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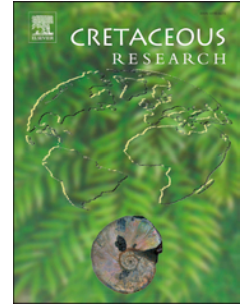
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1 A new genus and species of parasitic wasps (Hymenoptera: Diapriidae)
2 from Hkamti ‘mid-Cretaceous’ Burmese amber

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 ± 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 Proctotrupeoidea 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

249 **References**

250 Antropov, A.V., Belokobylskij, S.A., Compton, S.G., Dlussky, G.M., Khalaim, A.I., Kolyada,
251 V.A., Kozlov, M.A., Perlieva, K.S., Rasnitsyn, A.P., 2014. The wasps, bees and ants (Insecta:
252 Vespida = Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK.
253 Earth and Environmental Science Transactions of the Royal Society of Edinburgh 104, 335–446.
254 Archibald, S., Rasnitsyn, A., Brothers, D., Mathewes, R., 2018. Modernisation of the Hymenoptera:
255 ants, bees, wasps, and sawflies of the early Eocene Okanagan Highlands of western North
256 America. The Canadian Entomologist 150, 205–257.

- Journal Pre-proof
- 257 Ashmead, W.H., 1902. Classification of the pointed-tailed wasps, or the superfamily
258 Proctotrypidae. I. *Journal of the New York Entomological Society* 10, 240–247.
- 259 Brues, C.T., 1937. Hymenoptera superfamilies Ichneumonoidea, Serphoidea and Chalcidoidea. pp.
260 27–44. In: Carpenter, F.M., Folsom, J.W., Essig, E.O., Kinsley, A.C., Brues, C.T., Boesel,
261 M.W., Ewing, H.E. (eds). *Insects and arachnids from Canadian amber*, University of Toronto
262 Studies, Geology Series, 40.
- 263 Castro, L.R., Downton, M., 2006. Molecular analysis of the Apocrita (Insecta: Hymenoptera) suggest
264 that the Chalcidoidea are sister to the diaprioid complex. *Invertebrate Systematics* 20, 603–614.
- 265 Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern
266 Myanmar. *Journal of Asian Earth Sciences*, 21, 441–455.
- 267 Downton, M., Austin, A.D., Dillon, N., Bartowsky, E., 1997. Molecular phylogeny of the apocritan
268 wasps: the Proctotrupomorpha and Evaniomorpha. *Systematic Entomology* 22, 245–255.
- 269 Downton, M., Austin, A.D., 2001 Simultaneous analysis of 16S, 28S, COI and morphology in the
270 Hymenoptera: Apocrita – evolutionary transitions among parasitic wasps. *Biological Journal of*
271 *the Linnean Society* 74, 87–111.
- 272 Early, J.W., Masner, L., Naumann I.D., Austin, A.D., 2001a. Maamingidae, a new family of
273 proctotrupoid wasp (Insecta: Hymenoptera) from New Zealand. *Invertebrate Taxonomy* 15, 341–
274 352.
- 275 Early, J.W., Masner L., Naumann, I.D., Austin, A.D., 2001b. Maamingidae, a new family of
276 Proctotrupeoidea unique to New Zealand. In: Melika G., Thuoczy C. (eds), *Parasitic wasps:*
277 *evolution, systematics, biodiversity and biological control. International symposium: “Parasitic*
278 *Hymenoptera: Taxonomy and Biological Control”, 14–17 May 2001, Kőszeg, Hungary,*
279 *Agroinform Kiadó & Nyomda KFT, Budapest, 13–18.*
- 280 Engel, M.S., Ortega-Blanco, J., Delclòs, X., 2013. A new lineage of enigmatic diapiroid wasps in
281 Cretaceous amber (Hymenoptera: Diaprioidea). *American Museum Novitates* 3771, 1–23

Journal Pre-proof

282 Engel, M.S., Huang, D., Azar, D., Nel, A., Davis, S.R., Alvarado, M., Breitzkreuz, L.C.V., 2015.
283 The wasp family Spathiapterygidae in mid-Cretaceous amber from Myanmar (Hymenoptera:
284 Diaprioidea). *Comptes Rendus Palevol* 14, 95–100. <https://doi.org/10.1016/j.crpv.2014.11.002>.

285 Förster, A., 1856. *Hymenopterologische Studien*. II. Heft. Chalcidiae und Proctotrupii. Ernst ter
286 Meer, Aachen, 152 pp.

287 Goulet, H., Huber, J.T., 1993. *Hymenoptera of the world: An identification guide to families*. ed.
288 Agriculture Canada, Ottawa, Ontario, 680 pp.

289 Haliday, A.H., 1833. Essay on the classification of parasitic Hymenoptera, &c. *Entomological*
290 *Magazine* 1, 259–276.

291 Johnson, N.F., 1992. Catalog of the world species of Proctotrupeoidea excluding Platygasteridae
292 (Hymenoptera). *Memoirs of the American Entomological Institute* 51, 825 pp.

293 Johnson, N.F., Musetti, L., 2012. Genera of the parasitoid wasp family Monomachidae
294 (Hymenoptera: Diaprioidea). *Zootaxa* 3188, 31–41.

295 Johnson, N.F., Musetti, L., Cora, L., 2019. *Hymenoptera Online (HOL)*. Internet site:
296 <https://hol.osu.edu> (consulted 10 March 2020).

297 Klug, J.C.F., 1841. Die Arten der Gattung *Pelecinus* (Latr.). *Zeitschrift für die Entomologie* 3, 377–
298 385.

299 Königsmann, E., 1978. Das phylogenetische System der Hymenoptera. Teil 3: “Terebrantes”
300 (Unterordnung Apocrita). *Deutsche Entomologische Zeitschrift* 25, 1–55.

301 Krogmann, L., Azar, D., Rajaei, H., Nel, A., 2016. *Mymaropsis baabdaensis* sp. n. from Lower
302 Cretaceous Lebanese amber – the earliest spathiapterygid wasp and the first female known for
303 the family. *Compte Rendus Palevol* 15, 483–487. <https://doi.org/10.1016/j.crpv.2015.11.002>

304 Lak M., Nel A., 2009. An enigmatic diapriid wasp (Insecta, Hymenoptera) from French Cretaceous
305 amber. *Geodiversitas* 31, 137–144.

306 Latreille, P.A., 1802. *Histoire naturelle, générale et particulière des Crustacés et des Insectes*.
307 *Ouvrage faisant suite aux œuvres de Leclerc de Buffon et partie du cours complet d'Histoire*

Journal Pre-proof

308 naturelle rédigé par C.S. Sonnini. T. 3–4, an X. Familles naturelles et genres. Paris, Dufart, 1–
309 467 and 1–387.

310 Linnaeus, C. von, 1758. Systema Naturae per regna tria naturae secundum classes, ordines, genera,
311 species cum characteribus, differentiis, synonymis, locis. Ed. decima reformata. Holmiae, Laur.
312 Salvii, 1, 1–823.

313 Loiacono, M.S., 1987. Un nuevo diaprido (Hymenoptera) parasitoide de larvas de *Acromyrmex*
314 *ambiguus* (Emery) (Hymenoptera, Formicidae) en el Uruguay. Revista de la Sociedad
315 Entomologica Argentina 44, 129–136.

316 Masner, L., 1961. Ambositrinae, a new subfamily of Diapriidae from Madagascar and Central
317 Africa (Hymenoptera: Proctotrupoidea). Mémoires de l'Institut scientifique de Madagascar (E)
318 12, 289–295.

319 Masner, L., 1976. A revision of the Ismarinae of the New World (Proctotrupoidea: Diapriidae). The
320 Canadian Entomologist 108, 1243–1266.

321 Masner, L., 1993. Superfamily Proctotrupoidea, in Goulet, H., Hubert, J.T. (eds), Hymenoptera of
322 the World: an identification guide to families. Research Branch Agriculture Canada Publication,
323 Ottawa, 537–557.

324 Musetti, L., Johnson, N.F., 2000. First documented record of Monomachidae (Hymenoptera:
325 Proctotrupoidea) in New Guinea, and description of two new species. Proceedings of the
326 Entomological Society of Washington 102, 957–963.

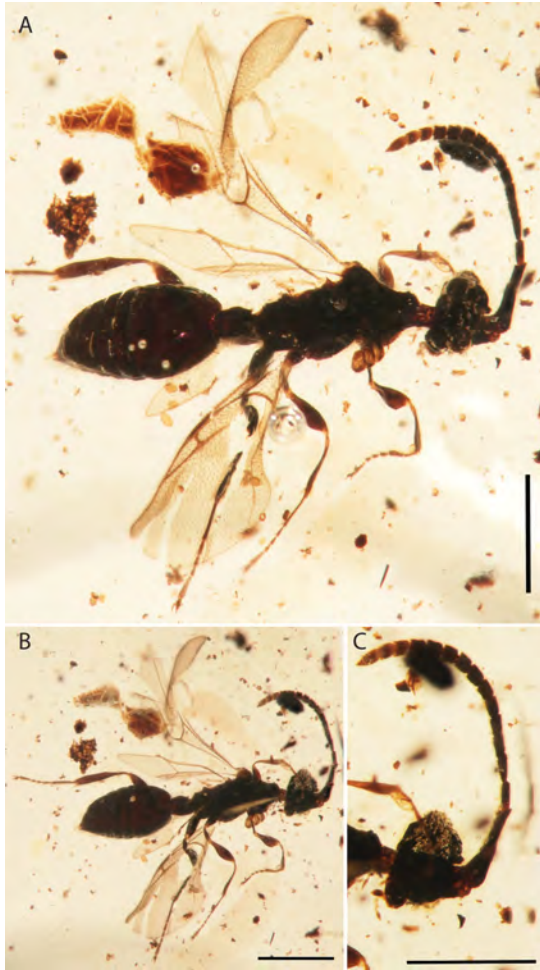
327 Naumann, I.D., 1988. Ambositrinae (Insecta: Hymenoptera: Diapriidae). Fauna of New Zealand 15,
328 1–168.

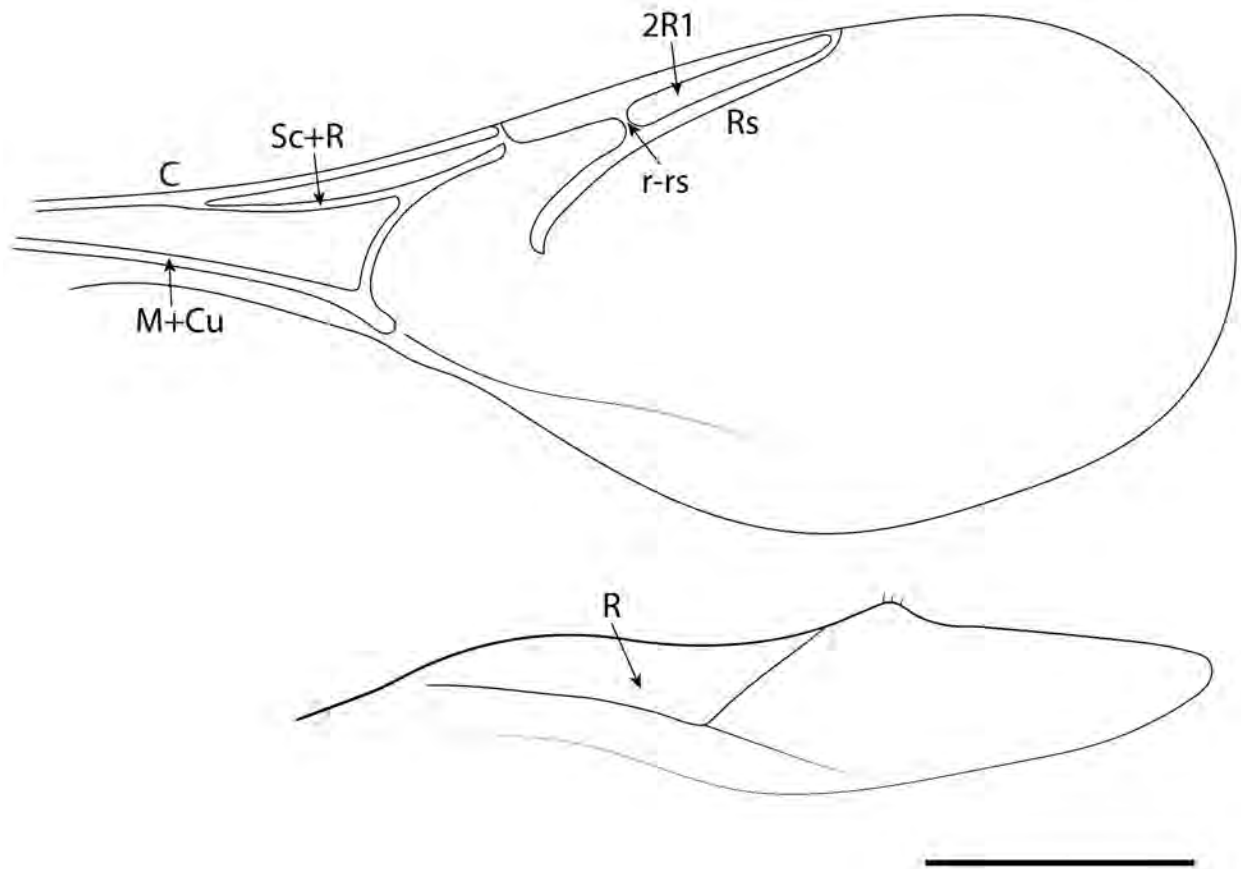
329 Naumann, I.D., Masner, L., 1985. Parasitic wasps of the proctotrupoid complex: a new family from
330 Australia and a key to world families (Hymenoptera: Proctotrupoidea *sensu lato*). Australian
331 Journal of Zoology 33, 761–783.

332 Nixon, G.E.J., 1957. Hymenoptera, Proctotrupoidea, Diapriidae, subfamily Belytinae. Handbooks
333 for the Identification of British Insects 8, 1–107.

- 334 Perrichot, V., Nel, A., 2008. A new belytine wasp in Cretaceous amber from France (Hymenoptera:
335 Diapriidae). *Alavesia* 2, 203–209.
- 336 Peters, R., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A.,
337 Podsiadlowski, L., Petersen, M., Lanfear, R., Diez, P., Heraty, J., Kjer, K., Klopstein, S., Meier,
338 R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Niehuis, O. 2017. Evolutionary history of the
339 Hymenoptera. *Current Biology* 27, 1013–1018.
- 340 Rasnitsyn, A.P., 1975. [Hymenoptera Apocrita of the Mesozoic.] *Trudy Paleontologicheskogo*
341 *Instituta Akademii nauk SSSR* 147, 1–134.
- 342 Rasnitsyn, A.P., 1988. An outline of evolution of hymenopterous insects (order Vespida). *Oriental*
343 *Insects* 22, 115–145.
- 344 Rasnitsyn, A.P. 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (= *Vespida*
345 *Laicharting, 1781*). In: *History of insects*, Rasnitsyn, A.P., Quicke, D.L.J. (eds), Kluwer
346 Academic Publishers, Dordrecht, The Netherlands, 242–254.
- 347 Rasnitsyn, A.P., Öhm-Kühnle, C., 2019. Revision of the Cretaceous Proctotrupomorpha (Insecta:
348 Hymenoptera) of Australia. *Cretaceous Research* 100, 91–96.
- 349 Ross, A.J., 2019. Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology*
350 2, 22–84.
- 351 Ross, A.J., 2020. Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019.
352 *Palaeoentomology* 3, 103–118.
- 353 Sharkey, M.J., 2007. Phylogeny and classification of Hymenoptera. *Zootaxa* 1668, 521–548.
- 354 Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.,
355 Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L., Wheeler, W.C., 2012.
356 Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* 27, 1–33.
- 357 Shi, G.-h., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, Ju., Yang, M.-c., Lei, W.-y., Li, Q.-l., Li,
358 X.-h., 2012. Age constraint on Burmese amber based on UePb dating of zircons. *Cretaceous*
359 *Research* 37, 155–163.

- 360 Szépligeti, V., 1903. Neue Evaniiden aus der Sammlung des Ungarischen National-Museums.
361 Annales Historico-Naturales Musei Nationalis Hungarici 1, 364–395.
- 362 Thomson, C.G., 1862. Försök till uppställning och beskrifning af Sveriges Figiter. Öfversigt af
363 Konglika Vetenskaps-Akademien Förhandlingar 18, 395–420.
- 364 Van de Kamp, T., Schwermann, A.H., dos Santos Rolo, T., Lösel, P.D., Engler, T., Etter, W.,
365 Faragó, T., Göttlicher, J., Heuveline, V., Kopmann, A., Mähler, B., Mörs, T., Odar, J., Rust, J.,
366 Jerome, N.T., Vogelgesang, M., Baumbach, T., Krogmann, L. (2018) Parasitoid biology
367 preserved in mineralized fossils. Nature Communications 9 (3325), 1–29.
- 368 Yoder, M. 2007. The Diapriidae. Version 12.2008.
369 <http://www.diapriid.org/public/site/diapriid/home> (last accessed the 30 January 2020).
- 370 Yu, Tingting, Kelly, R., Mu, Lin, Ross, A., Kennedy, J., Broly, P., Xia, Fangyuan, Zhang, Haichun,
371 Wang, Bo, Dilcher, D., 2019. An ammonite trapped in Burmese amber. Proceedings of the
372 National Academy of Sciences, 116, 11345–11350.
- 373 Zhang, Q., Rasnitsyn, A.P., Zhang, H.-c., 2018. Hymenoptera (wasps, bees and ants) in mid-
374 Cretaceous Burmese amber: a review of the fauna. Proceedings of the Geologists' Association,
375 129, 736–747.
- 376
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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