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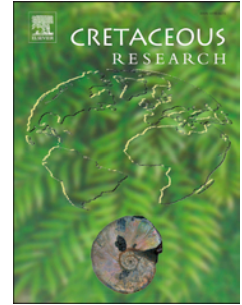


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1 A new genus and species of parasitic wasps (Hymenoptera: Diapriidae)  
2 from Hkamti ‘mid-Cretaceous’ Burmese amber

3

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12

13 **ABSTRACT**

14 *Protobelyta monsirei* gen. et sp. nov., a new genus and species of belytine wasp (Diapriidae:  
15 Belytinae), is described from a female preserved in ‘mid-Cretaceous’ Burmese (Albian–  
16 Cenomanian) amber from Hkamti. The new fossil is the first description of the family in Burmese  
17 amber and one of the oldest known Belytinae, providing evidence for the antiquity of modern  
18 diapriid lineages.

19

20 *Keywords:*

21 Hymenoptera, Apocrita, Diapriidae, Belytinae, Hkamti amber, Cretaceous.

22

23 **1. Introduction**

24 Diapriidae remain poorly documented in Cretaceous ambers, which is very surprising  
25 considering the number of pieces of amber containing representatives of this family (C.J pers. obs).  
26 Perrichot & Nel (2008) proposed a summary of the fossil record of the family and reported *ca.* fifty

27 inclusions, mainly Cenozoic and distributed among the subfamilies Diapriinae Haliday, 1833 and  
28 Belytinae Förster, 1856. After this paper, the fossil record of the family has increased, with the  
29 papers of Lak & Nel (2009), Engel et al. (2013) and Rasnitsyn and Öhm-Kühnle (2019) for the  
30 Cretaceous, and Antropov et al. (2014), Archibald et al. (2018), and Van de and Kamp et al. (2018)  
31 for the Cenozoic. Nevertheless, it remains largely underestimated for major deposits such as the  
32 Burmese and Baltic ambers.

33 Diapriid wasps are small endoparasitoids of flies, ants, and beetles (Loiacono, 1987; Masner,  
34 1993). Their modern diversity is greatly underestimated according to Johnson (1992), with ‘only’  
35 2088 described extant species (<https://hol.osu.edu>). This would represent half of the estimated  
36 extant diversity of this family. This family shows a wide distribution in most of the ecozones. As  
37 mentioned in Königsmann (1978), Rasnitsyn (1988), Dowton et al. (1997), Dowton & Austin  
38 (2001), Rasnitsyn (2002), and Castro & Dowton (2006), the superfamily Proctotrupoidea appears to  
39 be composed by paraphyletic groups. Sharkey (2007) separated the Diaprioidea from this  
40 superfamily. According to recent phylogenetic studies, the Diaprioidea seems to be the sister  
41 lineage of the Proctotrupoidea or of the Chalcidoidea, and possibly diverged at the beginning of the  
42 Jurassic (Dowton et al., 1997; Castro & Dowton, 2006; Peters et al., 2017). The concept of  
43 Diaprioidea also varied through time: Rasnitsyn (1980)’s concept of Diaprioidea comprised  
44 Platygastroidea, Mymaridae Haliday, 1833, Austroniidae Kozlov (in Rasnitsyn, 1975), Diapriidae  
45 Haliday, 1833, Monomachidae Ashmead, 1902 and the extinct Serphitidae Brues, 1937; while  
46 Sharkey et al. (2012)’s concept included Maamingidae Masner, Naumann & Austin, 2001,  
47 Diapriidae (with the Ismaridae as a subfamily), and Monomachidae. Engel et al. (2013) added the  
48 Mesozoic family Spathiopterygidae Engel & Ortega-Blanco, 2013 to the Diaprioidea.

49 Two putative synapomorphies allow a quick recognition of the Cynipoidea and  
50 Diaprioidea: the concave/convex vein M(+Cu) on the hind wing and the male basal flagellomere  
51 modified to accommodate the gland secretion releaser (Rasnitsyn, 1988, 2002). Sharkey et al.  
52 (2012: 99) proposed two different synapomorphies to support the clade Diaprioidea except *Ismarus*:

53 subantennal shelf present, and ventral transverse carina of metapleuron absent or weakly developed,  
54 but these authors added that they are ‘convergent in some members of most Proctotrupomorpha  
55 superfamilies’. Unlike the cosmopolitan and speciose Diapriidae, the Monomachidae and the  
56 †Spathiopterygidae are represented by a small number of species (less than 10 species for the later),  
57 and can be differentiated from the others families composing the Diaprioidea by a typical wing  
58 venation (Engel et al., 2013, 2015; Krogmann et al., 2016). The Ismarinae can be easily  
59 differentiated from the other Diapriidae by the lack of facial projection from which the antennae  
60 arise, and characterized by various degrees of fusion of the metasomal terga. The family  
61 Monomachidae is represented by the three genera *Monomachus* Klug, 1841 (with *Tetraconus*  
62 Szépligeti, 1903 as junior synonym), and *Chasca* Johnson & Musetti, 2012 (Naumann & Masner  
63 1985; Musetti & Johnson 2000; Johnson & Musetti, 2012), only found in the Neotropical and  
64 Australian regions. Females are readily recognized by ‘their elongate, loosely articulated, weakly  
65 sclerotized, and acuminate metasoma’, as a putative synapomorphy (Johnson & Musetti, 2012: 1).  
66 The Diapriidae can be differentiated by the medium to small sizes, the antennae elbowed, the scape  
67 inserted high above clypeus, usually on a prominent transverse ledge; fore wing without stigma but  
68 sometimes with slightly thickened marginal vein; metasoma distinctly petiolate with true or  
69 apparent tergum 2 the longest; ovipositor almost entirely retracted (Goulet & Huber, 1993). Four  
70 subfamilies are currently recognized within diapriids: Ambositrinae, Belytinae, Diapriinae, and  
71 Ismarinae. The Belytinae and Diapriinae seem to be the most diverse ones compared to the other  
72 subfamilies. The monophyly of Diapriidae except *Ismarus* is supported by six morphological  
73 character states not present in *Ismarus*, i.e., third maxillary palpomere enlarged, broader than the  
74 following palpomere, and triangular; pronotal transverse carina absent; lateroventral corners of  
75 pronotum with medial inflexions abutting mesopleuron; prophragma of mesonotum not subdivided  
76 by slit; a distinct longitudinal ridge of metapleuron ventral to propodeal spiracle present;  
77 metaphragma and metapleural apodeme fused (after Sharkey et al., 2012).

78 Herein we described and figure a new genus and species of Belytinae based on new  
79 material from Burmese amber.

80

## 81 **2. Material and methods**

82 The amber piece containing the specimen studied herein derive from the deposits of Hkamti site,  
83 Hkamti District, Sagaing Region, Myanmar. The Hkamti site is about 80 km southwest of the  
84 Angbamo site. Radiometric data established an early Cenomanian age ( $98.79 \pm 0.62$  Ma) for  
85 Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments  
86 (Shi et al., 2012). Some ammonites found in the amber-bearing deposits corroborates a late Albian–  
87 early Cenomanian age (Cruickshank & Ko, 2003; Yu et al., 2019).

88 Specimen examination was conducted under a Leica MZ APO stereomicroscope and  
89 pictures were taken with Canon EOS 5D mark II. All images are digitally stacked  
90 photomicrographic composites of several individual focal planes, which were obtained using  
91 HeliconFocus. The figures were composed with Adobe Illustrator CC 2019 and Adobe Photoshop  
92 CS19 software. The specimen presented in this study is housed in the amber collection of the  
93 Geological Department and Museum (IGR) of the University of Rennes, France under the  
94 collection number IGR.BU-011. The terminology of Huber & Sharkey (1993) is employed  
95 throughout for morphological features of the body and wing venation.

96 [urn:lsid:zoobank.org:pub:A0AE4A98-187C-4277-BF81-A0D00CAAB96D](https://zoobank.org/pub:A0AE4A98-187C-4277-BF81-A0D00CAAB96D)

97

## 98 **3. Systematic palaeontology**

99 Order: Hymenoptera Linnaeus, 1758

100 Superfamily: Diaprioidea Haliday, 1833

101 Family: Diapriidae Haliday, 1833

102 Subfamily: ?Belytinae Förster, 1856

103

104 Genus: *Protobelyta* gen. nov. Jouault & Nel

105 urn:lsid:zoobank.org:act:483AF931-4783-449D-9E79-9ACE673D95E2

106 Type species

107 *Protobelyta monsirei* sp. nov.

108 *Etymology*

109 The genus name is a combination of the Greek «*prôtos*» meaning ‘primitive’ and *Belyta*, type  
110 genus of the Belytinae. Gender feminine.

111 *Diagnosis*

112 Head short; eyes glabrous; antenna 15-segmented, inserted high above clypeus on a distinct shelf;  
113 scape long, slightly longer than head height; pedicel, first and second flagellomeres cylindrical and  
114 subequal, other flagellomeres broadened distally; fore wing with radial cell [2R1] as long as  
115 pterostigma, entirely closed at apex, vein r-rs reaching pterostigma after mid-length; hind wing with  
116 basal cell well defined, with three hamuli; deep and long notauli on mesoscutum; metanotum  
117 without dorso-lateral teeth; propodeum coarsely aerolate; petiole slightly longer than wide;  
118 metasoma ellipsoidal, dorso-ventrally flattened, not narrowly pointed at apex; second metasomal  
119 sternite the longest, fifth and sixth slightly longer than third and fourth.

120

121 *Protobelyta monsirei* sp. nov. Jouault & Nel

122 (Figs 1–2)

123 urn:lsid:zoobank.org:act:1FFDFE5C-9B8D-4E04-9D1B-818D395F0276

124 *Etymology*

125 The specific epithet is a patronym honoring Mathieu Monsire, a friend of one of us (J.C.). The  
126 species epithet is to be treated as a noun in the genitive case.

127 *Studied material*

128 Holotype IGR.BU-011 (female, a nearly complete and well-preserved specimen in a rectangular  
129 piece of amber measuring 6 × 3 × 1 mm).

130 *Locality and horizon*

131 Hkamti site, Hkamti District, Sagaing Region, Myanmar; Albian–Cenomanian, Upper Cretaceous.

132 *Diagnosis*

133 As for the genus.

134 *Description*

135 Female specimen. Head: hypognathous, short; occipital carina conspicuous; compound eyes large  
136 and glabrous; ocelli hardly visible but present, apparently equidistant; several long hairs on front;  
137 mandibles short (not clearly visible due to preservation). Antenna with 13 flagellomeres, not  
138 clubbed, inserted high above clypeus on a distinct transverse shelf; antennal sockets facing  
139 upwards; scape elongated slightly longer than head height as seen in frontal view, with short hairs;  
140 pedicel, first and second flagellomeres nearly equal in length, cylindrical, about twice as long as  
141 wide; following flagellomeres shorter but increasing gradually in length and width, broadened  
142 distally, about as long as broad; apical one ovoid, tapering apically; lengths of antennomeres: 0.31;  
143 0.1; 0.1; 0.1; 0.08; 0.06; 0.06; 0.06; 0.06; 0.06; 0.06; 0.06; 0.05; 0.05; 0.05; 0.06; 0.011.

144 Mesosoma: with short, sparse pilosity; notauli deep and long, scutellum without tooth; metanotum  
145 smooth (without teeth); propodeum coarsely areolate. Fore wing covered with punctuation and  
146 bordered with small setae increasing in size on ventral margin, vein Rs not forked; pterostigma  
147 narrow, almost linear; radial cell [2R1] closed, as long as pterostigma; vein r-rs reaching  
148 pterostigma after mid-length; veins Sc + R, M + Cu, M, distal parts of Rs, M and Cu visible, other  
149 veins not sclerotized. Hind wing narrow elongate, covered with punctuation and bordered with  
150 small setae increasing in size on ventral margin; basal cell [R] closed; with three distal hamuli. Legs  
151 with sort sparse pubescence; hind coxa much thicker than fore and mid ones; femora medially  
152 enlarged; fore and mid legs thinner than hind legs; tibiae broadened at about fourth-fifths of length  
153 (hind tibia the broadest); basitarsus shorter than combined length of other ones; tibial spur formula  
154 1-2-2, no false spur on fore tibia; tarsal claws simple; arolium as long as tarsal claws.

155 Metasoma: with each segments wearing a numerous hairs; ellipsoidal, dorso-ventrally flattened, not  
156 narrowly pointed at apex; petiole slightly longer than wide with several longitudinal carina; second  
157 metasomal tergite the longest, tergum 2 about 5.3 times longer than tergum 3, each tergite and  
158 sternite separated by a clear groove; longitudinal ridge between sternum 2 and lateral margin of  
159 tergum 2; fifth and sixth tergites slightly longer than third and fourth; ovipositor internalized, not  
160 visible.

161 Measurements (in mm). Total length (in dorsal view) ; head length 0.22, height 0.35 (mandibles  
162 excluded); mesosomal length 0.77; fore wing length 1.14, width 0.44 (as preserved); hind wing  
163 length 0.86, width 0.13; legs: fore femur length 0.23, tibia 0.21, tarsi 0.42; mid femur 0.24, tibia  
164 0.31, tarsi 0.43; hind femur 0.36, tibia 0.44, tarsi 0.47; metasomal length 0.84, width ca. 0.4; petiole  
165 length 0.19; metasomal tergum 2 length 0.43; metasomal tergum 3 length 0.08.

166 Male unknown.

167

#### 168 **4. Discussion.**

169 Following the key of the extant Proctotrupoidea from Goulet & Hubert (1993) the specimen keys  
170 out in Diapriidae because it possesses an elongated scape (more than 2.5 longer than wide); head in  
171 lateral view with antennal shelf distinct; fore wing pterostigma linear. These characters are also  
172 proposed by Sharkey (2007) to define the Diaprioidea and fit with the specimen. *Protobelyta*  
173 *monsirei* gen. et sp. nov. differs from the Spathiopterygidae in the complete wing venation and the  
174 15 antennomeres, instead of 14 (Engel et al., 2013). *Protobelyta monsirei* gen. et sp. nov. has a first  
175 metasomal segment petiole-like (cylindrical-shaped), allowing a quick differentiation from the  
176 Maamingidae. It also differs from the Monomachidae readily recognized by their elongate, loosely  
177 articulated, weakly sclerotized, and acuminate metasoma, while it is short, stout, and fully  
178 sclerotized in *Protobelyta* gen. nov. As mentioned above, *Protobelyta* gen. nov. has antennae  
179 inserted on a facial shelf, which is considered by Early et al. (2001a,b) as a putative synapomorphy  
180 of the (Diapriidae + Maamingidae), and less evidently of the Monomachidae (see Johnson &

181 Musetti, 2012 figs 2-3). Some Proctotrupoidea and even Cynipoidea Latreille, 1802 also have a low  
182 facial antennal shelf (*e.g.* Figitidae Thomson, 1862), but all the representatives of these groups have  
183 their antennae generally inserted lower on the face, and the structure and arrangement of the first  
184 and second metasomal segments are clearly different, thus precluding the placement of *Protobelyta*  
185 *gen. nov.* in these families. Sharkey et al. (2012), as afore mentioned, proposed six characters states  
186 to defined the Diapriidae. *Protobelyta gen. nov.* possesses some of them such as a third maxillary  
187 palpomere enlarged, broader than the following palpomere, and triangular; a distinct longitudinal  
188 ridge of metapleuron ventral to propodeal spiracle present; and do not display pronotal transverse  
189 carina. However, due the preservation in amber some external and internal structures such as the  
190 lateroventral corners of pronotum and the phragma, cannot be discerned.

191 Additionally, *Protobelyta monsirei gen. et sp. nov.* differs from both Maamingidae and  
192 Monomachidae in having the second metasomal tergite and sternite the longest. According to  
193 Goulet & Hubert (1993) and Lak & Nel (2009), this character is only recorded in the Diapriinae and  
194 Belytinae. But diapriine wasps have a reduced number of flagellomeres with a maximal number of  
195 11 in both sexes (Goulet & Hubert, 1993). Thereby, *Protobelyta gen. nov.* cannot be assigned to the  
196 Diapriinae and seems closer to the Belytinae that have 13 flagellomeres in female specimens.  
197 Additionally, *Protobelyta gen. nov.* displays a complete wing venation with three closed cells, a  
198 plesiomorphic state of character ‘generally used’ to define the Belytinae. Nevertheless, the putative  
199 synapomorphy of the Belytinae ‘two longitudinal grooves on metasomal sternum 2’ (after Masner,  
200 1993) is absent in *Protobelyta gen. nov.* Our fossil can be excluded from Ismarinae because of the  
201 presence of notauli and the absence of a false spur on fore tibia (Masner, 1961, 1976, 1993;  
202 Naumann, 1988); and because its antennae are inserted on a shelf and conspicuously separated from  
203 the clypeus (Yoder, 2007). The second metasomal sternite clearly longer than third one excludes  
204 affinities with the Ambositrinae. The presence of a split between laterosternite and ventral sternite  
205 on sternite 2 and the petiole-gaster junction not covered by tergite 2, are characters that would  
206 strengthen affinities with the Belytinae. In view of these data, we propose to place *Protobelyta*

207 *monsirei* gen. et sp. nov. among the Belytinae, possibly as stem-group of this subfamily, in  
208 particular because of its complete forewing venation. The 15-segmented antennae allow us to  
209 assume that the specimen is a female.

210 According to Ross (2019, 2020), no Diapriidae has been described from Burmese amber, even if  
211 Zhang et al. (2018) indicated the presence of the family. The oldest described representatives of the  
212 family would be from the French and Spanish ‘mid’-Cretaceous amber (Lak & Nel, 2009; Perrichot  
213 & Nel, 2008; Engel et al., 2013). *Protobelyta monsirei* gen. et sp. nov. clearly differs from the  
214 specimens described Lak & Nel (2009) in having antennae 15-segmented, even if this unnamed  
215 specimen was mis-reconstructed (A.N. pers. obs. and V.P., pers. comm.) because one antennal  
216 segment is missing; long scape about twice as long as head length. Additionally, *Protobelyta* gen.  
217 nov. differs from *Gaugainia electrogallica* Perrichot & Nel, 2008 by its size (body 1.9 vs. 1.2 mm  
218 long), in having glabrous eyes (vs. pilose); scape slightly longer than head height (vs. fully equal to  
219 head height); pedicel, first and second flagellomeres cylindrical and subequal (vs. only pedicel and  
220 first flagellomeres cylindrical and subequal); fore wing with radial cell [2R1] as long as pterostigma  
221 (vs. longer than pterostigma), vein r-rs reaching pterostigma after mid-length (vs. before  
222 midlength); hind wing with three hamuli; metanotum without two small dorso-lateral teeth (vs.  
223 present); propodeum coarsely aerolate vs. apparently smooth (see Perrichot & Nel, 2008: fig 2A);  
224 metasoma ellipsoidal, dorso-ventrally flattened vs. apparently rounded (see Perrichot & Nel, 2008:  
225 figs 1A-2A). *Protobelyta* gen. nov. differs from *Iberopria perialla* Engel, Ortega-Blanco & Delclòs  
226 2013 in having a clear hypognathous head (vs. prognathous in *I. perialla*); fore wing with cell [2R1]  
227 present (vs. absent); long pterostigma (vs. short); veins Rs, M, Cu present (vs. absent); shortest  
228 petiole; tergum 2 slightly shorter than the combined length of remaining tergite, vs. subequal to  
229 tergum 2 (see Engel et al., 2013: fig 9A).

230 Based on the key to Palearctic genera of Nixon (1957), the new genus would key out near  
231 *Pantolyta* Förster 1856 but it differs from the latter in not having a stouter habitus; head short; first

232 flagellomere clavate; fore wing with pterostigma much developed and cell [2R1] larger; tergum 2  
233 about 5.3 times longer than tergum 3 and about shorter than combined length of remaining tergites.

234

## 235 **5. Conclusion**

236 Even if the modern Belytinae are found worldwide and arbor a wide diversity in moist temperate  
237 forests of the southern hemisphere (Masner, 1993), the fossil record of the Diapriidae in  
238 paratropical habitat like that of the Cretaceous Burmese amber is poor. However, the subfamily was  
239 already widely distributed during the Albian–Cenomanian since it is now recorded in the French,  
240 Spanish, and now Burmese amber deposits. This new description confirms that the Proctotrupoidea  
241 are already well-diversified in Lower Cretaceous assemblages. However, their diversity seems to be  
242 largely underestimated, mainly because of a lack of study on these taxa.

243

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248

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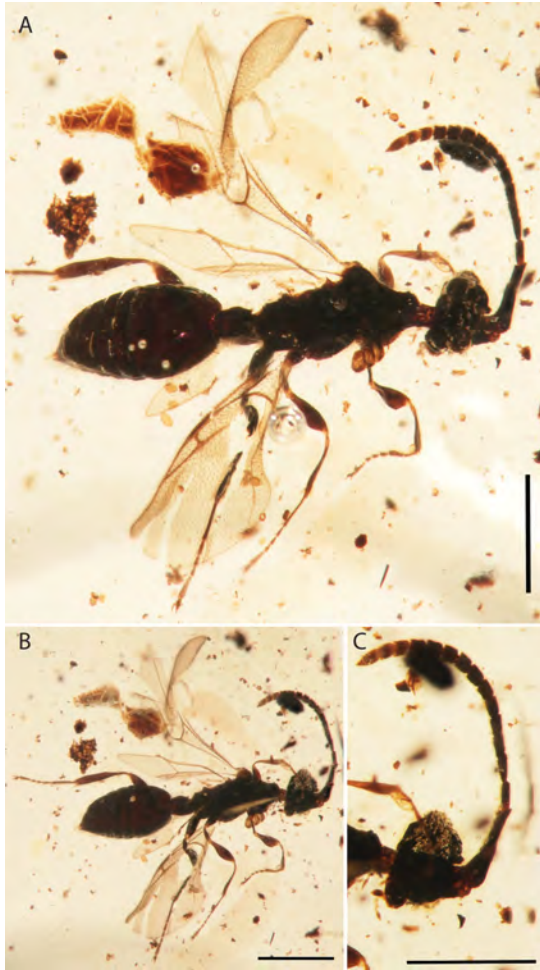
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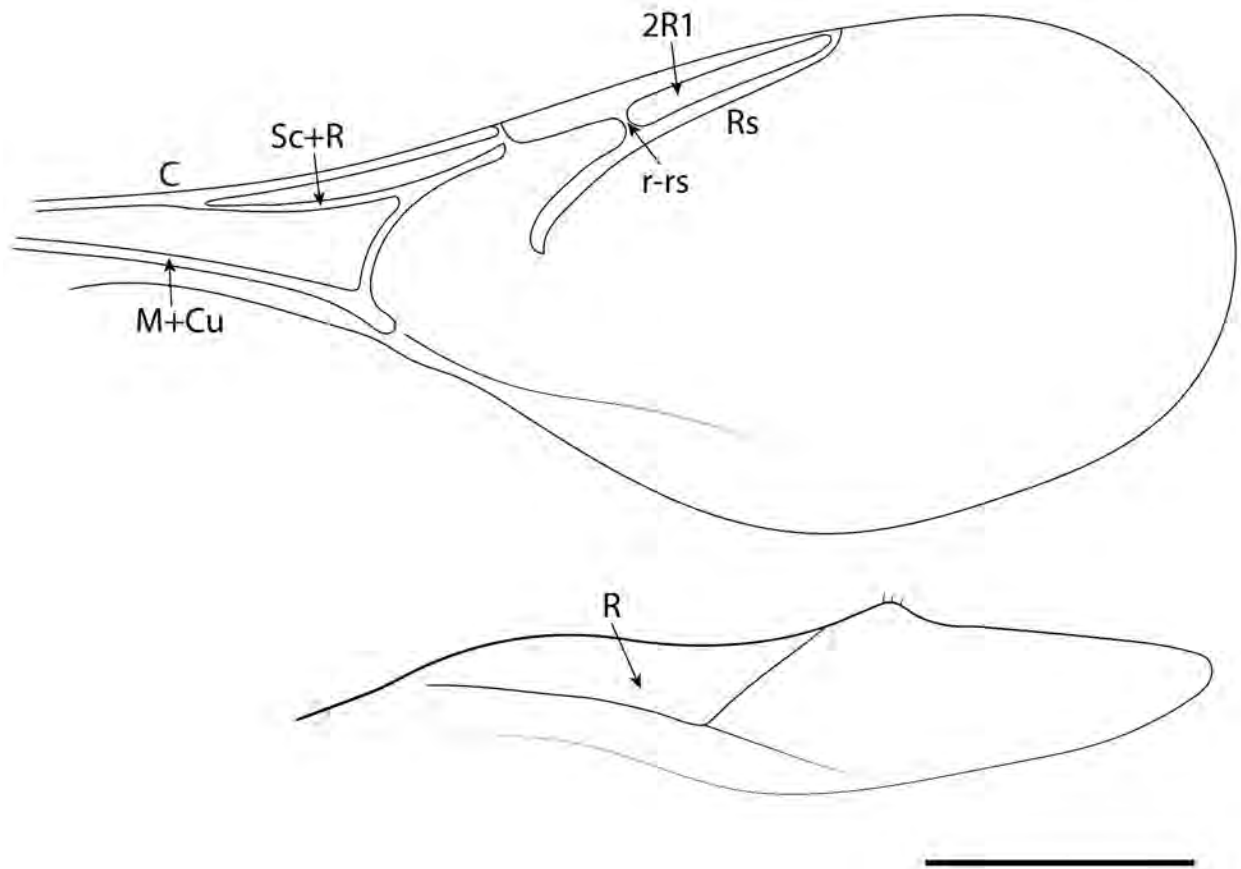
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377
- 378 **Fig. 1.** *Protobelyta monsirei* gen. et sp. nov., holotype IGR.BU-011. **A**, habitus, in dorsolateral  
379 view; **B**, habitus, in ventral view; **C**, detailed view of head. Scale bars: 0.5 mm.
- 380 **Fig. 2.** *Protobelyta monsirei* gen. et sp. nov., holotype IGR.BU-011. Reconstruction of wing  
381 venation. Scale bar: 0.25 mm.





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We attest that the three authors equally participate to the paper

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We declare that we have no conflict of interest

Yours sincerely

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