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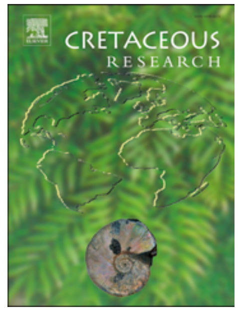

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A new genus and species of parasitic wasps (Hymenoptera: Diapriidae) from Hkamti 'mid–Cretaceous' Burmese amber

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ABSTRACT

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

Keywords:

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

1. Introduction

Diapriidae remain poorly documented in Cretaceous ambers, which is very surprising considering the number of pieces of amber containing representatives of this family (C.J pers. obs). Perrichot & Nel (2008) proposed a summary of the fossil record of the family and reported *ca*. fifty inclusions, mainly Cenozoic and distributed among the subfamilies Diapriinae Haliday, 1833 and Belytinae Förster, 1856. After this paper, the fossil record of the family has increased, with the papers of Lak & Nel (2009), Engel et al. (2013) and Rasnitsyn and Öhm-Kühnle (2019) for the Cretaceous, and Antropov et al. (2014), Archibald et al. (2018), and Van de and Kamp et al. (2018) for the Cenozoic. Nevertheless, it remains largely underestimated for major deposits such as the Burmese and Baltic ambers.

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

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

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

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

2. Material and methods

The amber piece containing the specimen studied herein derive from the deposits of Hkamti site, Hkamti District, Sagaing Region, Myanmar. The Hkamti site is about 80 km southwest of the Angbamo site. 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 deposits corroborates a late Albian–early Cenomanian age (Cruickshank & Ko, 2003; Yu et al., 2019).

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

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3. Systematic palaeontology

Order: Hymenoptera Linnaeus, 1758

Superfamily: Diaprioidea Haliday, 1833

Family: Diapriidae Haliday, 1833

Subfamily: ?Belytinae Förster, 1856

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

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Type species

Protobelyta monsirei sp. nov.

Etymology

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

Diagnosis

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

Protobelyta monsirei sp. nov. Jouault & Nel

(Figs 1–2)

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Etymology

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

Studied material

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

Locality and horizon

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

Diagnosis

As for the genus.

Description

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

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

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

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

Male unknown.

4. Discussion.

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

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

Additionally, *Protobelyta monsirei* gen. et sp. nov. differs from both Maamingidae and Monomachidae in having the second metasomal tergite and sternite the longest. According to Goulet & Hubert (1993) and Lak & Nel (2009), this character is only recorded in the Diapriinae and Belytinae. But diapriine wasps have a reduced number of flagellomeres with a maximal number of 11 in both sexes (Goulet & Hubert, 1993). Thereby, *Protobelyta* gen. nov. cannot be assigned to the Diapriinae and seems closer to the Belytinae that have 13 flagellomeres in female specimens. Additionally, *Protobelyta* gen. nov. displays a complete wing venation with three closed cells, a plesiomorphic state of character 'generally used' to define the Belytinae. Nevertheless, the putative synapomorphy of the Belytinae 'two longitudinal grooves on metasomal sternum 2' (after Masner, 1993) is absent in *Protobelyta* gen. nov. Our fossil can be excluded from Ismarinae because of the presence of notauli and the absence of a false spur on fore tibia (Masner, 1961, 1976, 1993; Naumann, 1988); and because its antennae are inserted on a shelf and conspicuously separated from the clypeus (Yoder, 2007). The second metasomal sternite clearly longer than third one excludes affinities with the Ambositrinae. The presence of a split between laterosternite and ventral sternite on sternite 2 and the petiole-gaster junction not covered by tergite 2, are characters that would strengthen affinities with the Belytinae. In view of these data, we propose to place *Protobelyta* *monsirei* gen. et sp. nov. among the Belytinae, possibly as stem-group of this subfamily, in particular because of its complete forewing venation. The 15-segmented antennae allow us to assume that the specimen is a female.

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

Based on the key to Palaearctic genera of Nixon (1957), the new genus would key out near *Pantolyta* Förster 1856 but it differs from the latter in not having a stouter habitus; head short; first flagellomere clavate; fore wing with pterostigma much developed and cell [2R1] larger; tergum 2 about 5.3 times longer than tergum 3 and about shorter than combined length of remaining tergites.

5. Conclusion

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

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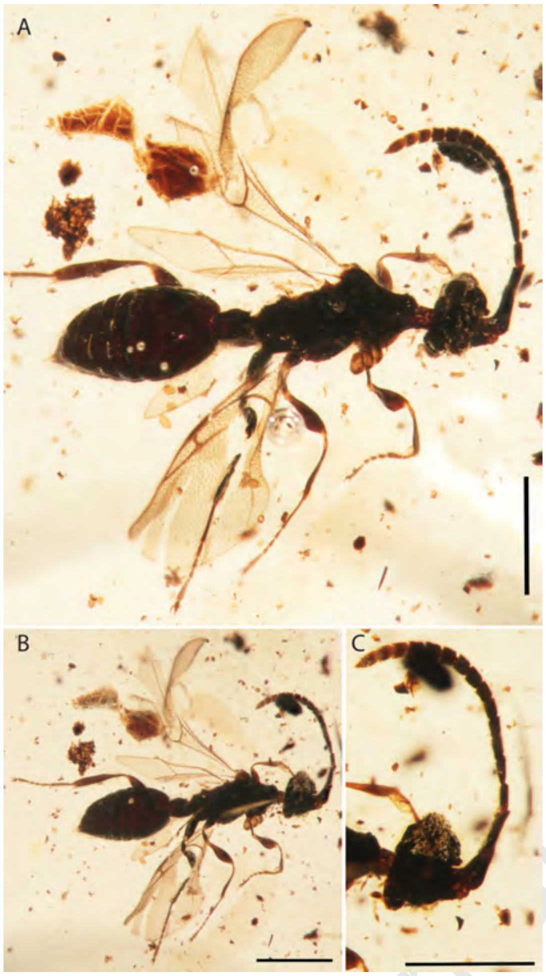
Fig. 1. ***Protobelyta monsirei*** gen. et sp. nov., holotype IGR.BU-011. **A**, habitus, in dorsolateral view; **B**, habitus, in ventral view; **C**, detailed view of head. Scale bars: 0.5 mm.

Fig. 2. ***Protobelyta monsirei*** gen. et sp. nov., holotype IGR.BU-011. Reconstruction of wing venation. Scale bar: 0.25 mm.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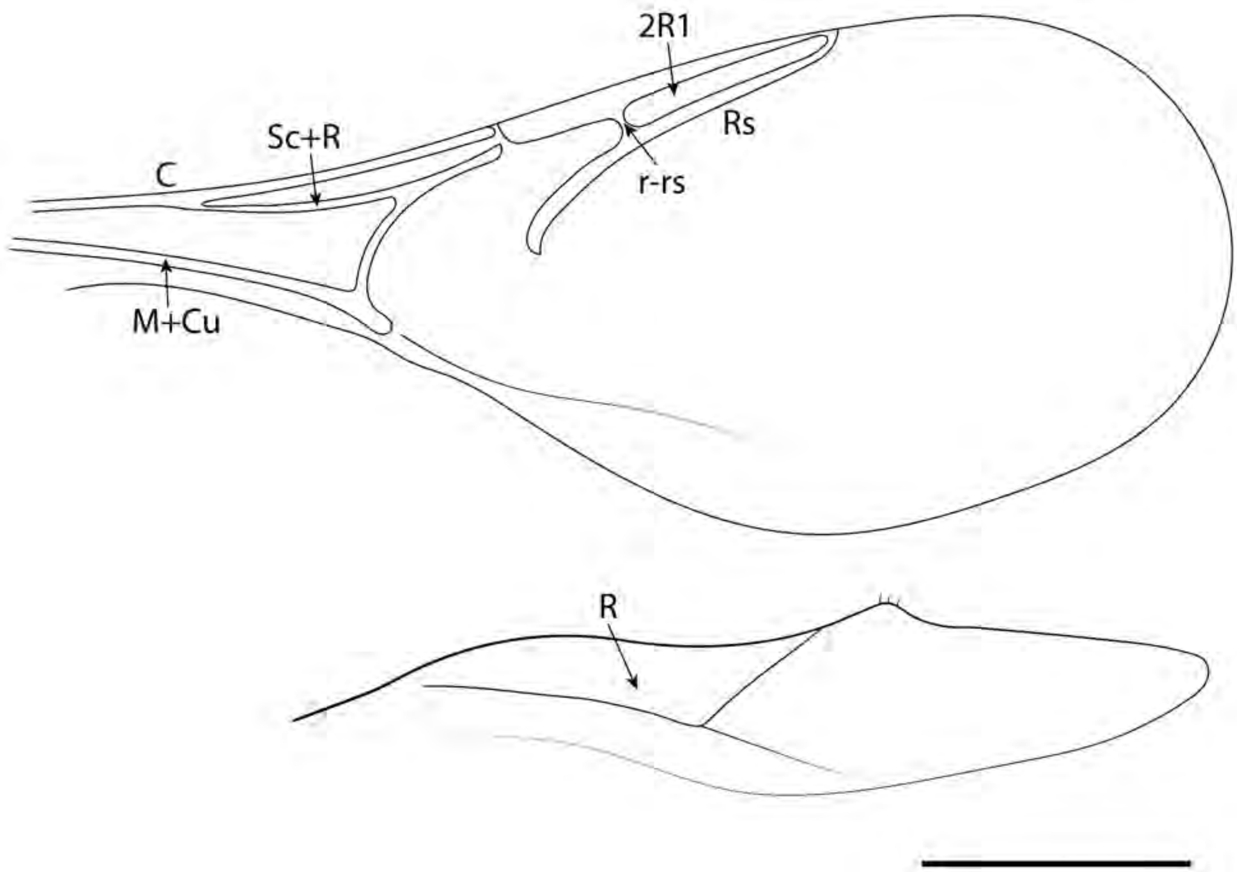
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We attest that the three authors equally participate to the paper

We declare that we have no conflict of interest

Yours sincerely

Andre nel