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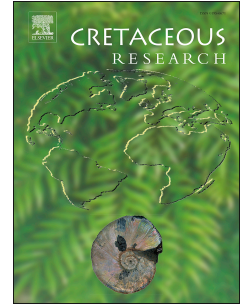
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Corenne Jouault: Conceptualization, Data curation, Investigation, Methodology, visualization, writing - original draft, Writing - review & editing. Vincent Perrichot: Data curation, Investigation, Writing - original draft, Writing - review & editing. André Nel: Supervision, Data curation, Investigation, Writing - original draft, Writing - review & editing.

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1 New Hymenoptera wasps from mid-Cretaceous Burmese amber deposits highlight the
2 Bethyloid antiquity and paleobiogeography (Hymenoptera: Chrysidoidea)

3

4 Corentin Jouault ^{a*}, Vincent Perrichot ^a, André Nel ^b

5

6 ^a Univ. Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France E-mail:

7 jouaultc0@gmail.com / vincent.perrichot@univ-rennes1.fr

8 ^b Institut de Systématique, Évolution, Biodiversité (ISYEB) – UMR 7205 – Muséum national

9 d’Histoire naturelle, CNRS, SU, EPHE, Université des Antilles, CP50, 57 rue Cuvier F-75005 Par-

10 is, France. E-mail: anel@mnhn.fr

11 *Corresponding author: jouaultc0@gmail.com

12

13 **Abstract**

14 Examination of Hkamti and Tanai Burmese ambers reveals two new genera and species of
15 †Lancepyrinae: *Protopyris myanmarensis* Jouault & Nel gen. et sp. nov. and *Burmapyris azevedoi*
16 Jouault, Perrichot & Nel gen. et sp. nov. *Protopyris* Jouault & Nel gen. nov. is the first Bethyloidea
17 described from amber of the Hkamti deposit (lower Albian, mid-Cretaceous) in Myanmar. These
18 specimens provide useful clues to understand the paleobiogeographic evolution of the
19 †Lancepyrinae, since they are only predated by genera described from Lebanese and Spanish amber.
20 These new taxa suggest a major paleobiogeographic scenario, since Burmese amber was probably
21 produced on an island that separated from Gondwana during the Late Jurassic to Early Cretaceous.
22 It thus suggests a possible earlier origin for the †Lancepyrinae, and thereby for the Bethyloidea, in
23 the Late Jurassic to earliest Cretaceous.

24

25 **Key words.** Hkamti amber, Bethyloidea, †Lancepyrinae, paleobiogeography, Albian

26

27 **Introduction**

28 The †Lancepyrinae are a small extinct bethylid subfamily, originally described from Barremian
29 Cretaceous Lebanese amber (Azevedo and Azar, 2012). Members can be easily distinguished from
30 related taxa mainly by having fore wing venation with an unusual combination of closed lanceolate
31 cell 2R1, tubular and well-pigmented vein Rs+M, and angled vein Rs&M (Azevedo and Azar 2012).
32 Later, this work was supplemented by the additions of Ortega and Engel (2013) and Engel et al.
33 (2016), with descriptions of further lancepyrine genera and species, challenging the constant pres-
34 ence of a tubular Rs+M vein. †Lancepyrinae were hitherto known only by five species from Leba-
35 nese, Spanish, and Taimyr amber (Evans, 1973; Azevedo and Azar, 2012; Ortega-Blanco and Engel,
36 2013; Engel et al., 2016), but remained unknown from the Burmese amber biota. As for the other
37 bethylid fossil subfamilies, we do not have a record of behavior or clue to understand
38 †Lancepyrinae biology (Azevedo et al., 2018).

39 Recently, two phylogenies have been proposed to investigate the relationships between
40 Bethylidae subfamilies (Jouault et al., 2020a; Colombo et al., 2020). However, if their results do not
41 record †Lancepyrinae at exactly the same position, both recover them as an early diverging lineage
42 among Bethylidae. In Jouault et al. (2020a: fig 6), they fall as a part of separate radiation
43 (†Lancepyrinae + †Protopristocerinae) sister group of the clade (Mesitiinae + Pristocerinae +
44 Epyrinae + Scleroderminae); while Colombo et al. (2020: fig 1B) recorded them as sister group to
45 the clade (Mesitiinae + †Elektroepyrinae + Pristocerinae + Epyrinae + Scleroderminae +
46 †Protopristocerinae). It is therefore probable that new phylogenies will be necessary to clarify this
47 placement, above all a molecular phylogeny updating the results of Carr et al. (2010).

48 Herein, we describe the first records of †Lancepyrinae from two Cretaceous Burmese amber depos-
49 its, and we discuss their placement and the implication on the paleobiogeographic history of the
50 subfamily.

51

52 **Material and methods**

53 The amber piece containing the type of *Protopyris myanmarensis* gen. et sp. nov. derives from the
54 deposits of Hkamti site (about 80 km southwest of the Angbamo site), Hkamti District, Sagaing
55 Region, Myanmar, see detailed map in Zheng et al. (2018: supplementary figure 2) or in Xing and
56 Qiu, (2020: fig. 1). Zircon U-Pb analyses established an early Albian age (109.7 ± 0.4 Ma) for
57 Hkamti amber, based on zircon analyses of clastic deposits at the surface (Xing & Qiu, 2020). The
58 paleobiota from this deposit is almost unknown, with only one ostracod and one Diapriidae de-
59 scribed to date (Xing et al., 2018; Jouault et al., 2020b). The amber piece containing the type of
60 *Burmapyris azevedoi* gen. et sp. nov. derives from the deposits of Noiye Bum in the Hukawng Val-
61 ley ($26^{\circ} 29' N$, $96^{\circ} 35' E$), Kachin State, northern Myanmar (see detailed map in Grimaldi and Ross,
62 2017: fig. 2). Radiometric data established an earliest Cenomanian age (98.79 ± 0.62 Ma) for Ka-
63 chin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi et
64 al., 2012). Some ammonites found in the amber-bearing bed and within amber corroborate a late
65 Albian–early Cenomanian age (Cruickshank and Ko, 2003; Yu et al., 2019).

66 The specimens were examined and photographed using a Leica MZ APO stereomicroscope
67 equipped with a Canon EOS 5D Mark II camera. All images are digitally stacked photomicrograph-
68 ic composites of several individual focal planes, which were obtained using HeliconFocus 6.7. The
69 figures were composed with Adobe Illustrator CC 2019 and Adobe Photoshop CS19 software. The
70 specimens are housed in the amber collection of the Geological Department and Museum (IGR) of
71 the University of Rennes, France. We follow the nomenclature, classification, and terminology for
72 morphological features of the body and wing venation of Azevedo et al. (2018).

73 Main measurements and abbreviations used are as follows: length of fore wing (LFW);
74 length of head, mandibles excluded (LH); width of head (WH); width of frons (WF); height of eye
75 (HE); length of eye (LE); ocello-ocular line (OOL); width of ocellar triangle (WOT); diameter of
76 anterior ocellus (DAO); vertex-ocular line (VOL). The nomenclature of integument sculpture fol-
77 lows Harris (1979).

78 Published work and nomenclatural acts are registered in ZOOBank (<http://www.zoobank.org>,
79 last access: 18 November 2020), with the following LSID (reference):
80 urn:lsid:zoobank.org:pub:42C094B2-B116-4F29-B118-8724D288FAE0

81

82 **Systematic paleontology**

83 Class Insecta Linnaeus, 1758

84 Order Hymenoptera Linnaeus, 1758

85 Superfamily Chrysidoidea Latreille, 1802

86 Family Bethylidae Haliday, 1839

87 Subfamily †Lancepyrinae Azevedo and Azar, 2012

88

89 Genus *Protopyris* gen. nov. Jouault & Nel

90 Figs 1-2

91 urn:lsid:zoobank.org:act:8C12080A-83F2-48D3-AC6D-7C92DA4C6710

92

93 *Type species. Protopyris myanmarensis* sp. nov. Jouault & Nel

94 *Etymology.* The genus name is a combination of the Greek « *prôtos* » meaning ‘primitive’ and the
95 generic name *Epyris*, commonly used as a stem for many bethylid genera. Gender masculine.

96 *Diagnosis.* Body depressed; mandibles dentate with four(?) teeth along masticatory margin and one
97 long apical tooth; clypeus reduced, not projecting; antennae with 11 flagellomeres; scape less than
98 twice as long as pedicel; notauli conspicuous; fore wing venation developed, with cells C, R, 1Cu,
99 1M, and 2R1 delimited by tubular veins; M and cu-a veins aligned; 2Cu not clearly delimited; 2R1
100 opened at apex; pterostigma narrow, elongate; propodeum rectangular and not spinose; legs with
101 slightly enlarged femora.

102

103 *Protopyris myanmarensis* sp. nov. Jouault & Nel

105

106 *Holotype*: Specimen identifier IGR.BU-015 (a nearly complete specimen, with right antenna de-
107 stroyed, in a rectangular piece of amber measuring $5 \times 4 \times 1.5$ mm).

108 *Etymology*. Named after the originating country of the amber piece, Myanmar. The specific epithet
109 is to be treated as an adjective in the genitive case.

110 *Locality and horizon*. Hkamti site, Hkamti District, Sagaing Region, Myanmar; lower Albian (ca.
111 110 Ma), mid-Cretaceous.

112 *Diagnosis*. As for the genus.

113 *Description*. Sex unknown; body ca. 2.10 mm long, depressed, almost smooth and not strongly fo-
114 veolate; wings clear, setose, LFW 1.25 mm. LH 0.50 mm; WH 0.53 mm; WF 0.31 mm; LE 0.25
115 mm; OOL 0.15 mm; WOT ca. 0.12 mm; DAO 0.03 mm; VOL 0.11 mm. Head sub-quadrate, not
116 pubescent, with small dorsal median depression, finely punctate but not sculptured; mandible pro-
117 jecting forward, ca. 0.12 mm long, dentate, apparently with four equal, sharp, small teeth along
118 masticatory margin and one longer apical tooth; only two maxillary palpomeres visible (but certain-
119 ly more are present); flagellomeres with cylindrical cross-section; measurable antennomere lengths
120 (in mm) scape 0.11 mm, pedicel 0.07 mm, F1 ca. 0.03 mm, F2 ca. 0.03 mm, F3 0.05 mm, F4 to F10
121 sub-equal to equal ca. 0.06 mm (all flagellomeres compressed due to preservation, thereby useful
122 width measurements not provided); occipital carina slightly marked; posterior head margin nearly
123 straight with small median concavity; compound eye without microsetae, closer to mandibular in-
124 sersion than posterior to head margin; ocellar triangle nearly equilateral, with two posterior ocelli
125 slightly more distant from each other than from anterior.

126 *Mesosoma* with dorsum smooth, not roughly sculptured; femora slightly thickened, tibia thin, tarsal
127 claws simple; tibial spur formula 1-2-2; arolium present; notauli well-marked, posteriorly conver-
128 gent; parapsidal furrows weak; metanotum developed medially and overlapping mesoscutellum
129 posteriorly; metapectal-propodeal complex rectangular, not foveolate, with marginal carinae and no

130 posterior spines, posterior margin of propodeum straight. Fore wing covered with microtrichiae and
131 bordered with small microtrichiae; elongated with apical margin gently rounded; anterior border not
132 angularly incurved anterior to pterostigma; veins C, Sc+R, A, R1, Rs, Rs+M, 2r-rs&Rs, M+Cu, M,
133 cu-a, Cu and cells C, R, 1Cu, 1M and 2R1 present; M and cu-a veins aligned; cell 2Cu open, virtu-
134 ally enclosed by spectral vein; cell 2R1 distally opened; Rs+M prolonged as a spectral vein origi-
135 nating from 1M at level of pterostigma base; pterostigma long and narrow; prestigmal abscissa of
136 R1 conspicuous. Hind wing with only veins C and Sc+R, hamuli uncountable.

137 Metasoma with short petiole; six tergites present, T1 reduced, T2 enlarged, all tergites convex, part-
138 ly covering sternites; sting not preserved (apical part of metasoma destroyed); length of clearly visi-
139 ble tergites: T1 0.26 mm, T2 0.15 mm, T3 ca. 0.15 mm, more distal tergites impossible to measure
140 because of bent metasoma.

141

142 Genus *Burmapyris* gen. nov. Jouault, Perrichot & Nel

143 Figs 3-4

144 urn:lsid:zoobank.org:act:A627B4D5-35BB-48F5-B198-A2721DDB01D1

145 *Type species. Burmapyris azevedoi* Jouault, Perrichot & Nel sp. nov.

146 *Etymology.* The generic epithet is a combination of 'Burma' referring to Burmese amber and the
147 generic name *Epyris*, commonly used as a suffix for many bethylid genera. Gender masculine.

148 *Diagnosis.* Female (sting visible) with body weakly depressed; mandibles heavily dentate with
149 five(?) sharp teeth along masticatory margin, with apical tooth longer and stouter; clypeus triangular
150 and slightly projecting; antennae stout, with 11 flagellomeres; scape nearly twice as long as pedicel;
151 notauli conspicuous; fore wing venation developed, with cells C, R, 1Cu, and 2R1 delimited by
152 tubular veins; M and cu-a veins aligned; pre- and post-stigmal R1 abscissae present; 1M and 2Cu
153 not clearly delimited; 2R1 opened at apex; pterostigma short, wide in apical one-third of length;
154 hind wing with four hamuli; propodeum rectangular and not spinose; legs with slightly enlarged
155 femora.

156

157 *Burmapyris azevedoi* sp. nov. Jouault, Perrichot & Nel

158 urn:lsid:zoobank.org:act:9EE1F4FE-9B6C-43AB-8C2A-823D4A48F0E1

159 *Holotype*: Specimen identifier IGR.BU-016 (complete female, in a rectangular piece of amber
160 measuring $5 \times 4 \times 2$ mm).

161 *Etymology*. The specific epithet is a patronym honoring Dr. Celso O. Azevedo, a world authority in
162 Bethyridae taxonomy. The specific epithet is to be treated as a noun in a genitive case.

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

165 *Diagnosis*. As for the genus.

166 *Description*. Female (sting slightly visible); body ca. 2.5 mm long, almost smooth and not strongly
167 foveolate; wings clear and setose, LFW at least 1.50 mm (bent). LH 0.57 mm; WH 0.53 mm; WF
168 0.31 mm; HE 0.18 mm; LE ca. 0.25 mm; OOL 0.15 mm; WOT ca. 0.15 mm; DAO 0.05 mm; VOL
169 ca. 0.12 mm. Head slightly longer than wide, not pubescent, without dorsal median depression,
170 sculpture apparently absent; mandible bent downward and slightly curved backwards, ca. 0.18 mm
171 long; only four maxillary palpomeres visible (but certainly more numerous); flagellomeres with
172 cylindrical cross-section; measurable antennomere lengths (in mm): scape ca. 0.15 mm, pedicel
173 0.08 mm, F1 to F7 ca. 0.12 mm, F8 to F10 ca. 0.11 mm, F11 0.18 mm; occipital carina conspicuous;
174 posterior head margin curved; compound eye without microsetae, closer to mandibular insertion
175 than to posterior head margin; ocellar triangle nearly equilateral, situated posteriorly on head, with
176 two posterior ocelli slightly more distant from each other than from anterior.

177 *Mesosoma* with dorsum smooth, not roughly sculptured; femora slightly thickened, tibia thin, tarsal
178 claws simple; tibial spur formula 1-2-2; arolium present; notauli well-marked, slightly posteriorly
179 convergent; parapsidal furrows weak; metanotum developed medially and overlapping mesoscutel-
180 lum posteriorly; metapectal-propodeal complex rectangular, not foveolate, with marginal carinae
181 and no posterior spines; posterior margin of propodeum straight. Fore wing covered with mi-

182 crenulae and bordered with small microtrichia, with apical margin gently rounded, anterior bor-
 183 der not angularly incurved anterior to pterostigma; veins C, Sc+R, A, R1, Rs, Rs+M, 2r-rs&Rs,
 184 M+Cu, M, cu-a and cells C, R, 1Cu, and 2R1 present; M and cu-a veins aligned; cell 2Cu and 1M
 185 open, virtually enclosed by spectral vein; cell 2R1 distally opened; Rs+M long and prolonged as a
 186 spectral vein originating from 1M after pterostigma apex; pre- and post-stigmal abscissae of R1
 187 conspicuous. Hind wing with only veins C and Sc+R, and 4 hamuli.

188 Metasoma with short petiole; apex interiorized, but six tergites visible, T1 reduced, T2 enlarged, all
 189 tergites convex, partly covering sternites; sting not preserved; length of clearly visible tergites: T1
 190 0.43 mm, T2 0.27 mm, T3 0.22 mm, T4 ca. 0.12 mm, other tergites not measurable since interior-
 191 ized.

192

193

194 Key to genera of †Lancepyrinae (modified from Azevedo et al., 2018):

195 1. Fore wing with Rs+M vein conspicuous and tubular 2

196 – Fore wing with Rs+M vein apparently absent, weak or spectral 5

197

198 2. Fore wing with 2R1 cell closed *Lancepyris* Azevedo & Azar, 2012 (Ain Dara am-
 199 ber, Lebanon)

200 – Fore wing with 2R1 cell opened 3

201

202 3. Fore wing with a short pterostigma and Rs+M vein short (not enclosing 1M cell or reaching apex
 203 of pterostigma) *Archaeopyris* Evan, 1973 (Taimyr amber, Russia)

204 – Fore wing with an elongate pterostigma and Rs+M long (enclosing 1M cell or reaching apex of
 205 pterostigma) 4

206

- 207 4. Rs+M long, continuing after 1M cell, 1M cell not fully enclosed by tubular
 208 veins *Burmapyris* Jouault, Perrichot & Nel gen. nov. (Kachin amber, My-
 209 anmar)
- 210 – Rs+M short, only cancelling 1M cell, 1M cell fully enclosed by tubular
 211 veins *Protopyris* Jouault & Nel gen. nov. (Hkamti amber, My-
 212 anmar)
- 213
- 214 5. Fore wing with cu-a vein postfurcal with M vein *Zophepyris* Engel et al.,
 215 2016 (Peñacerrada amber, Spain)
- 216 – Fore wing with cu-a vein aligned or antefurcal with M vein 6
 217
- 218 6. Fore wing with 2r-rs&Rs vein arising on distal half of pterostig-
 219 ma *Cretepyris* Ortega-Blanco & Engel,
 220 2013 (Peñacerrada amber, Spain)
- 221 – Fore wing with 2r-rs&Rs vein arising on basal half of pterostig-
 222 ma *Liztor* Ortega-Blanco & Engel,
 223 2013 (Peñacerrada amber, Spain)
- 224

225 Discussion

226 *Systematic placement and phylogenetic hypothesis*

227 Following the key to superfamilies proposed in Goulet and Huber (1993), our specimens
 228 key out in Chrysoidea because of their pronotum being more than half as long as their mesoscu-
 229 tum, and their metasomal terga 1 and 2 having very weak constriction at their junction dorsally and
 230 laterally or with no constriction at all. Following the key to Chrysoidea families in Goulet and
 231 Huber (1993), they key out in Bethyridae because of their antenna with 10 or 11 flagellomeres, the
 232 presence of wings, their profemora not enlarged or swollen, metasoma with six or seven exposed

233 terga, pronotum touching tegula, and prognathous heads. Additionally, our specimens could be con-
234 fused with Scolebythidae but differ from the latter in having a pronotal anterior flange rendering
235 propleura visible in dorsal aspect; the propleura closely situated so that the prosternum is not large,
236 exposed, and diamond-shaped; and the prothrochanter inserted ventrally on procoxa (Engel and Gri-
237 maldi, 2007). Our specimens also differ from †Chrysobythidae at least in lacking a shallow medial
238 line on head (vs. present in †Chrysobythidae); in having the clypeus more or less triangular (vs.
239 raised as a convex, somewhat squared lobe), the fore wing with a reduced number of closed cells
240 (vs. six enclosed cells) and the cells 1R1 and 2R1 open (Melo and Lucena, 2020).

241 Following the key to subfamily of Azevedo et al. (2018), *Protopyris* gen. nov. and *Bur-*
242 *mapyris* gen. nov. key out in †Lancepyrinae because of their developed wings; the fore wings with
243 Rs+M vein tubular and straight, at least as stub, with at most six closed cells; the clypeus not pro-
244 jecting backward onto frons; and the tarsal claws slightly curved. Following the key to genera of
245 †Lancepyrinae of Azevedo et al. (2018), *Protopyris* gen. nov. keys out near *Archaeopyris* Evans,
246 1973 because of the fore wing with Rs+M vein conspicuous and tubular, and 2R1 cell opened.
247 However, *Protopyris* gen. nov. differs from *Archaeopyris* in having an elongate fore wing, an elon-
248 gate pterostigma, 1M cell conspicuous and closed, 2Cu cell virtually delimited by spectral veins,
249 and M and cu-a veins aligned. Unfortunately, Evans (1973) did not provide extensive illustrations
250 as for the other species he described. Thus, it is difficult to make a full comparison with our speci-
251 men. Following the key to genera of †Lancepyrinae of Azevedo et al. (2018), *Burmapyris* gen. nov.
252 also keys out near *Lancepyris* because of the fore wing with Rs+M vein conspicuous and tubular
253 and 2R1 opened, but it differs from the latter in having a fore wing with a long and wide pterostig-
254 ma, a tubular Rs+M, 1M and 2Cu cells closed by conspicuous spectral veins, M and cu-a veins
255 aligned, and R1 poststigmatal present. Both new genera differ from each other in having the body
256 respectively depressed vs. weakly depressed, and different fore wing venations (see. Figs
257 1,2C,3,4D).

258 Rasnitsyn (1969, 1980), proposed a general trend among various hymenopteran lineages
259 consisting in the miniaturization, reduction of venation, enlargement of the pterostigma, and reduc-
260 tion of number of antennal flagellomeres. The reduction of wing venation has been recently investi-
261 gated in two bethylid subfamilies (viz. †Holopsenellinae and Scleroderminae) by Jouault et al.
262 (2020a), in accordance with Rasnitsyn's observations. Thereby, by comparing the age and the wing
263 venation of the new species described herein and previously described genera, it is possible to infer
264 some phylogenetic placement of *Protopyris* gen. nov. and *Burmapyris* gen. nov. (Fig. 5) and to pro-
265 pose a hypothetical phylogeny of the †Lancepyrinae. *Lancepyris* and *Protopyris* display a relatively
266 more complete and complex wing venation than other representatives, with numerous closed cells.
267 Thereby, it is likely that they diverged earlier than other lancepyrine wasps (Fig. 2C) (Azevedo et
268 al., 2018: fig 92D). This hypothesis is also supported by their age, in fact, *Lancepyris* is the oldest
269 record of the subfamily, which would be congruent with a relatively 'basal' position in the
270 †Lancepyrinae. Proposing relationships between the other taxa is more complicated since the dif-
271 ferences in venation are reduced. However, *Zophepyris* and *Burmapyris* share a tubular Rs+M vein
272 (Fig. 4D) (Azevedo et al., 2018: fig 92F), not recorded in other 'advanced' genera (viz. *Liztor*, *Ar-*
273 *chaepyris*, *Cretepyris*), suggesting that they could be closely related. *Liztor*, *Archaepyris*, and
274 *Cretepyris* all have closed R and 1Cu cells (Azevedo et al., 2018: figs 92A,B,C,E), but only *Liztor*
275 has a reduced 2r-rs&Rs vein while *Archaepyris* and *Cretepyris* display an elongated and tubular 2r-
276 rs&Rs vein. Thereby, we assume that these two genera could be closely related to each other than to
277 *Liztor*, which could be the sister group of (*Archaepyris* + *Cretepyris*) since the rest of their wing
278 venations is similar.

279

280 *Paleobiogeographic implications*

281 Correlation between paleogeography and fossil record often provided interesting hypotheses
282 on taxa antiquity. The Burma Terrane, where the amber was initially produced, displays an interest-
283 ing geological and paleobiogeographic history allowing consistent hypothesis on origin and antiqui-

284 ty of taxa composing the Burmese amber biota. In fact, during the Early Jurassic, the Terrane was
285 located near the Australian block in East Gondwana (van Hinsbergen et al., 2012; Seton et al., 2012)
286 and separated from East Laurasia (Asian region) by the Mesotethys Ocean. In addition, the extant
287 Pacific islands (Malaysia, Papua, Borneo, etc.) did not yet exist (Neall and Trewick, 2008), making
288 it almost impossible to transfer wildlife from East Laurasia to the East Gondwana (Australia and
289 Burmese Terranes). Following this period, the Burmese Terrane began to break away from the Aus-
290 tralian block to go north (as for the Indian block) to the Asian region between the Late Jurassic and
291 the Early Cretaceous (Heine et al., 2004; Heine and Müller, 2005). The Burma Terrane is supposed
292 to have been separated from the Gondwana after 125 Ma ago, but close to its margin ca. 120 Ma
293 ago (Metcalf, 1990, 1996; Scotese, 2014; Westerweel et al., 2019). Later, it was isolated geograph-
294 ically and occupied an island position in the Tethys Ocean between Asia and the Indian block dur-
295 ing the mid-Cretaceous (Westerweel et al., 2019) for more than 20 Ma (Heine et al., 2004; Seton et
296 al., 2012). It is very likely that the stem group of the Bethyloidea was already present on the Burma
297 Terrane before its complete separation from Gondwana, ca. 125-120 Ma ago, since we already have
298 fossil record of the family in Lebanese amber during the Barremian (Fig. 6) (Azevedo and Azar,
299 2012). The record of lancepyrine wasps in Lebanese and Spanish amber (in southern Laurasia), re-
300 spectively located in the central part of the southern Tethyan margin and the western Tethyan mar-
301 gin (Peris et al., 2016: fig. 1), suggests that the †Lancepyrinae were already diversified along the
302 western Tethys. However, the record of *Protopyris* gen. nov. and *Burmapyris* gen. nov. on the
303 Burma Terrane suggests that the †Lancepyrinae had also conquered the eastern Gondwana before
304 the break-up of the Burma Terrane. Ezcurra and Agnolin (2012: fig. 2) proposed the paleogeograph-
305 ic Eurogondwana model, according to which Gondwanan lineages could colonize Laurasia and
306 North America via an Apulia microplate from 145 to 99 Ma, prior to continental drift. This scenario
307 is in accordance with the presence of other †Lancepyrinae in Spain and Lebanon during the Early
308 Cretaceous (Azevedo and Azar, 2012; Ortega-Blanco and Engel, 2013; Engel et al., 2016). The rec-
309 ord of *Archaeopyris* in Taimyr amber (Late Cretaceous) (Evans, 1973) may also indicate that the

310 †Lancepyrinae already colonized the eastern Laurasia during the mid-Cretaceous. According to this
311 peculiar geological history, it is very likely that the †Lancepyrinae and, therefore the Bethylidae,
312 arose before the break-up of the Burma Terrane from South-East Gondwana, indicating at least an
313 Early Cretaceous (or even Late Jurassic) origin for the family.

314

315 **Conclusion**

316 Both new genera described herein are the first †Lancepyrinae described from Burmese amber and
317 *Protopyris myanmarensis* gen. et sp. nov. is the first Bethylidae described from the lower Albian
318 Hkamti amber. These discoveries highlight the underestimated diversity of bethylid wasps in Bur-
319 mese biota. The peculiar palaeogeographic history of the Burma Terrane provides evidence for the
320 antiquity of the †Lancepyrinae and, therefore, of the entire Bethylidae family. It is likely that the
321 Bethylidae arose during the earliest Cretaceous, before the Gondwana breakup, and maybe during
322 the Late Jurassic. It stands to reason that a morphological- and molecular-based phylogeny with
323 time divergence estimates has become a necessity for our understanding of this family.

324

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328

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424

425 **Figure captions.**

426

427 Figure 1. *Protopyris myanmarensis* sp. nov. Jouault & Nel, holotype IGR.BU-015. Photographs of
428 habitus. A: Dorsal view. B: Ventral view. Scale bars: 0.5 mm.

429

430 Figure 2. *Protopyris myanmarensis* sp. nov. Jouault & Nel, holotype IGR.BU-015. A: Mesosoma.
431 B: Head. C: Wing. D: Line drawing of fore wing with vein and cell nomenclature (cell names in
432 bold). Scale bars: 0.25 mm (A,B); 0.5 mm (C).

433

434 Figure 3. *Burmapyris azevedoi* sp. nov. Jouault, Perrichot & Nel, holotype IGR.BU-016. Photo-
435 graphs of habitus A: Right view. B: Left view. Scale bars: 0.5 mm.

436

437 Figure 4. *Burmapyris azevedoi* sp. nov. Jourd'ant, FENICHOI & NEI, holotype IGR.BU-010. A: Head
438 in left view. B: Mesosoma. C: Wings (with hamuli indicated by black arrows). D: Line drawing
439 of fore wing with vein and cell nomenclature (cell names in bold). Scale bars: 0.25 mm.

440

441 Figure 5. Hypothetical phylogeny of Lancepyrinae with affixed geological time scale.

442

443 Figure 6. Global paleogeographic reconstruction for the mid-Cretaceous (100 Ma) period, showing
444 distribution of Lancepyrinae; modified from Global Paleogeography and Tectonics in Deep Time
445 © 2016 Colorado Plateau Geosystems Inc., localities of amber-producing forests after Wester-
446 weel et al. (2019).

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.

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