

Please cite this article as: Jouault, C., Nel, A., A new genus and species of Aulacidae (Hymenoptera: Evanioidea) from mid-Cretaceous Burmese amber, *Cretaceous Research*, <https://doi.org/10.1016/j.cretres.2021.104799>.

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

3
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11
12 **ABSTRACT**

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

21
22 **Keywords.** Hymenoptera, Evanioidea, Aulacidae, Cenomanian, fossil record

23
24 **1. Introduction**

25

26 The superfamily Evanioidea comprises the families Aulacidae, Evaniidae, Gasteruptiidae,
27 †Praeaulacidae, †Anomopterellidae, †Andreneliidae, †Baissidae, and †Othniodellithidae. These
28 wasps were clearly more diverse during the Mesozoic than in the extant fauna, with records of fos-
29 sils of all these families. Notice that Engel et al. (2016), Engel (2017), and Turrisi & Ellenberger
30 (2019) considered the praeaulacid subfamily †Nevaniinae as a different family but did not provide a
31 clear phylogenetic argument or synapomorphy justifying such a placement. Thus we prefer to fol-
32 low Zhang & Rasnitsyn (2007) and Li et al. (2018), keeping the †Nevaniinae as a subfamily of
33 †Praeaulacidae.

34 Among the Evanioidea, the aulacid wasps are easily recognizable by an anterior margin of
35 metasomal segment 1 distinctly separated from metanotum, and metatibia at most slightly widened
36 toward apex (vs. metasomal segment 1 with anterior margin almost touching metanotum, and me-
37 tatibia gradually enlarged or markedly swollen toward apex, appearing club-shaped) according to
38 Goulet & Huber (1993). The Aulacidae comprise extant and fossil species, distributed in two sub-
39 families †Hyptiogastritinae (Engel, 2006, 2017) and Aulacinae (Shuckard, 1841). Furthermore, the
40 monophyly of the family is well-supported (Jennings & Austin, 2000; Smith, 2001; Turrisi, 2006,
41 2007, 2014; Turrisi et al., 2009; Turrisi & Madl, 2013). Mesozoic Aulacidae are not uncommon but
42 only known from Burmese amber (burmite, Kachin, northern Myanmar) inclusions (Turrisi & El-
43 lenberger, 2019) with 11 described species (Cockerell, 1917a, 1917b; Engel, 2017; Li et al., 2018;
44 Turrisi & Ellenberger, 2019; Jouault et al., 2020). Cockerell (1916a, 1916b, 1917a, 1917b, 1920a,
45 1920b) provided the first scientific studies on this amber. This resin is now renowned for its pletho-
46 ric insect inclusions (Ross, 2019, 2020). One more time, it has delivered a new genus and species
47 which is described and illustrated herein.

48

49 **2. Material and methods**

50 The amber piece containing the specimen studied herein derives from the deposits of Noiye Bum in
51 the Hukawng Valley (26° 29' N, 96° 35' E), Kachin State, northern Myanmar (Fig. 1). Radiometric

52 data established an early Cenomanian age (98.79 ± 0.62 Ma) for Kachin amber, based on zircons
53 from volcanic clasts found within the amber-bearing sediments (Shi et al., 2012). Some ammonites
54 found in the amber-bearing bed and within amber corroborate a late Albian–early Cenomanian age
55 (Cruikshank and Ko, 2003; Yu et al., 2019).

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

64 Published work and nomenclatural acts are registered in ZooBank (<http://www.zoobank.org/>, last
65 access: 07/12/2020), with the following LSID (reference): urn:lsid:zoobank.org:pub:478D05C9-
66 6F3D-4395-A7B0-45030873215B

67

68 **3. Systematic paleontology**

69 Order Hymenoptera Linnaeus, 1758

70 Suborder Apocrita Gerstaecker, 1867

71 Superfamily Evanioidea Latreille, 1802

72 Family Aulacidae Shuckard, 1841

73 Subfamily Aulacinae Shuckard, 1841

74 See summary of fossil species in Table 1

75

76 Genus *Paleoaulacus* gen. nov.

77 Type species: *Paleoaulacus minutus* sp. nov.

78 urn:lsid:zoobank.org:act:5FD961F6-7D8C-4D30-A80E-86F56A95A9B9

79 *Etymology*. Named after ‘paleo’ in reference to its antiquity, and the extant genus *Aulacus* Jurine,
80 1807. Gender masculine.

81 *Diagnosis*. Head hypognathous; compound eye very large, prominent, ovoid; forewing long and
82 narrow; venation well developed, with veins 1rs-m, 2rs-m present but spectral and 2m-cu tubular;
83 cell 1M narrow with parallel vein 1Rs+M and 1cu; vein 1M short (more than six times shorter than
84 1Rs); vein 2Rs+M short (twice as short as 2Rs); vein 1cu and M+Cu practically aligned.

85

86 ***Paleoaulacus minutus*** sp. nov.

87 urn:lsid:zoobank.org:act:7745BB59-C62E-40A1-BF7F-BB738EF1A7A4

88 Figs 1–2.

89 *Material*. Holotype IGR.BU-014 (male; preserved in a flat triangular piece of amber measuring
90 8×5×3 mm with a Psychodidae).

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

93 *Etymology*. From the Latin word *minutus* meaning ‘small’, referring to the small size of the species.
94 The specific epithet is to be treated as an adjective in a genitive case.

95 *Diagnosis*. As for the genus.

96 *Description*. Head globulous, practically hypognathous, higher than wide (in full face view); occipi-
97 tal carina absent; malar space narrow, almost inexistant; gena angled and slightly protruding; com-
98 pound eye very large, prominent, ovoid, without circum-ocular carina, inner margins slightly angled
99 (maximal distance between eyes near upper margin); ocelli small, arranged in a small triangle on
100 top of vertex above compound eyes and separated by at least their diameter. Antennal toruli broadly
101 separated, situated above head mid-length, distinctly separated from clypeus, near eyes apex; scape
102 robust, 0.13 mm long, longer than wide, more than twice as long as pedicel, enlarged medially,
103 slightly longer than or sub-equal to first flagellomere; pedicel almost as long as wide, 0.06 mm long;

104 flagellum filiform, with nine preserved flagellomeres, all longer than wide and cylindrical. Mandi-
105 bles present but closed and not projected forward; palpal formula not clearly visible, at least com-
106 posed by maxillary palps six-segmented and labial palps bi-segmented.

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

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

115 Forewing with moderately wide costal space of comparatively consistent width along its length,
116 slightly narrower than pterostigma; pterostigma longer than wide, expanded in width medially, ta-
117 pering gradually in width to acute apex; r-rs vein originating at widest part of pterostigma (slightly
118 distad pterostigmal midlength); cell 1Cu long, separated from cell 2Cu by angled and curved vein
119 1cu-a; cell R slightly wider than 1Cu; cell 1R1 large compared to other cells, vein 1Rs slightly
120 longer than 2Rs, both slightly curved, vein 2Rs+M short (more than twice as short as 2Rs), vein
121 1Rs+M straight and parallel to 1Cu, more than twice as long as 2Rs+M and enclosing cell 1M rec-
122 tangular shaped, conspicuously longer than wide; cell 1M separated from 2M by a small vein 1m-cu
123 sub-parallel to 2Rs and as long as 1M; cell 2Cu wider than long, slightly elongated basally with
124 presence of vein 2cu-a and separated from 2M by vein 2Cu; cell 2M elongated, enclosed by vein
125 2m-cu and 3Cu; cell 2R1 broad and elongated (twice as long as wide), with greatest width near vein
126 2rs-m; vein 1rs-m and 2rs-m spectral and subequal, slightly curved; cell 1Rs shorter but as wide as
127 2Rs. Hind wing hidden under forewing, without visible venation except C+R.

128 Metasoma elongated in profile, cylindrical, longer than mesosoma; inserted well after metano-
129 tum; first metasomal segment long with anterior part modified into a petiole, remaining part cone

130 shaped; first tergite and sternite longer than remaining ones; tergites and sternites equal to sub-equal
 131 in lengths and separated by conspicuous sutures; last segment shorter than preceding ones. Hypo-
 132 pygium divided ventrally to form an elongate, apically rounded lobe on each metasomal side. Apex
 133 of gaster projected apically into rounded parameres.

134 Measurements (in mm). Total length as preserved (excluding antennae) 3.1; head length (excl.
 135 mandibles) 0.37; compound eye 0.31 long, 0.24 wide; mesosomal length 1.0, maximum height 0.47;
 136 dorsal length of propodeum (between metanotum and petiolar insertion) 0.19; metasomal length
 137 1.35; profemur length 0.46, protibial length 0.43, probasitarsi length 0.31, combined lengths of re-
 138 maining tarsomeres 0.23; mesofemur length 0.53, mesotibial length at least 0.5, mesobasitarsus
 139 length 0.27, combined lengths of remaining tarsomeres not measurable; metafemur length 0.53, me-
 140 tatibial length 0.62; metabasitarsus length 0.27, combined lengths of remaining tarsomeres 0.35;
 141 forewing length 2.1; hind wing length 1.2.

142

143 **4. Discussion.**

144 *Paleoaulacus* gen. nov. is assigned to the Aulacidae based on the geniculate antenna with a distinct
 145 elbow between scape and pedicel, which differentiates it from Baissidae. Also its propleuron is ex-
 146 tending forward to form a pronounced ‘neck’ (not present in †Baissidae). However, the current fami-
 147 ly rank of Baissidae might be challenged since lacking clear apomorphies (Rasnitsyn, 2013) and
 148 retaining several plesiomorphies (listed in Engel, 2017). With 11 preserved antennomeres, and a
 149 reduced hind wing venation (viz. without 1r cell closed by tubular vein). *Paleoaulacus* gen. nov. vs.
 150 cannot be assigned to the †Praeaulacidae that have more than 20 flagellomeres. The family
 151 †Praeaulacidae is currently considered as the ‘ancestral’ group of Evanioidea and is characterized
 152 by a complete wing venation, except for some species of the subfamily †Cretocleistogastrinae (Ras-
 153 nitsyn, 1988; Li et al., 2013). Hence, *Paleoaulacus* gen. nov. cannot be assigned to this family since
 154 it has not such a wing venation. *Paleoaulacus* gen. nov. has not the typical horn with toruli, the long
 155 scape and the high number of antennomeres (20-21) proper to the †Othniodellithidae. It cannot be

156 assigned to the †Anomopterellidae because it has only 12(?) antennomeres vs. at least 18 for the
157 latter family.

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

166 Engel (2017) proposed to use the relative positions of the eyes and antennae to separate Gas-
167 teruptiidae (see. Engel, 2017: Appendix: ‘toruli never at or bordering ventral tangent of compound
168 eyes’) and Aulacidae (see. Engel, 2017: Appendix: ‘toruli usually at or near ventral tangent of com-
169 pound eyes’). Following this character *Paleoaulacus* gen. nov. also keys out as an Aulacidae. *Pale-*
170 *oaulacus* gen. nov. has a forewing venation developed as in some other Aulacidae, with the veins
171 1rs-m, 2rs-m and 2m-cu present (absent in Hyptiogastritinae). In view of all these characters, we
172 assigned *Paleoaulacus* gen. nov. to the subfamily Aulacinae.

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

180 Similarly, *Paleoaulacus* gen. nov. could fall in the †Electrofoenini because of the mesoscu-
181 tum not transversely carinate. It also shares with the recently described *Electrofoenia jehani* Jouault

182 et al., 2020 (in †Electrofoenini) a forewing with 2Rs+M shorter than 1Rs+M, and similar shape of
183 the metasoma, unlike the remaining †Electrofoenini. Additionally, *Paleoaulacus* gen. nov. shares
184 with most †Electrofoenini (except *Electrofoenia jehani* Jouault et al., 2020) subequal veins 2Rs and
185 1Rs but *Paleoaulacus* gen. nov. lacks the projected mandibles typical of the †Electrofoenini (see
186 Engel, 2017; Jouault et al., 2020). The complete wing venation with veins 1rs-m, 2rs-m and 2m-cu
187 present is recorded in the Cretaceous tribe †Electrofoenini (e.g. Engel, 2017; Jouault et al., 2020)
188 but also in the tribe Aulacini (e.g. Chen et al., 2016; Ramage and Jouault, 2020).

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

193 Among Aulacinae, it seems that *Paleoaulacus* gen. nov., shares with the extant genus *Aula-*
194 *cus* similar habitus and wing venation (e.g. cell and vein disposition really similar, see Fig. 2C).
195 However, it has a long and cylindrical metasoma while the two extant aulacid genera, *Pristaulacus*
196 Kieffer, 1900 and *Aulacus*, usually have a trapezoidal one (see Goulet and Hubert, 1993; Chen et al.,
197 2016; Ramage and Jouault, 2020). *Paleoaulacus* gen. nov. shares this putative plesiomorphic char-
198 acter state (see Engel and Wang, 2016) with the Gasteruptiidae from which it can be differentiated
199 in its metasomal insertion clearly separated from metanotum. The Gasteruptiinae can also be distin-
200 guished by peculiar connected U-shaped notauli (synapomorphic character) (Grimaldi & Engel,
201 2005: 419), present since Early Cretaceous (Rasnitsyn, 1991), while the notauli are not connected in
202 *Paleoaulacus* gen. nov. Basibuyuk and Quicke (1997) proposed to characterize the extant Gas-
203 teruptiidae by the presence of three hamuli. Unfortunately this character is not visible in the holo-
204 type of *Paleoaulacus* gen. nov. Moreover, *Paleoaulacus* gen. nov. does not share the synapo-
205 morphies of the aulacid sister group (†Kotujellitinae + Gasteruptiinae), viz. forewing vein 2rs-m
206 spectral or conspicuous (absent or spectral in *Paleoaulacus* gen. nov.), without any indication of a
207 meeting between Rs and M (while present in *Paleoaulacus* gen. nov.), and vein 2m-cu absent (pre-

208 sent in *Paleoaulacus* gen. nov.). *Paleoaulacus* gen. nov. would rather display the ‘groundplan’ ve-
209 nation features of Evanioidea (Basibuyuk et al., 2002).

210 Chen et al. (2016) proposed to separate *Aulacus* and *Pristaulacus* on the basis of the follow-
211 ing characters: occipital carina absent in *Aulacus* vs. present in *Pristaulacus*; forewing with
212 crossvein 2r-m, with 2Rs+M long in *Aulacus* vs. short in *Pristaulacus*; hind coxa of female without
213 groove or notch on inner lateral surface in *Aulacus* vs. present in *Pristaulacus*; pretarsal claw not
214 pectinate, without tooth-like processes along inner margin in *Aulacus* vs. pectinate, with tooth-like
215 processes along inner margin in *Pristaulacus*. Even if we cannot discern the presence of a ‘groove
216 or notch on inner lateral surface of hind coxa’, all the others characters allow us to assume that
217 *Paleoaulacus* gen. nov. shares more characters with *Aulacus* than with *Pristaulacus*. However,
218 *Paleoaulacus* gen. nov. differs from *Aulacus* in having more developed eyes (completely occupying
219 the sides of head); cylindrical metasoma; cell 1M narrow with parallel to sub-parallel sides; and
220 2Rs+M short.

221

222 **5. Conclusion.**

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

231

232 **Acknowledgment**

233 We sincerely appreciate critical reviews and comments from the editor (Dr. Eduardo Koutsoukos),
234 an anonymous reviewers, and Prof. Alexandr Rasnitsyn in improving our manuscript. We are grate-
235 ful to Dr. Valérie Ngô-Muller (ISYEB, MNHN) who has kindly imaged the specimen.

236

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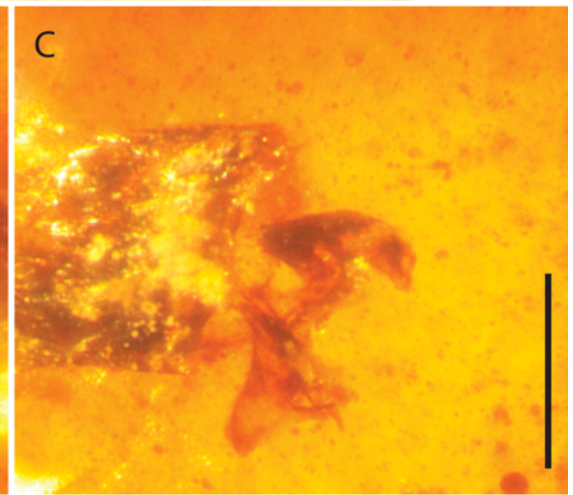
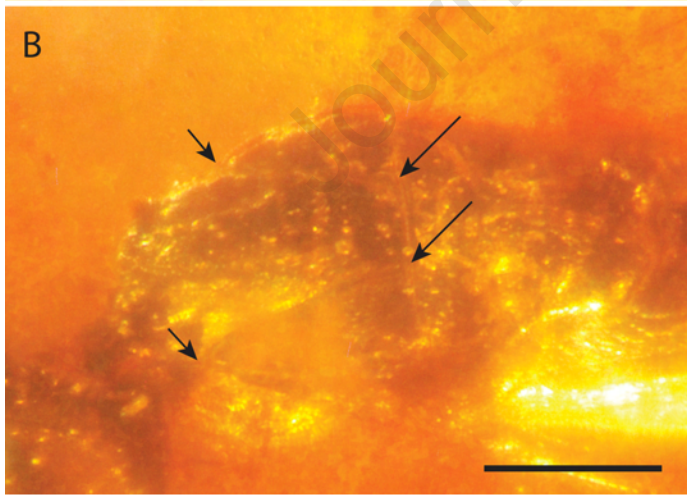
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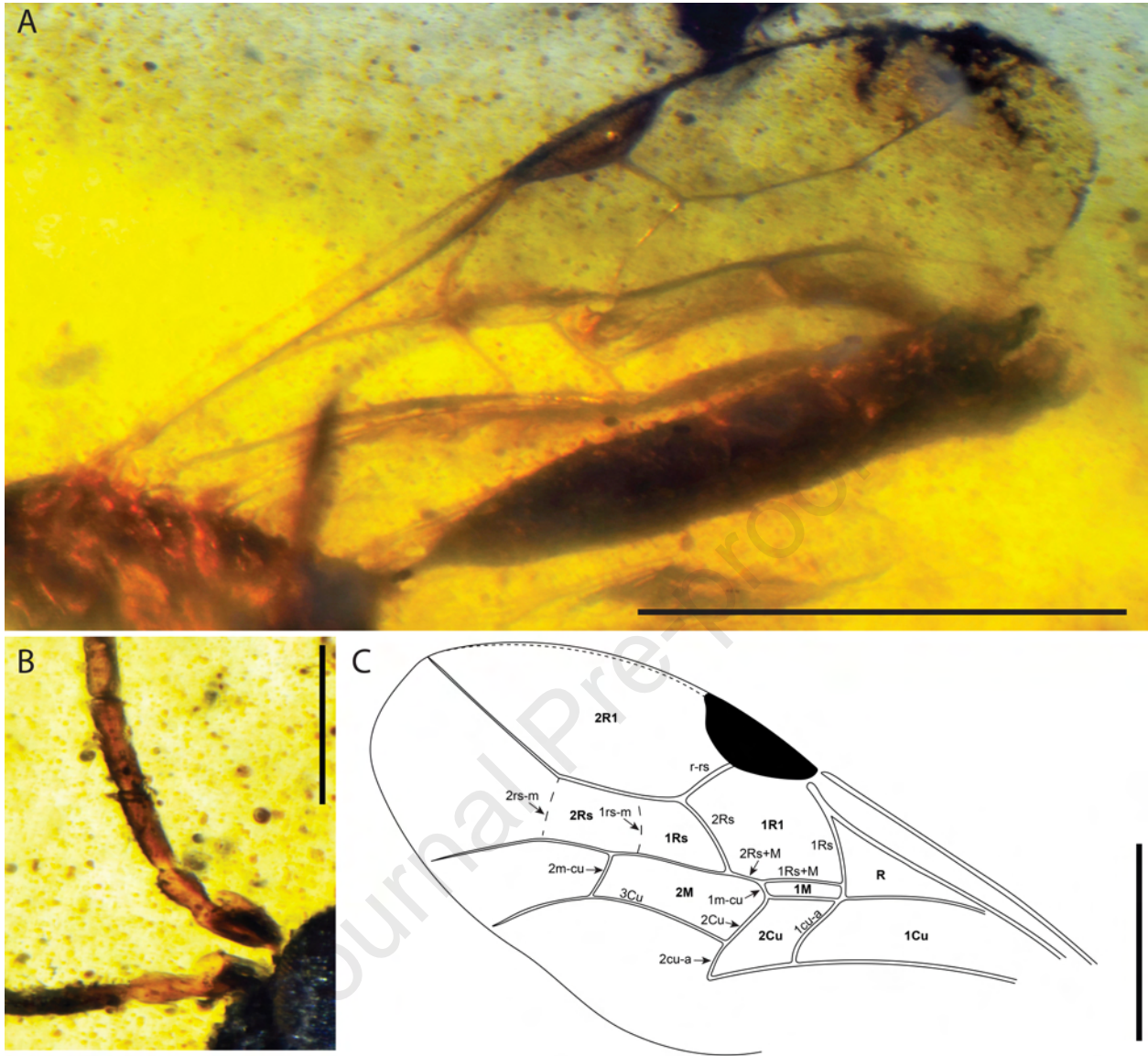
337 Table 1. List of fossil Aulacidae with their distribution.

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

341 Figure 2. *Paleoaulacus minutus* sp. nov. Jouault & Nel, holotype IGR.BU-014. A: Photograph of
342 wings. B: Photograph of antennae basal part. C: Line drawing of forewing venation (cell name in
343 bold). Scale bars 0.5 mm (A,C); 0.125 (B).

Families/Subfamilies / Genera	Species	Distribution	Period	References
Aulacidae				
<i>Vectevania</i> Cockerell	1	United Kingdom	Eocene	Cockerell, 1922
Hyptogastritinae				
<i>Hyptogastrites</i> Cockerell	1	Myanmar	Late Cretaceous	Cockerell, 1917
<i>Archeofoenus</i> Engel	2	Myanmar	Late Cretaceous	Engel, 2017; Turrisi and Ellenberger, 2019
<i>Protofoenus</i> Cockerell	1	Myanmar	Late Cretaceous	Cockerell, 1917
Aulacinae				
<i>Electrofoenops</i> Engel	3	Myanmar	Late Cretaceous	Engel, 2017; Turrisi and Ellenberger, 2019
<i>Electrofoenus</i> Cockerell	1	Myanmar	Late Cretaceous	Cockerell, 1917
<i>Aulacus</i> Jurine	1	France	Eocene	Nel et al., 2004
	2	Baltic amber	Eocene	Brues, 1933;
	1	USA	Oligocene	Bruce, 1910
<i>Exilaulacus</i> Li et al.	2	Myanmar	Late Cretaceous	Li et al., 2018
<i>Pristaulacus</i> Kieffer	3	USA	Eocene	Brues, 1910; Cockerell, 1916
	3	Baltic amber	Eocene	Brues, 1923 ;Brues, 1933; Jennings and Krogmann, 2009
<i>Electrofeonia</i> Jouault et al.	1	Myanmar	Late Cretaceous	Jouault et al., 2020
<i>Paleoaulacus</i> Jouault & Nel	1	Myanmar	Late Cretaceous	Jouault and Nel, 2021





Jouault C: Conceptualization, writing original draft, visualization, analysis, revise manuscript. Nel A: Supervision, writing original draft, revise manuscript.

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We declare that we have no conflict of interest

Yours sincerely

Corentin

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