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Two new genera of belytine wasps (Hymenoptera: Diapriidae) from Cretaceous Burmese amber

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ABSTRACT

Christophus myanmarensis gen. et sp. nov., *Christophus ohmkuhnlei* gen. et sp. nov., and *Mintara parva* gen. et sp. nov., three new species and two new genera of belytine wasps (Diapriidae: Belytinae) are described and figured from males preserved in mid-Cretaceous Kachin (Burmese) amber. These new fossils enrich the fossil record of Cretaceous diapriids, summarized here, demonstrating the diversity of the family before the K/Pg extinction and suggesting an older origin for the family.

Keywords: Fossil record; Diaprioidea; taxonomy; mid-Cretaceous; Cenomanian.

1. Introduction

The Diapriidae is a speciose family of small parasitoid wasps with more than 2,000 extant valid species (Johnson et al., 2021), which may correspond to half of the estimated diversity (~4,500 sp.; Johnson, 1992). The biology of most diapriid species is unknown even if some species are assumed to be primarily endoparasitoid on Diptera or Coleoptera or Hymenoptera (Loiacono, 1987; Masner, 1993). The diapriid's representatives are

widely distributed and more abundant in the southern hemisphere even if their diversity is clearly underestimated in all the ecozones.

The family Diapriidae is traditionally divided into the four subfamilies Ambositrinae, Belytinae, Diapriinae, and Ismarinae. Six characters allow quick recognition of diapriid wasps: antennae inserted apically on a shelf, elongate scape, male with antennomeres 3 and/or 4 modified, fore wing without clearly defined stigma and with at most three closed cells, hind wing with at most one closed cell, tubular petiole (Masner, 1993). The monophyly of Diapriidae excluding *Ismarus* Haliday, 1835 is well supported by the characters ‘third maxillary palpomere enlarged and broader than the following palpomere, transverse carina on the pronotum absent, lateroventral corners of the pronotum with medial inflexions abutting mesopleuron, prophragma of the mesonotum not subdivided by split, distinct ridge ventral to propodeal spiracle on the metapleuron, metaphragma and metapleural apodeme fused’ (Sharkey et al., 2012). These last authors have raised the Ismarinae to family-level, a systematic change followed in several recent papers. The phylogenetic relationships and the position of the Diapriidae among the Proctotrupeoidea *sensu lato* are not resolved, because of the probable paraphyly of the superfamily (Königsmann, 1978; Rasnitsyn, 1988; Sharkey, 2007; Klopstein et al., 2013; Peters et al., 2017). Depending on the method and the dataset, different sister-lineages are retrieved: morphological and molecular analyses suggest respectively Cynipoidea (Rasnitsyn, 1988; Sharkey and Roy, 2002; Vilhelmsen et al., 2010) and (Chalcidoidea + Platygastroidea) (Castro and Dowton, 2006; Heraty et al., 2011; Klopstein et al., 2013; Peters et al., 2017) as sister lineages of the Diaprioidea complex (i.e. Diapriidae + Monomachidae + Maamingidae + †Spathiopterygidae). Sharkey et al. (2012) characterized this group with the synapomorphies ‘subantennal shelf present, ventral transverse carina on the metapleuron absent or weakly developed’ (Sharkey et al., 2012). Recently, Rasnitsyn and Öhm-Kühnle (2020) proposed a redefinition of the Diaprioidea (Diapriidae + Ismaridae + †Spathiopterygidae), supported by the synapomorphies ‘long scape, oligomeric antenna, presence of specialized petiolar segment and metasomal apex tightly closed at rest’, and included in the higher informal group Microprocta.

The subfamily Belytinae is, by morphological and biological aspects, assumed to be the subfamily which diverged the earlier within the Diapriidae (Masner, 1993). The fore wing venation with three closed cells is considered to be plesiomorphic (Quadros and Brandão, 2017) and the search for hosts reflects the biological

groundplan of the family (endoparasitism on Diptera larvae; Masner, 1993). However, as for the Diapriidae, not so much is known about the specific hosts. Currently, 54 genera and almost 700 valid species are comprised within the Belytinae (Johnson et al., 2021), which are cosmopolite and often associated to wet and shady environments (Quadros and Brandão, 2017). To date, around sixty fossils of Diapriidae have been documented (see detailed list in Perrichot and Nel, 2008: Appendix 1; and a summary of the posterior discoveries in Jouault and Nel, 2020), most of them being identified at the genus, subfamily or even family-level only. Among this sparse fossil record, only 26 species have been described, meaning that numerous new species are to be expected in the case of a focused detailed study on the family.

In the fossil record, the subfamilies Belytinae and Diapriinae are the most encountered and seem to be the most abundant and diversified whereas the Ambositrinae and the Ismarinae are both only known by two specimens. Most of the diapriid fossil record comes from Cenozoic deposits, especially the Eocene Baltic amber and the latest Eocene – earliest Oligocene from the Isle of Wight, while the Cretaceous diapriids are rare (Perrichot and Nel, 2008). Cretaceous belytines are known by two species, *Protobelyta monsirei* Jouault and Nel, 2020 (in Jouault et al., 2020) from Albian Hkamti amber, and *Gaugainia electrogallica* Perrichot and Nel, 2008 from Albian French amber; ismarines are known by *Cretapria tsudakai* Fujiyama, 1994 from Aptian Choshi amber (Fujiyama, 1994) as the oldest described fossil of the family, and another undetermined specimen from Cenomanian French amber (Schlüter, 1978). One undetermined diapriine is mentioned from Cenomanian Taimyr amber (Zherikin and Sukatcheva, 1973) and other representatives of the family are known from Campanian Canadian amber (Schlüter, 1978), Turonian Timmerdyakh amber (Rasnitsyn, 1980), Cenomanian French amber (Lak and Nel, 2009), and Albian Peñacerrada amber (*Iberopria perialla* Engel, Ortega-Blanco and Delclòs, 2013 in Engel et al., 2013). The recent molecular phylogenetic analyses assumed that the family probably diverged at the beginning of the Jurassic (Castro and Dowton, 2006; Peters et al., 2017), and diversified after the Cretaceous-Paleocene crisis (Rasnitsyn, 2002). However, it appears that a true diversity already existed during the Cretaceous, as is suggested by recent discoveries from Hkamti amber (Jouault et al., 2020).

Here, we report and describe three new species belonging to two new genera in Burmese amber and we provide a summary of the Cretaceous Diapriidae (Table 1).

2. Material and methods

The present study is based on four fossil individuals fossilized in two amber pieces from the deposits of Noije Bum in the Hukawng Valley (26° 29' N, 96° 35' E), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross, 2017: fig. 2). Radiometric data and taphonomic analysis of pholadids 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; Smith and Ross, 2017). Some ammonites found in the amber-bearing bed and within amber corroborate a late Albian – early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

One piece containing three individuals was kindly donated to the Geology Department and Museum of the University of Rennes, France (IGR), by Dr. Christoph Öhm-Kühnle (Herrenberg, Germany). The other piece was accessed by one of us (C.J.). The material is deposited in the amber collection of the IGR and summarized in Table 2. Both amber pieces were trimmed and polished using thin silicon carbide papers on a Buehler Metaserv 3000 polishing machine to optimize the views of the specimens. The specimens were examined and photographed with a Nikon SMZ25 with an attached Nikon D800 camera or a Leica MZ APO with an attached Canon EOS 5D Mark II camera. Images taken with the Nikon D800 camera have been enhanced using Capture NXD software. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The figures were composed with Adobe Illustrator CC2019 and Photoshop CC2019 softwares. The description of the characters follows the nomenclature of Nixon (1957).

Published work and nomenclatural acts are registered in ZooBank (<http://www.zoobank.org/>, last access: 10 September 2021), with the following LSID (reference): urn:lsid:zoobank.org:pub:5C80141B-A6CF-43EE-9A9F-44314387CE20

3. Systematic paleontology

Superfamily Proctotrupoidea Latreille, 1802

Family Diapriidae Haliday, 1833

Subfamily Belytinae Förster, 1856

***Christophus* gen. nov.**

urn:lsid:zoobank.org:act:216D54F4-BEEA-4150-A48F-131513686F56

Etymology: The genus name is a patronym honoring Dr. Christoph Öhm-Kühnle, who generously donated the specimen to the IGR. Gender masculine.

Diagnosis (Male). Minute size (< 2 mm); head short, ovoid in lateral view; eye glabrous; 14 antennomeres, scape shorter than pedicel + flagellomere 1 combined length, inner portion of apical circumference of scape forming a short teeth covering base of pedicel, flagellomeres cylindrical but not elongate, always longer than wide, flagellomere 1 distinctly emarginate, flagellomere 12 the longest; mesosoma shorter than metasoma; mesoscutum smooth, with apparent notauli; petiole short and narrow, three to five times longer than wide; gaster suboval with sternum 2 and tergum 2 the longest; fore wing with radial cell closed, marginalis swollen and short, as long as r-rs, postmarginalis extending far beyond radial cell, almost reaching wing tip; hind wing with three distal hamuli.

***Christophus myanmarensis* sp. nov.**

(Figs. 1, 2.A)

urn:lsid:zoobank.org:act:095C1E4C-7396-4ADF-AADC-499405A22E89

Etymology: The species name refers to the Myanmar origin of the amber piece containing the holotype. The specific epithet is to be treated as an adjective.

Material studied. Holotype IGR.BU-017d (a male in a piece of amber measuring 19 × 11 × 4 mm) housed in the Geological Department and Museum (IGR) of the University of Rennes, France.

Type locality: Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar.

Type horizon: upper Albian to lower Cenomanian, mid-Cretaceous.

Diagnosis. Flagellomere 1 shorter than pedicel (Fig. 1.B); fore wing with radial cell reduced in length, as long as wide, anterior segment of Rs nebulous to inconspicuous, directed toward anal margin; hind wing with basal

cell closed (Figs. 1.A, 2.A); hind basitarsomere 1.3 times shorter than the length of three following tarsomeres combined (Figs. 1.A).

Description. Minute size; melanic. Head hypognathous, oval in lateral view, reduced in length, compound eyes rounded, not covering head length; mandibles not forming a beak; antennae inserted on a shelf, antennal sockets protruding, separated by a deep cleft, scape as long as pedicel + flagellomere 1 combined, inner portion of apical circumference of scape raised to cover base of pedicel, pedicel pear-shaped, 12 cylindrical flagellomeres, all distinctly longer than wide, flagellomere 1 emarginate on its anterior third, widen at base of emargination, flagellomere 2 slightly longer than following flagellomeres 3-11, F3-11 shorter and subequal in length, apical flagellomere ovoid (antennomeres length, in mm: P-0.069, F1-0.073, F2-0.062, F3-0.059, F4-0.062, F5-0.061, F6-0.073, F7-0.069, F8-0.063, F9-0.069, F10-0.073, F11-0.067, F12-0.094).

Mesosoma elongate, narrow, slightly pubescent; mesoscutum large with notauli; pronotum visible in dorsal view; epomia distinct; propodeum with longitudinal ridges. Fore wing hyaline, covered with microtriches, rounded, shorter than body, C, Sc+R, M+Cu, basalis, marginalis, postmarginalis, r-rs and Rs pigmented, C and Sc+R separated from marginalis, marginalis short, postmarginalis extending far beyond radial cell, almost three times longer, radial cell triangular, very reduced in length, Rs closing radial cell, fading anteriorly to r-rs toward anal margin, M inconspicuous, Cu nebulous; hind wing narrow, bordered with long setae, C pigmented with tree long hamuli at its apex, basal cell closed. Legs slender, not very pubescent; tibial spur formula 1-2-2; tibiae and first tarsomeres bearing erect setae on margin; hind basitarsomere shorter than the length of the three following tarsomeres combined; tarsal claws simple.

Metasoma. Petiole narrow and short; gaster suboval, tightening at apex; sternum 2 and tergum 2 the longest.

Measurements (in mm). Body length 1.451; head length 0.182; antenna length 1.019; scape length 0.134; scape width 0.022; mesosoma length 0.604; fore wing length 1.047; petiole length 0.119; petiole width 0.027; total metasoma length 0.672.

***Christophus ohmkuhnlei* sp. nov.**

(Figs. 2.B, 3)

urn:lsid:zoobank.org:act:0550D253-51DF-4E42-8C74-0F4FE2D77DED

Etymology: Named after Christoph Öhm-Kühnle. The specific epithet is to be treated as a noun in a genitive case.

Material studied. Holotype male IGR.BU-017a; paratypes male IGR.BU-017b, IGR.BU-017c (in the same piece of amber measuring $19 \times 11 \times 4$ mm) housed in the Geological Department and Museum (IGR) of the University of Rennes, France.

Type locality: Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar.

Type horizon: upper Albian to lower Cenomanian, mid-Cretaceous.

Diagnosis. Pedicel shorter than flagellomere 1 (Figs. 3.A-C, 3.E); radial cell elongate, anterior segment of Rs directed toward wing base and conspicuous; hind wing with basal cell opened (Fig. 2.B); hind basitarsomere as long as the length of the three following tarsomeres combined (Figs. 1.B, 1.E).

Description. Minute size; melanic. Head short, hypognathous, ovoid in lateral view; eye almond-shaped, glabrous, not covering head length; mandibles simple, slightly crossing at tip; 14 antennomeres, with short hairs, inserted on a transverse shelf, antennal sockets facing upwards, scape as long as pedicel + first flagellomere length combined, inner portion of apical circumference of scape raised to form an angular projection, pedicel bulbous, flagellomere 1 the second longest, cylindrical, twice longer than wide, deeply but shortly emarginate at the base, flagellomere 2-11 shorter but subequal in length, apical flagellomere tapering toward apex, longer than flagellomere 1 (antennomeres length of the holotype, in mm: P-0.097, F1-0.110, F2-0.091, F3-0.078, F4-0.083, F5-0.079, F6-0.087, F7-0.087, F8-0.083, F9-0.84, F10-0.088, F11-0.086, F12-0.134).

Mesosoma shorter than metasoma; mesoscutum as wide as large, smooth, with deep slightly convergent notauli, not meeting, mesoscutum posterior margin straight; scutellum oval, wider than long without foveae; pronotum not elongate, epomia forming a distinct keel between propodeal shoulder and front coxa; meso and meta-pleuron minutely shagreened; propodeum with longitudinal ridges, median keel not forked. Fore wing homogeneously micropubescent, without infumate patterns, extending beyond metasoma, C, Sc+R, M+Cu, basalis, marginalis, postmarginalis, r-rs and Rs pigmented, C and Sc+R separated from marginalis, marginalis shorter than its distance from basalis, swollen, postmarginalis twice longer than radial cell, Rs closing radial cell, directed in straight line toward base of the wing; M nebulous but visible to the wing tip;

Cu nebulous, slightly arched; hind wing reduced, hyaline, C strongly pigmented on two thirds of wing with three hamuli on its apex, basal cell not closed. Legs slender, hind pair being just slightly wider; tibial spur formula 1-2-2; tibiae and first tarsomeres bearing erect setae; meta basitarsomere as long as the length of the three following tarsomeres combined; tarsal claws simple.

Metasoma. Petiole strongly narrowed and short, sculpture indistinct; gaster ovoid, enlarged, dorsoventrally flattened, glabrous; tergum 2 the longest, 1.5 times longer than other tergites combined, sternum 2 the longest, half-length of gaster; genitalia externalized.

Measurements (in mm; paratypes IGR.BU-017b, IGR.BU-017c when measurable in brackets, '?' indicates unmeasurable data). Body length 1.690 (1.910; 1.065); head length 0.254 (0.266; 0.151); antenna length 1.342 (1.353; 0.953); scape length 0.149 (0.153; 0.134); scape width 0.029 (0.032; 0.026); mesosoma length 0.680 (0.726; 0.422); fore wing length 1.391 (1.657; ?); petiole length 0.131 (0.146; 0.094); petiole width 0.031 (0.035; 0.026); total mesosoma length 0.764 (0.909; 0.512).

***Mintara* gen. nov.**

urn:lsid:zoobank.org:act:136B7BCA-434C-48E7-B4BB-0A8B46BAE859

Etymology. The *Mintara* is one of the 37 nat spirit, a deity of the Burmese pantheon. Gender feminine.

Diagnosis (Male). Minute size (< 2 mm). Head hypognathous; eye without pilosity; antennae inserted on a shelf (reduced), 14 antennomeres, scape unarmed, six times longer than wide, pedicel bulbous, flagellomeres cylindrical, not clubbed, marked emargination on the anterior quarter of F1, F2 longest flagellomere, following ones decreasing in size, except apical flagellomere longer than preceding one (Figs. 4.A, B); mesosoma shorter than metasoma; petiole convex with both extremity wider, twice longer than its middle height; gaster subovoid, not flattened; tergum 2 the longest, half-length of gaster; each tergite and sternite separated by a groove; sternum 2 the longest (Fig. 4.C); marginalis short, postmarginalis present on half-length of radial cell, radial cell reduced in length, closed by Rs in straight line from middle to anterior margin of wing (Fig. 5); legs slender; meta femora stouter than pro- and meso femora; row of erected setae on metatibia (Fig. 4.A).

***Mintara parva* sp. nov.**

(Figs 4-5)

urn:lsid:zoobank.org:act:297D2E73-7544-44D1-860C-8179DEC44912

Etymology: The specific epithet derives from the Latin word *parvus*, meaning small, it refers to the tiny size of the species, and is to be treated as an adjective.

Material studied. Holotype IGR.BU-026 (a male in a piece of amber measuring $5 \times 4 \times 1$ mm) housed in the Geological Department and Museum (IGR) of the University of Rennes, France.

Type locality: Noije Bum Hill, Hukawng Valley, Kachin State, Myanmar.

Type horizon: upper Albian to lower Cenomanian, mid-Cretaceous.

Diagnosis. As for genus.

Description. Minute size. Head hypognathous, subtriangular in frontal view; compound eye large and without pilosity; mandibles just slightly crossing at tips, not forming a beak; 14 antennomeres, covered with short setae, inserted on a slightly protruding transverse shelf, scape unarmed at least six times longer (0.110 mm) than wide (0.018), pedicel bulbous, wider at apex, as long as first flagellomere, flagellomeres not clubbed, longer than wide, cylindrical, F1 with emargination strongly marked on its anterior quarter (sex-segment), F2 longest flagellomere, F3-F11 slightly decreasing in length toward apex, apical flagellomere conoid, second longest (lengths of antennomeres, in mm: P-0.066, F1-0.062, F2-0.086, F3-0.078, F4-0.074, F5-0.066, F6-0.066, F7-0.062, F8-0.064, F9-0.064, F10-0.062, F11-0.056, F12-0.084).

Mesosoma shorter than metasoma, twice as long as high; epomia not distinct, probably absent. Fore wing hyaline, almost as long as body, covered with homogeneous micropubescence and bordered by setae; C, Sc+R, M+Cu, distal segment of Rs, basalis, marginalis, postmarginalis and r-rs tubular; basalis connected to Sc+R and M+Cu, Sc+R and C separated from marginalis, marginalis slightly thickened to form a stigma, much shorter than its distance from basalis, postmarginalis projecting just a little after stigma, hardly longer than r-rs, r-rs short, extending obliquely from stigma to Rs, Rs in straight line from middle to anterior margin of wing, just notched at intersection with r-rs, Cu pigmented on a segment as long as distance between marginalis and basalis, directed toward posterior wing margin, then arched and disappearing toward margin; radial

cell closed, triangular, reduced in length; basal cell closed; costal cell opened. Legs slender with sparse pubescence; no false spurs on fore tibia; hind femur stouter than fore and mid ones; row of erect setae on hind tibia; basitarsomere as long as the length of the three following tarsomeres combined; tarsal claws simple.

Metasoma. Petiole hardly twice as long as its middle height, convex with both extremities wider, bearing numerous longitudinal carina; gaster subovoid, not flattened, each segment easily distinct from one another; tergum 2 the longest, reaching half-length of gaster, roughly four times longer than tergum 3, following tergites 4-5-6-7 nearly of same lengths; each tergite and sternite separated by a groove; sternum 2 the longest, more than half-length of gaster; hypopygium flattened; genitalia slightly externalized.

Measurements (in mm). Body length 1.283; head length 0.223; head height 0.278; antenna length 1.119; scape length 0.221; scape width 0.036; mesoma length 0.483; mesosoma height 0.243; fore wing length 1.139; petiole length 0.140; petiole height 0.061; total metasoma length 0.578; metasoma height 0.178.

4. Discussion

Despite different conceptions of the Diaprioidea, the synapomorphies respectively proposed by Rasnitsyn and Öhm-Kühnle (2020) and Sharkey et al. (2012) and listed in introduction can all be observed in *Christophus* gen. nov. and *Mintara* gen. nov. Sharkey et al. (2012) recognized four families within the Diaprioidea complex: Diapriidae (including Ismarinae), Maamingidae, Monomachidae and Engel et al. (2013) added the extinct family Spathiopterygidae whereas Rasnitsyn and Öhm-Kühnle (2020) only recognize Diapriidae, Ismaridae and Spathiopterygidae. *Christophus* gen. nov. and *Mintara* gen. nov. can be excluded from the Spathiopterygidae because these genera have a much more complete fore wing venation (at least with the veins C and Sc complete and absence of defined cells; Engel et al., 2013). Both can be excluded as well from the Maamingidae because the representatives of the family possess an highly reduced petiole-like first metasomal segment that is present in our specimens, and 12 antennomeres without emargination in males (Early et al., 2001). *Christophus* gen. nov. and *Mintara* gen. nov. differ from the Monomachidae by displaying a shorter and stouter mesosoma than the representatives of this family (Johnson and Musetti, 2012). Among the six apomorphic characters states defining the Diapriidae (Sharkey et al., 2012) and mentioned afore, *Christophus* gen. nov. and *Mintara* gen. nov. have the third maxillary palpomere enlarged and triangular, broader than the

following palpomere, the longitudinal ridge of metapleuron ventral to propodeal present and the absence of pronotal transverse carina. All these characters ensure the placement of both new genera in the family Diapriidae (+ Ismarinae). Other characters proposed for extant Diapriidae cannot be observed on amber-preserved specimens.

The second metasomal tergite and sternite the longest would assign *Christophus* gen. nov. and *Mintara* gen. nov. either in the Diapriinae or the Belytinae, excluding the Ambositrinae and the Ismarinae (Masner, 1993). But males Diapriinae rarely possess 14 antennomeres (exceptions in van de Kamp et al. (2018): *Xenomorphia* Krogmann, van de Kamp and Schwermann, 2018 (in van de Kamp et al., 2018); Oglobin (1959): *Xenismarus* Oglobin, 1959; Masner and Garcia (2002): *Chilomicrus* Masner and Garcia, 2002) and when they do, the modified flagellomere is always the second, never the first. Therefore, *Christophus* gen. nov. and *Mintara* gen. nov. are placed within the subfamily Belytinae.

Following the key to the European genera of Nixon (1957), *Christophus myanmarensis* gen. et sp. nov. and *Christophus ohmkuhnlei* gen. et sp. nov. key out near *Pantoclis* Förster, 1856. However, they differ from this genus in having a narrower petiole, much longer than wide (Hou et al., 2016). The diagnostic characters of *Christophus* gen. nov. are the length of the postmarginalis, that is two to three times longer than the radial cell and the very narrow petiole (Figs. 1.C, 2, 3.D). Extant genera that possess a similar configuration of the fore wing differ from *Christophus* gen. nov. as follow: *Cinelaptus* Nixon, 1957 has the radial cell shorter and narrower, the marginalis longer and the epomia absent (Nixon, 1957); *Belyta* Förster, 1856 has the radial cell not conspicuously closed (Nixon, 1957); *Gladicauda* Early, 1980 has the marginalis very long (Early, 1980). Among the Cretaceous described diapiid wasps, *Christophus* gen. nov. differs from *Gaugainia* Perrichot and Nel, 2008, described from a female specimen, in having the eyes without pilosity, the gaster oval and dorso-ventrally flattened rather than ellipsoidal and a narrower petiole (Perrichot and Nel, 2008); from *Protobelyta* Jouault and Nel, 2020, described from a female specimen, in having the postmarginalis extending beyond the radial cell, the r-rs more developed, a narrower petiole and the presence of erect setae on the hind legs (Jouault et al., 2020); from *Iberopria* Engel, Ortega-Blanco and Delclòs, 2013, described from a male specimen, in having a closed radial cell, a narrower petiole and more elongate flagellomeres (Engel et al., 2013). The similar fore wing venation (Fig. 2), the general shape of the body, the small apical projection on the scape (Figs. 1.B,

3.C), the size of the petiole lead us to consider *Christophus myanmarensis* gen. et sp. nov. and *Christophus ohmkuhnlei* gen. et sp. nov. as belonging to one same genus. Their diagnostic features are the relative lengths of the pedicel compared to the first flagellomere and of the metatarsomeres, the shape of the radial cell and the hind wing venation. The first three characters are clearly not sufficient to place *Christophus myanmarensis* gen. et sp. nov. and *Christophus ohmkuhnlei* gen. et sp. nov. in two separate genera. However, the presence of a closed basal cell on the hind wing of *Christophus myanmarensis* gen. et sp. nov. whereas it is opened in *Christophus ohmkuhnlei* gen. et sp. nov., is more dubious: this character is often used to separate extant genera as a diagnostic trait. However, the numerous features shared by *Christophus myanmarensis* gen. et sp. nov. and *Christophus ohmkuhnlei* gen. et sp. nov. and listed above on their respective descriptions are preponderant. Furthermore, we cannot confidently ensure that the basal cell is closed on our specimens of *Christophus ohmkuhnlei* gen. et sp. nov. as the venation, if slight, can fade during the embedding process. Thus, supplementary material of both *Christophus myanmarensis* gen. et sp. nov. and *Christophus ohmkuhnlei* gen. et sp. nov. would be helpful to confirm or infirm our attribution.

Using Nixon's (1957) key, *Mintara parva* gen. et sp. nov. keys out between *Acropiستا* Förster, 1856 and *Aclista* Förster, 1856. However, it does not match this identification because of the mesoscutum not pubescent, the epomia not distinct, the cleft inter-antennal sockets (*Aclista*) and the gaster oval, the apical tergite not upturned, the stouter shape of the body (*Acropiستا*). Following the key of Diapriidae (<http://www.diapriid.org/public/site/diapriid/jome>), *Mintara parva* gen. et sp. nov. keys out near *Acropiستا* and *Pantoclis*. However, *Mintara parva* gen. et sp. nov. differs from *Pantoclis* in having the petiole convex and longer and F1 shorter than F2 (Hou et al., 2016). Other genera not listed by Nixon (1957) or described later but listed by Johnson (1992), differ from *Mintara parva* gen. et sp. nov. as follows: *Stylaclista* Dodd, 1915 has the marginalis distinctly longer than r-rs (Dodd, 1915); *Aclistoïdes* Dodd, 1916 has an open radial cell and the apical abdominal segments are telescoping (Dodd, 1916); *Gladicauda* has a concave petiole with the extremities narrower than the middle and the scape as long as the first flagellomere (Early, 1980); *Probelyta* Brues, 1922 has a shorter petiole (Brues, 1922); *Ctenopria* Oglobin, 1966 has no ocelli and the petiole just slightly longer than wide, with the poster extremity wider than the anterior (Oglobin, 1966); *Masnerosoma* Sundholm, 1970 lacks the basalis and the radialis on the fore wing (Sundholm, 1970); *Panbelista* Chambers, 1985 has 13

antennomeres with long setae in males (Chambers, 1985); *Psilommacra* Máček, 1990 has an opened radial cell (Máček, 1990); *Masnerolyta* Buhl, 1997 and *Masneretus* Buhl, 1997 have the marginalis as long or longer than its distance from the basalis and the postmarginalis extending beyond the radial cell (Buhl, 1997); *Eccinetus* Muesebeck and Walkley, 1956 has an elongate radial cell and a very long marginalis (Muesebeck and Walkley, 1956; Liu and Xu, 2011). Other Cretaceous diapriid wasps differ from *Mintara parva* gen. et sp. nov. in having the postmarginalis as long as the radial cell (*Protobelyta*; Jouault et al., 2020), the radial cell opened (*Iberopria*; Engel et al., 2013), an ellipsoidal gaster with the segments not separated by a distinct groove (*Gaugainia*; Perrichot and Nel, 2008) and a narrower petiole (*Christophus* gen. nov.).

5. CONCLUSION

Modern belytine species occupy an important place in the hymenopteran assemblages of the moist temperate forests of the southern hemisphere and this study show that the belytine presence in this type of habitat dates back to the Lower Cretaceous. The previous studies on fossil Diapriidae from Cretaceous amber deposits also suggested that their diversity was underestimated before the K/Pg crisis. We confirm this tendency, as well as the early worldwide distribution of Diapriidae since they are known from various Cretaceous amber deposits around the world.

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References

- Brues, C.T., 1922. Some parasitic Hymenoptera from New Zealand. *Psyche* 29, 216–225.
<https://doi.org/10.1155/1922/41808>
- Buhl, P.N., 1997. Two new genera of Belytinae from Argentina (Hymenoptera, Diapriidae). *Entomofauna* 18, 89–92.
- Castro, L.R., Downton, M., 2006. Molecular analysis of the Apocrita (Insecta: Hymenoptera) suggest that the Chalcidoidea are sister to the diaprioid complex. *Invertebrate Systematics* 20, 603–614.
<https://doi.org/10.1071/IS06002>
- Chambers, V.H., 1985. A new genus of the Belytinae (Hym, Proctotrupoidea, Diapriidae). *Entomologist's Monthly Magazine* 121, 207–209.
- Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* 21(5), 441–455. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- Dodd, A.P., 1915. Australian Hymenopteran Proctotrypoidea. NO 3. *Transactions of the Royal Society of South Australia* 39, 384–454.
- Dodd, A.P., 1916. Australian Hymenopteran Proctotrypoidea. NO 4. *Transactions of the Royal Society of South Australia* 40, 9–32.
- Early, J.W., 1980. The Diapriidae (Hymenoptera) of the southern islands of New Zealand. *Journal of the Royal Society of New Zealand* 10, 153–171.
- Early, J.W., Masner, L., Naumann, I.D., Austin, A.D., 2001. Maamingidae, a new family of proctotrupoid wasp (Insecta: Hymenoptera) from New Zealand. *Invertebrate Taxonomy* 15, 341–352.
<https://doi.org/10.1071/IT00053>
- Engel, M.S., Ortega-Blanco, J., Soriano, C., Grimaldi, D.A., Delclòs, X., 2013. A new lineage of enigmatic diaprioid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). *American Museum Novitates* 3771, 1–23. <https://doi.org/10.1206/3771.2>
- Fujiyama, I., 1994. Two parasitic wasps from Aptian (Lower Cretaceous) Choshi amber, Chiba, Japan. *Natural History Research* 3, 1–5.

- Grimaldi, D., Ross, A.J., 2017. Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fräser, N.C., Sues, H.D. (Eds.), *Terrestrial conservation Lagerstätten: windows into the evolution of life on land*. Dunedin Academic Press, Edinburgh, pp. 287–342.
- Heraty, J., Ronquist, F., Carpenter, J.M., Hawks, D., Schulmeister, S., Dowling, A.P., Murray, D., Munro, J., Wheeler, W.C., Schiff, N., Sharkey, M., 2011. Evolution of the hymenopteran megaradiation. *Molecular Phylogenetics and Evolution* 60, 73–88. <https://doi.org/10.1016/j.ympev.2011.04.003>
- Hou, Z., Yang, S., Xu, Z., 2016. First record of the genus *Pantoclis* Förster, 1856 from China, with descriptions of two new species (Hymenoptera: Diapriidae). *Zoological Systematics* 41, 280–285. <https://doi.org/10.1186/zs.201229>
- Johnson, N.F., 1992. Catalog of the world species of Proctotrupeoidea excluding Platygasteridae (Hymenoptera). *Memoirs of the American Entomological Institute* 51, 825 pp. <http://doi.org/10.5281/zenodo.23657>
- Johnson, N.F., Musetti, L., 2012. Genera of the parasitoid wasp family Monomachidae (Hymenoptera: Diaprioidea). *Zootaxa* 3188, 31–41. <https://doi.org/10.11646/zootaxa.3188.1.2>
- Johnson, N.F., Musetti, L., Cora, L., 2021. Hymenoptera Online (HOL). Internet site: <https://hol.osu.edu> (consulted 09/09/2021).
- Jouault, C., Nel, A., 2020. A new species of parasitoid wasps (Hymenoptera: Diapriidae: Belytinae) from Eocene Baltic amber. *Paleoentomology* 3, 614–622. <https://doi.org/10.11646/palaeoentomology.3.6.13>
- Jouault, C., Perrichot, V., Nel, A., 2020. A new genus and species of parasitic wasps (Hymenoptera: Diapriidae) from Hkamti “mid-Cretaceous” Burmese amber. *Cretaceous Research* 115, 104533. <https://doi.org/10.1016/j.cretres.2020.104533>
- Klopfstein, S., Vilhelmsen, L., Heraty, J.M., Sharkey, M., Ronquist, F., 2013. The Hymenopteran Tree of Life: Evidence from protein coding genes and objectively aligned ribosomal data. *PLoS ONE* 8(8), e69344. <https://doi.org/10.1371/journal.pone.0069344>
- Königsmann, E., 1978. Das phylogenetische System der Hymenoptera. Teil 3: “Terebrantes” (Unterordnung Apocrita). *Deutsche Entomologische Zeitschrift* 25, 1–55. <https://doi.org/10.1002/mmnd.19780250102>
- Lak, M., Nel, A. 2009. An enigmatic diapriid wasp (Insecta, Hymenoptera) from French Cretaceous amber. *Geodiversitas* 31, 137–144. <https://doi.org/10.5252/g2009n1a12>

- Liu, J.X., Xu, Z.F., 2011. Two new species of *Eccinetus* Muesebeck and Walkley, 1956 (Hymenoptera: Diapriidae) from China, with a key to the World species. *Entomological News* 122, 65–73.
<https://doi.org/10.3157/021.122.0109>
- Loiacono, M.S., 1987. Un nuevo diáprido (Hymenoptera) parasitoide de larvas de *Acromyrmex ambiguus* (Emery) (Hymenoptera, Formicidae) en el Uruguay. *Revista de la Sociedad Entomologica Argentina* 44, 129–136.
- Máček, J., 1990. Revision of European *Psilommina* (Hymenoptera, Diapriidae). 1. *Psilomma* and *Acanosema* complex. *Acta Entomologica Musei Nationalis Pragae* 43, 335–360.
- Masner, L., 1993. Superfamily Proctotrupoidea. In: Goulet, H., Huber, J.T. (Eds), *Hymenoptera of the world: An identification guide to families*. Research Branch Agriculture Canada, Ottawa, pp. 537–557.
- Masner, L., Garcia, J.L., 2002. The genera of Diapriinae (Hymenoptera: Diapriidae) in the New World. *Bulletin of the American Museum of Natural History* 268, 1–138. <http://hdl.handle.net/2246/476>
- Muesebeck, C.F.W., Walkley, L.M., 1956. Type species of the genera and subgenera of parasitic wasps comprising the superfamily Proctotrupoidea (order Hymenoptera). *Proceedings of the United States National Museum* 105, 319–419. <https://doi.org/10.5479/si.00963801.3359.319>
- Nixon, G.E.J., 1957. Hymenoptera, Proctotrupoidea, Diapriidae, subfamily Belytinae. *Handbooks for the Identification of British Insects* 8, 1–107.
- Oglobin, A.A., 1959. Un género nuevo de la familia Diapriidae (Hymenoptera). *Revista de la Sociedad Entomologica Argentina* 21, 43–46.
- Oglobin, A.A., 1966. *Ctenopria* un género nuevo de la familia Diapriidae (Hymenoptera). *Revista de la Sociedad Entomologica Argentina* 28, 61–64.
- Perrichot, V., Nel, A., 2008. A new belytine wasp in Cretaceous amber from France (Hymenoptera: Diapriidae). *Alavesia* 2, 203–209.
- Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Pedersen, M., Lanfear, R., Diez, P.A., Heraty, J., Kjer, K.M., Klopstein, S., Meier, R., Polidori, C., Schmitt, T., Liu, S., Zhou, X., Wappler, T., Rust, J., Misof, B., Niehuis, O., 2017. Evolutionary history of the Hymenoptera. *Current Biology* 27, 1013–1018. <https://doi.org/10.1016/j.cub.2017.01.027>

- Quadros, A.L., Brandão, C.R.F., 2017. Genera of Belytinae (Hymenoptera: Diapriidae) recorded in the Atlantic dense ombrophilous forest from Paraíba to Santa Catarina, Brazil. *Papéis Avulsos de Zoologia* 57(6): 57–91. <https://doi.org/10.11606/0031-1049.2017.57.06>
- Rasnitsyn, A.P., 1980. Origin and evolution of Hymenoptera. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* 174, 1–192 [in Russian].
- Rasnitsyn, A.P., 1988. An outline of evolution of hymenopterous insects (order Vespida). *Oriental insects* 22, 115–145. <https://doi.org/10.1080/00305316.1988.11835485>
- Rasnitsyn, A.P., 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linnei, 1789 (=Vespida Laicharting, 1781). In: Rasnitsyn, A.P., Quicke, D.L.J. (Eds.), *History of insects*. Kluwer academic Publisher, Dordrecht, The Netherlands, pp. 242–254.
- Rasnitsyn, A.P., Öhm-Kühnle, C., 2020. Taxonomic revision of the infraorder Proctotrupomorpha (Hymenoptera). *Paleoentomology* 3, 223–234. <https://doi.org/10.11646/paleoentomology.3.3.2>
- Schlüter, T., 1978. Zur Systematik und Palökologie harzkonserverter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich. *Berliner Geowissenschaftliche Abhandlungen (A)* 9, 150 pp.
- Sharkey, M.J., 2007. Phylogeny and classification of Hymenoptera. *Zootaxa* 1168, 521–548. <https://doi.org/10.11646/zootaxa.1668.1.25>
- Sharkey, M.J., Roy, A., 2002. Phylogeny of the Hymenoptera: a reanalysis of the Ronquist et al. (1999) reanalysis, emphasizing wing venation and apocritan relationships. *Zoologica Scripta* 31, 57–66. <https://doi.org/10.1046/j.0300-3256.2001.00081.x>
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L., Wheeler, W.C., 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* 27, 1–33. <https://doi.org/10.1111/j.1096-0031.2011.00366.x>
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>

- Smith, R.D.A, Ross, A.J., 2017. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resinproducing forests to brackish waters, and the age of the amber. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 107, 1–9.
<https://doi.org/10.1017/S1755691017000287>
- Sundholm, A., 1970. Chapter 16. Hymenoptera: Proctotrupoidea. *South African Animal Life* 14, 306–401.
- van de Kamp, T., Schwermann, A.H., dos Santos Rolo, T., Lösel, P.D., Engler, T., Etter, W., Faragó, T., Göttlicher, J. Heuveline, V. Kopmann, A., Mähler, B., Mörs, T., Odar, J., Rust, J., Jerome, N.T., Vogelgesang, M., Baumbach, T., Krogmann, L., 2018. Parasitoid biology preserved in mineralized fossils. *Nature communications* 9(3235), 1–29. <https://doi.org/10.1038/s41467-018-05654-y>
- Vilhelmsen, L., Mikó, I., Krogmann, L., 2010. Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society* 159, 22–194. <https://doi.org/10.1111/j.1096-3642.2009.00576.x>
- Yu, T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F., Zhang, H., Wang, B., Dilcher, D., 2019. An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences* 116, 20182192. <https://doi.org/10.1073/pnas.1821292116>
- Zherikhin, V.V., Sukatcheva, I.D., 1973. On the Cretaceous insect-bearing “ambers” (retinites) from North Siberia. In: Narchuk, E.P. (ed.), *Problems in Insect Palaeontology: XXIV annual lectures in memory of N.A. Kholodovsky (1-2 april 1971)*, Nauka, Leningrad, pp. 3–48 [in Russian].

Figure captions:

Figure 1: *Christophus myanmarensis* gen et sp. nov., holotype IGR.BU-017d. A. Habitus in lateral view; B. Head in dorsal view; C. Petiole in lateral view (scale bars: A = 0.5 mm; B,C = 0.125 mm // abbreviations: EF1 = emargination of flagellomere 1; ST = scape apical teeth).

Figure 2: Comparison of fore and hind wings of the two species of *Christophus* gen. nov.; A. *C. myanmarensis* sp. nov. B. *C. ohmkuhnlei* sp. nov.; (scale bars = 0.5 mm).

Figure 3: *Christophus ohmkuhnlei* gen. et sp. nov.; A. Holotype IGR.BU-017a, habitus in lateral view; B. Paratype IGR.BU-017b, habitus in dorsal view; C. Holotype IGR.BU-017a, head in dorsal view; D. Paratype IGR.BU-017b, petiole in dorsal view; E. Paratype IGR.BU-017c, habitus in lateral view (scale bars: A, B= 1 mm; C, D = 0.125 mm; E = 0.5 mm // abbreviations: EF1 = emargination of flagellomere 1; FS = frontal shelf; ST = scape apical teeth).

Figure 4: *Mintara parva* gen. et sp. nov., holotype IGR.BU-026. A. Habitus in lateral view; B. Head in frontal view; C. Metasoma in lateral view (scale bars: A = 0.5 mm; B, C = 0.25 mm // abbreviation: FS = frontal shelf).

Figure 5: *Mintara parva* gen. et sp. nov., fore wing venation (scale bar = 0.5 mm).

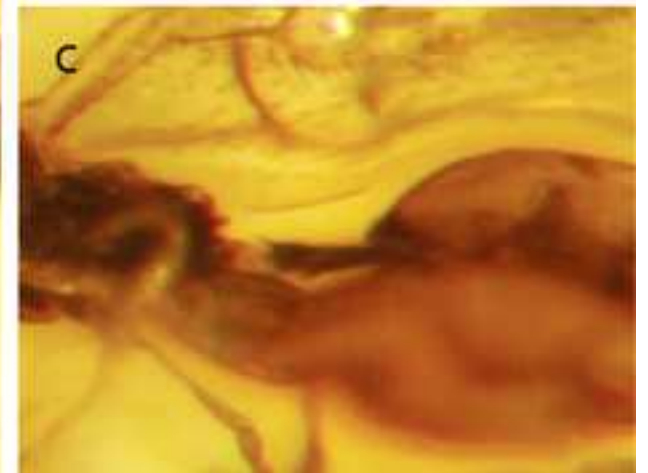
Table 1: Fossil record of the Cretaceous Diapriidae.

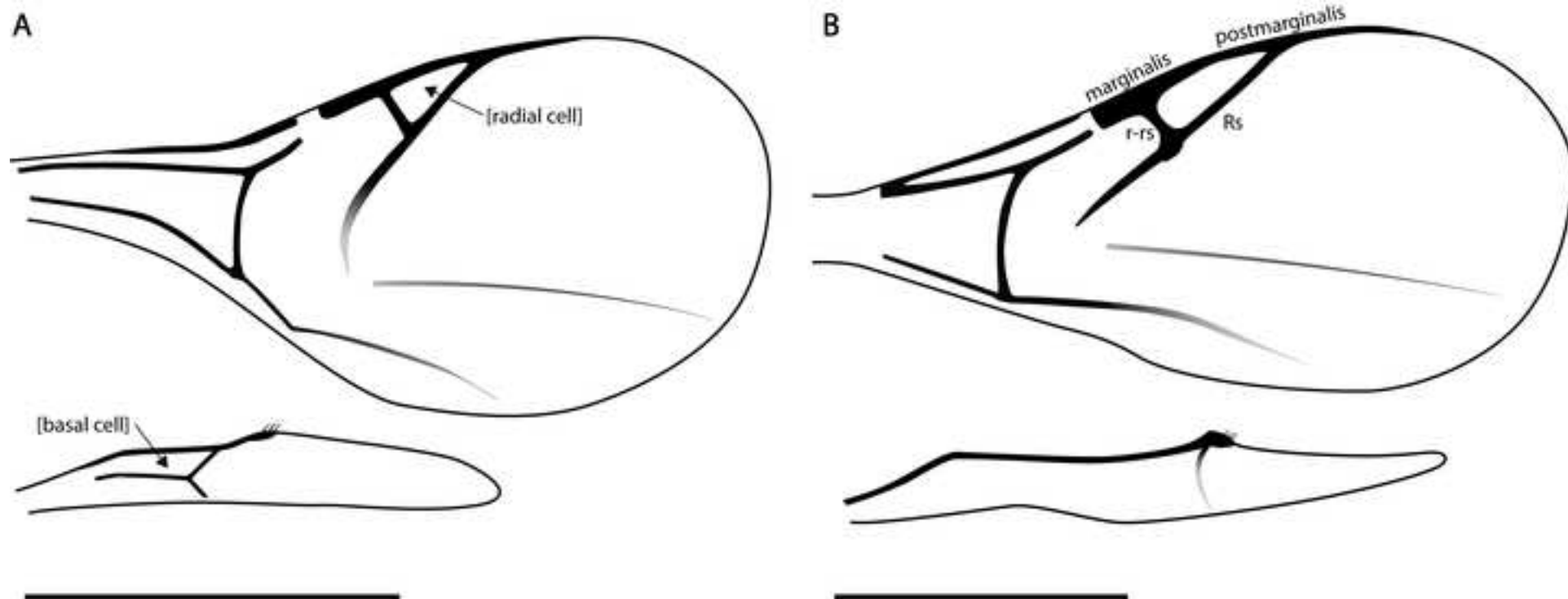
Table 2: Overview of the material studied herein.

Taxa	Age
<u>Belytinae</u>	
<i>Christophus myanmarensis</i> gen. et sp. nov.	Albian-Cenomanian
<i>Christophus ohmkunhlei</i> gen. et sp. nov.	Albian-Cenomanian
<i>Mintara parva</i> gen. et sp. nov.	Albian-Cenomanian
<i>Protobelyta monsirei</i> Jouault & Nel, 2020	Albian
<i>Gaugainia electrogallica</i> Perrichot & Nel, 2008	Albian
<u>Diapriinae</u>	
Diapriinae indet.	Cenomanian
Diapriinae (M.B., pers. obs.)	Cenomanian
<u>Ismarinae</u>	
Ismarinae indet.	Cenomanian
<i>Cretapria tsudakai</i> Fujiyama, 1994	Aptian
<u>Subfamily indet.</u>	
Diapriidae indet.?	Campanian
Diapriidae indet.	Turonian
<i>Iberopria perialla</i> Engel, Ortega-Blanco & Delclòs, 2013	Albian

Deposit	Reference	
Kachin amber (Myanmar)	this paper	
Kachin amber (Myanmar)	this paper	
Kachin amber (Myanmar)	this paper	
Hkamti amber (Myanmar)	Jouault et al., 2020	
SW French amber	Perrichot & Nel, 2008	
Taimyr amber (Russia)	Zherikin & Sukatcheva, 1973	
SW French amber	Lak & Nel, 2009	
NW French amber	Schlüter, 1978	
Choshi amber (Japan)	Fujiyama, 1994	
Canadian amber	Schlüter, 1978	
Timmerdyakh amber (Russia)	Rasnitsyn, 1980	
Peñacerrada amber (Spain)	Engel et al., 2013	

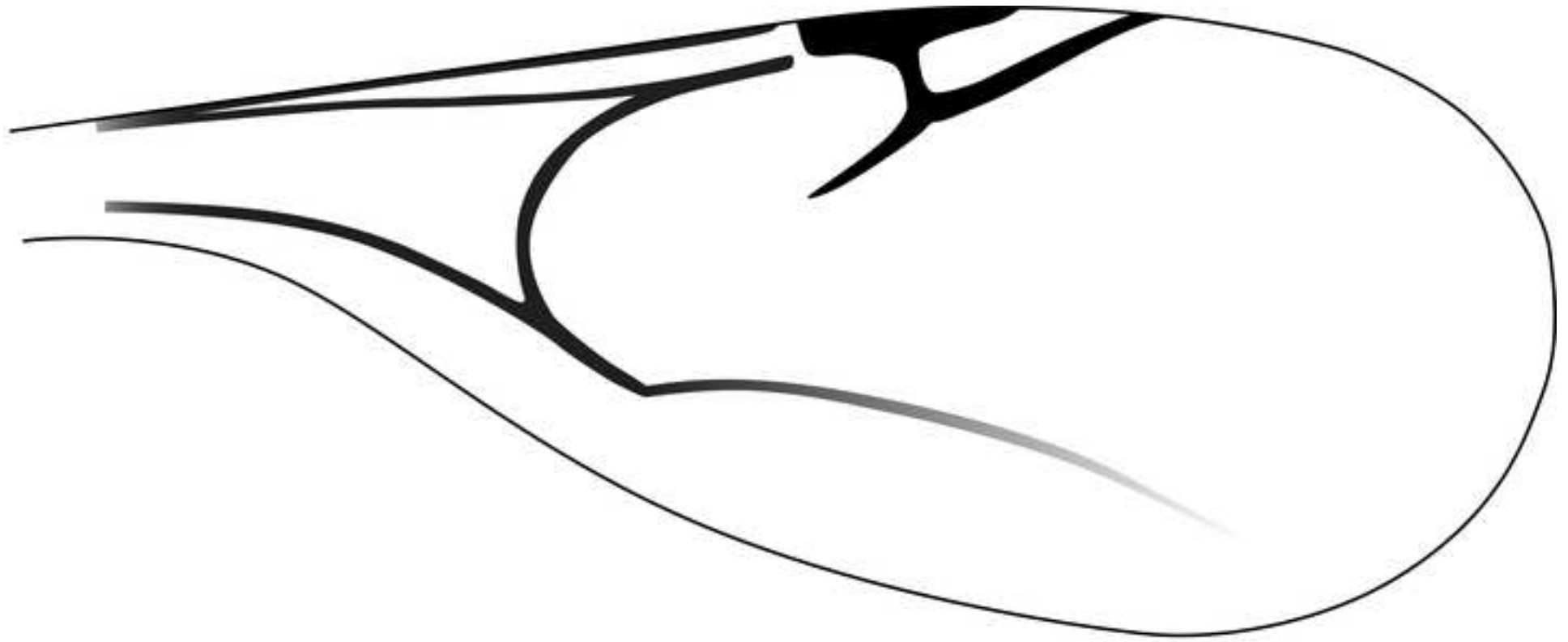
Species	Specimen number	Sex	Status
<i>Christophus myanmarensis</i> sp. nov.	IGR.BU-017d	Male	Holotype
<i>Christophus ohmkuhnlei</i> sp. nov.	IGR.BU-017a	Male	Holotype
	IGR.BU-017b	Male	Paratype
	IGR.BU-017c	Male	Paratype
<i>Mintara parva</i> sp. nov.	IGR.BU-026	Male	Holotype











Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.