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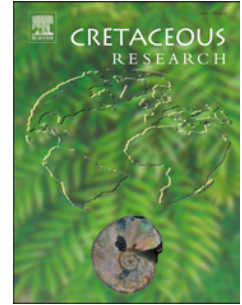
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CRediT authorship contribution statement

Corentin Jouault: Data curation, Formal analysis, Investigation, Writing - Original draft, Writing - Review & Editing. **Alexandr P. Rasnitsyn:** Conceptualization, Formal analysis, Resources, Investigation, Validation, Writing - Original draft. **Vincent Perrichot:** Conceptualization, Resources, Data curation, Investigation, Formal analysis, Validation, Writing - Original draft, Writing – Review & Editing, Supervision.

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1 *Ohlhoffiidae*, a new Cretaceous family of basal parasitic wasps

2 (*Hymenoptera: Stephanoidea*)

3
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11
12 **ABSTRACT** 0000-0002-7973-0430

13
14 A new family of stephanoid wasps is established based on Cretaceous amber inclusions and rock
15 imprints. *Ohlhoffiidae* fam. nov. comprises four species in three genera: *Ohlhoffia robusta* gen. et
16 sp. nov., and *Myanmephialtites bashkuevi* gen. et sp. nov., which are newly described and figured
17 from mid-Cretaceous amber of northern Myanmar; and *Cretephialtites pedrerae* Rasnitsyn &
18 Ansoerge, 2000, and *C.(?) hispanicus* (Rasnitsyn & Martínez-Delclòs, 2000) comb. nov., transferred
19 here from *Karataus hispanicus*, both from the Barremian of Spain. A key to the genera of the family
20 is proposed, and we also discuss the shifting proportion of non-aculeate wasps between the Early
21 Cretaceous and Cenozoic.

22
23 **Keywords.** Apocrita, *Ohlhoffiidae*, Kachin amber, Montsec, Cenomanian, Barremian

1. Introduction

The Stephanoidea is considered an old lineage of parasitoid wasps that previously diverged from the parasitoid Euhymenoptera (Grimaldi and Engel, 2005). In recent analyses of the higher-level hymenopteran relationships, the sole living family Stephanidae has been retrieved as the sister-group to the remaining Apocrita (Sharkey et al., 2012; Mao et al., 2015) or closer to the Evanioidea or Trigonaloidea (Peters et al., 2017; Tang et al., 2019). But little is known on the evolutionary history of Stephanidae, particularly its past distribution and diversity, since the family has a scant fossil record. Indeed, while there are about 350 extant species (Aguilar et al., 2013) and the earliest occurrences extend back to the mid-Cretaceous (ca. 100 Ma), only twelve extinct species of Stephanidae are currently recognized, five of which from the Cretaceous (Engel and Grimaldi, 2004, Engel et al., 2013; Engel and Huang, 2017; Li et al., 2017; Engel, 2019). The geological record provides a better glimpse into the remaining Stephanoidea, hitherto comprising three extinct-only families: the Ephialtitidae, known from 89 species ranging from early Jurassic to mid-Cretaceous of China, India, Kazakhstan, Kyrgyzstan, Mongolia, Russia, Spain, Germany, and Brazil (Li et al., 2020; Zhang, 2020 and references therein); the Aptenoperissidae, with eight species in mid-Cretaceous Burmese amber (Rasnitsyn et al., 2017; Rasnitsyn and Öhm-Kühnle, 2018; Zhang et al., 2018a, 2018d); and the Myanmarinidae, with four species similarly in mid-Cretaceous Burmese amber only (Li et al., 2018; Zhang et al., 2018b). Stephanoidea are thus mostly extinct except for the relictual, nominotypical family Stephanidae, with their generic diversity peak from the Jurassic to mid-Cretaceous.

Here we propose a fifth family, Ohlhoffiidae fam. nov., based on two specimens that are newly described from Albian–Cenomanian Burmese amber, in which we also tentatively place the genus *Cretephialtites* Rasnitsyn & Ansoerge, 2000, known from Lower Cretaceous rock imprints.

2. Material and methods

The two amber specimens described herein originate from mines of the Noiye Bum Hill in Hukawng Valley, Kachin State, northern Myanmar (see Grimaldi and Ross, 2017: fig. 2 for a

51 detailed map). After more than a century of uncertainty regarding the age of this amber, there
52 seems to be a recent consensus toward a latest Albian–earliest Cenomanian age, based on
53 radiometric studies of volcanic clasts from within the amber-bearing stratum (dated to 98.79 ± 0.62
54 Ma; Shi et al., 2012), the palynomorphs and ammonoid content of this amber bed (Cruickshank and
55 Ko, 2003), and ammonoid and bivalve inclusions in amber (Smith and Ross, 2018; Yu et al., 2019).

56 Specimen MB.I.12345 is complete and exquisitely preserved in a piece of clear yellow amber. It
57 was spotted by one of us (VP) among the amber collection of Rainer Ohlhoff (Saarbrücken,
58 Germany) who kindly provided it for study; it is now housed in the amber collection of the Museum
59 für Naturkunde, Berlin. It was examined and photographed using a Zeiss Axio Zoom.V16
60 stereomicroscope and Axiocam 512 digital camera with Zen software allowing for measurements
61 and digital photography. All images are digitally stacked photomicrographic composites of several
62 individual focal planes, which were processed using HeliconFocus software in B mode. The figures
63 were composed with Adobe CC 2019 softwares (Illustrator and Photoshop).

64 Specimen PIN no. 5608/55 is nearly complete, missing only the apex of fore wings, but is
65 somewhat distorted and altered by preservation, and surrounded by organic debris; it is preserved
66 in a piece of clear yellow amber that was donated to the Paleontological Institute, Russian
67 Academy of Sciences, Moscow (PIN), by Alexei Bashkuev. The piece was trimmed and polished by
68 Dr. Dmitry D. Vorontsov (Moscow) who also photographed the specimen. It was studied using a
69 Leica M165C stereomicroscope, and imaged using a compound microscope Nikon E-800 with dry
70 (4×) equipped with an Olympus OM-D E-M10II camera. A combination of brightfield and incident
71 light was used, and stacks of images were processed with Helicon Focus software in B mode. The
72 figures were composed with Adobe Photoshop CS2 and CorelDRAW 2019.

73 The morphological terminology used in description generally follows that of Huber and Sharkey
74 (1993), except van Achterberg (1993) or Quicke (2015) for the wing cell nomenclature, and Engel
75 et al. (2013) for the nomenclature of coronal teeth. This published work and the nomenclatural acts
76 it contains have been registered in ZooBank (<http://www.zoobank.org/>, last access: 18 June 2020),

77 with the following LSID (reference): [urn:lsid:zoobank.org:pub:51627020-1E4D-4D1D-B0D0-](http://urn:lsid:zoobank.org:pub:51627020-1E4D-4D1D-B0D0-97F960379A32)
78 97F960379A32.

79

80

81 **3. Systematic paleontology**

82 *Order Hymenoptera Linnaeus, 1958*

83 *Superfamily Stephanoidea Leach, 1815*

84

85 *Diagnosis. Fore wing with vein 1-RS short and proclivous, vertical, or reclivous (never long and*
86 *proclivous), and vein 2A, when present, never with complete sub-basal loop. In lateral view,*
87 *propodeum lacking a posterior surface or declivity, instead with a single, weakly sloping surface*
88 *not bent downward toward hind coxa, nor enclosed widely below metasomal articulatory orifice.*

89

90 *Included families. Stephanidae (mid-Cretaceous to Recent), Ephialtitidae (late Early Jurassic to*
91 *mid-Cretaceous), Ohlhoffiidae fam. nov. (Early to mid-Cretaceous), Aptenoperissidae and*
92 *Myanmarinidae (mid-Cretaceous only).*

93 *Comment. The superfamily Stephanoidea differs from the more basal Orussoidea (including*
94 *Karatavitidae, Orussidae and Paroryssidae) in the fore wing lacking the sub-basal loop of vein 2A,*
95 *which is indicative of the lost apparatus of wing fixation at resting position, as is retained in most*
96 *Orussoidea and more basal Hymenoptera. The Stephanoidea differs from higher Apocrita in the*
97 *propodeum that is not bent downward toward hind coxae (as in non-evanioid higher Apocrita) nor*
98 *widely sclerotized ventrally of the metasomal attachment (unlike Evanioidea).*

99

100 *Family **Ohlhoffiidae** fam. nov.*

101 *urn:lsid:zoobank.org:act:658F42E2-2BA7-4EAC-B7F1-6DC3A981C89A*

102 *Type genus: Ohlhoffia gen. nov.*

103 *Diagnosis. Males and females July winged. Head with series of teeth or tubercles arranged in*
104 *transverse rows on frons and vertex. Antenna polymerous, with more than 20 segments, not*
105 *geniculate. Mesosoma not much elongate nor strictly cylindrical, with standard sclerotization (no*
106 *fused carapace); mesonotum with median, longitudinal sulcus and notauli. Fore wing with vein 1-*
107 *Rs reclivous, 2m-cu entering second submarginal cell, and cu-a not distinctly postfurcal. Hind wing*
108 *with marginal cell widely open, vein 2-M+Cu long. Legs, including metacoxae and all femora, long*
109 *and slender; tibiae not inflated (without hypertrophied vibration detector inside), protibia with one*
110 *apical spur. Basal metasomal segments I and II transformed into petiole and postpetiole,*
111 *respectively; ovipositor short.*

112
113 *Included genera. Type genus Ohlhoffia gen. nov., Myanmephialtites gen. nov., and Cretephialtites*
114 *Rasnitsyn & Ansorge, 2000.*

115 *Comment. The new family is placed in Stephanoidea based on the following combination of*
116 *characters unique of the latter: (i) propodeum not bent downward to hind coxae (apparently*
117 *without free posterior surface) and not widely sclerotized below metasomal base, unlike in*
118 *remaining Apocrita with metasomal articulatory orifice small due to propodeum either bent*
119 *downward to hind coxae (in majority of taxa), or posterior propodeal surface widely sclerotized*
120 *below metasomal base (in Evanioidea); (ii) fore wing vein 2A, if present, lacking complete sub-*
121 *basal loop indicative of wing coupling apparatus (metanotal cenchri and rough area on lower wing*
122 *surface within 2A loop that fits to fix on cenchrus): the coupling mechanism is characteristic of*
123 *lower Hymenoptera including Orussoidea (Orussidae, Paroryssidae and Karatavitidae; see*
124 *Rasnitsyn and Zhang, 2010).*

125 *Ohlhoffiidae is mostly similar to Stephanidae in the presence of teeth or tubercles on the head, a*
126 *nearly complete wing venation, and the tibiae not inflated. But it differs notably from Stephanidae*
127 *and all other Stephanoidea by its two-segmented metasomal petiole. Additionally, Ohlhoffiidae*
128 *differs from Stephanidae and Ephialtitidae: Ephialtitinae by its short ovipositor, and from*
129 *Ephialtitidae: Symphyopterinae by its fore wing crossvein cu-a not far postfurcal. It differs from*

130 *Aptenoperissidae* by its antennae not geniculate, the fore tibia bearing a single spur, the female
131 winged and with a standard mesosomal sclerotization (*aptenoperissid* females are wingless and
132 with a mesosomal carapace), and the male with fore wing vein cu-a interstitial or antefurcal (cu-a
133 well postfurcal in *aptenoperissid* males). And it differs from *Myanmarinidae* by a more complete
134 wing venation (deeply reduced and modified in *Myanmarinidae*), polymerous antennae (11-14
135 segments in *Myanmarinidae*), a standard mesosomal sclerotization (elongate, cylindrical
136 mesosoma with smooth and desclerotized dorsum in *Myanmarinidae*, particularly in female), and a
137 short ovipositor.

138
139 Genus ***Ohlhoffia*** gen. nov.
140 urn:lsid:zoobank.org:act:7A7ADDB7-11F6-4786-A4D1-5E9FBDE0B366
141 Type species: *Ohlhoffia robusta* sp. nov.

142
143 *Etymology.* The generic name is a patronym honoring Rainer Ohlhoff who provided the type
144 specimen described here. The name is feminine.

145 *Diagnosis.* Stature stout, with body and appendages long and robust. Frons and vertex with 10-12
146 transverse ridges, 6 of which surmounted by series of distinct teeth or tubercles. Mandibles small,
147 tridentate. Fore wing with costal space much narrow, pterostigma narrow and elongate, marginal
148 cell long and narrow, third submarginal cell 3× as short as second submarginal cell, vein 2m-cu
149 well basad 2r-m. Hind wing vein 2A absent. Petiolar segments hardly longer than high. Tibial spurs
150 relatively short.

151
152 ***Ohlhoffia robusta*** sp. nov.
153 urn:lsid:zoobank.org:act:8E78F44A-D299-4E61-8B0C-8BAE91B17F59

154 (Figs. 1–3)
155 *Holotype.* MB.I.12345, a complete female exquisitely preserved in a small piece of polished,
156 translucent, yellow amber; housed in the Museum für Naturkunde Berlin, Germany.

157 *Horizon and locality. Mia-Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma), in amber*
158 *from the Hukawng Valley, Kachin State, Myanmar.*

159 *Etymology. The specific epithet is taken from the Latin robustus, meaning strong, in reference to the*
160 *robust appearance of this morphotype.*

161 *Diagnosis. As for the genus.*

162 *Description. Total body length 6.30 mm. Integument apparently thick. Head globose, 0.98 mm high;*
163 *compound eye large, 0.74 mm high, 0.51 mm wide, occupying much of lateral surface of the head;*
164 *gena apparently coriaceous, rounded (Figs. 2B, 2E, 3B). In lateral view, vertex strongly rounded*
165 *above compound eye, with distinct ocelli, ocellar diameter about as large as pedicel width. Frons*
166 *with median-anterior tubercle (tbA) followed by slightly larger, second median-anterior tubercle*
167 *(tbB); and row of two large tubercles (tbC-tbC') located right in front and at either side of median*
168 *ocellus. Vertex with one row of two large tubercles (tbD-D') located just behind median ocellus and*
169 *in front of lateral ocelli, at about the same position and size as tbC-C'; one single, large, median*
170 *tubercle (tbE) located between lateral ocelli; and one single, median tubercle (tbF) smaller than*
171 *tbE and located posterior to lateral ocelli (Figs. 2B, 2D, 3B). Each row or tubercle extending*
172 *laterally into transverse ridges reaching margin of compound eyes; additionally, 1–2 similar ridges*
173 *between each row of tubercles. Occiput slightly concave and roughened; malar space slightly*
174 *longer than first flagellomere, 0.24 mm long, with malar sulcus. Antenna relatively short (3.83 mm*
175 *long), filiform, with 21 flagellomeres gradually slightly decreasing in width toward apex; scape*
176 *robust, pedicel short (0.12mm), longer than wide, and slightly narrower than scape; individual*
177 *flagellomeres longer than wide, each about 0.06 mm wide; length of first flagellomere 0.16 mm,*
178 *second 0.22 mm; flagellomeres decreasing in length after antennal midlength; mandibles short,*
179 *stout, projecting forward, the outer surface strongly convex and with apical half densely covered by*
180 *long, fine, decumbent setae; masticatory margin of mandible with 3 blunt teeth, the apical tooth*
181 *large, the others progressively decreasing in size toward base. Maxillary palps with four long*
182 *palpomeres, labial palps much shorter, with apical palpomere the only visible segment, which*
183 *barely surpasses the first maxillary palpomere (Figs. 2E, 3B).*

184 *mesosoma* (Figs. 2A, 3A) with only few pronounced sculpturing, densely covered by minute
185 setae; mesosomal length 2 mm, maximal height 1.10 mm. Pronotum slightly elongate into a neck,
186 reaching tegula, pronotal fold reduced; anterior declivity of pronotum smooth; neck without
187 distinctive sculpture; dorsal mesonotal area convex, with weak median longitudinal sulcus not
188 reaching to posterior mesonotal margin, and distinct notauli converging but not touching
189 posteriorly; mesoscutellum short; mesopleuron with a depression for reception of leg delimited
190 above with furrow running from mesopleural pit (entrance of mesopleural apodeme) to small
191 triangular external part of prepectus; metanotum and mesoscutellum subequal in length, slightly
192 costulate; metanotal trough (metapostnotum) foveate; metapleuron fused immovably with
193 propodeum, posteriorly with transverse, foveate groove; propodeum flat to slightly convex,
194 anteriorly with a transverse row of shallow foveae, with long, slit-like spiracle.

195 Fore wing (Fig. 3C) 4.30 mm long, with ten cells (incl. costal one) entirely enclosed by tubular
196 veins; C and R adjacent for 2/3 of their length, then slightly diverging to form a narrow costal cell
197 which is mostly distinct above prestigma; pterostigma elongate, more than 8× as long as wide, only
198 feebly swollen medially; 1-Rs reclivous, 1.5× as long as 1-M, nearly straight, aligned with slightly
199 arched 1-M; 2r-rs proclivous, about as long as RS+M; fork of 2-RS and 2-M only slightly anterior
200 to 1m-cu (2-M very short); 2-Rs distinctly arched basally, with no trace of 1r-rs; 2r-m oblique,
201 slightly sinuate, meeting RS slightly behind 2r-rs, and well behind 2m-cu, enclosing long and
202 almost triangular submarginal cell 2; 3r-m sinuate, subparallel to 2r-m, delimitating short and
203 skewed submarginal cell 3; 5-RS almost half length of marginal cell, meeting R1 at acute angle
204 near wing apex; 1m-cu subequal in length and subparallel to 1-M (discal cell subparallel-sided,
205 more than twice as long as high); 2r-m, 3r-m, and 2m-cu each with two bullae; cu-a only slightly
206 anterior to fork of 1-M and 1-Cu, oblique, longer than 1-M; 2-Cu longer than 1m-cu; A straight,
207 prolonged apically by claval furrow which forms a spurious vein margined with incrassate
208 membrane. Hind wing (Fig 3C) 2.70 mm long, with basal and sub-basal cells entirely enclosed by
209 tubular veins; basal cell long, 1.5× as long as sub-basal one; neither longitudinal vein reaching
210 wing margin as a tubular vein; 1-RS and 1-M long, subequal in length, more than twice as long as

211 subvertical *r-m*, *1-M* distinctly arched basally, *2-M+Cu* only slightly shorter than *1-M*, longer than
212 *cu-a*; fork of *1-M* and *1-Cu* basal to fork of *RS* and *R1*; *2A* present, jugal lobe only incipiently
213 delimited; anterior margin of wing with 8 distal hamuli.

214 Legs elongate, without distinct sculpturing (Figs. 1, 3A); tibial spur formula 1-2-2; protibial
215 spur bifid at apex, shorter than meso and meta-tibial spurs that are subequal in length, straight and
216 simple; metacoxa distinctly larger than pro- and meso-coxae, its outer margin expanded apically by
217 a lateral flange covering articulation of metatrochanter; metafemur moderately swollen medially
218 (0.30 mm at maximum width) and nearly as long as metatibia (1.95 vs 2.00 mm); tarsi
219 pentamerous; metabasitarsus (0.91 mm) as long as remaining ones combined, second metatarsus
220 0.43 mm long; fourth metatarsomere shortest; pretarsal claws with small preapical tooth.

221 *Metasoma bipetiolate* (Figs. 1, 2A, 2C, 3A), both petiolar segments cushion-shaped, short and
222 thick, hardly as long as high (0.50 and 0.53 mm long, respectively), without tergosternal fusion and
223 with deep, foveate pretergite; remaining metasoma ('gaster') oval, short, only twice as long as
224 petiolar segments combined; first and second gastral tergites largest of metasomal tergites,
225 following gastral tergites gradually decreasing in size toward apex. Ovipositor short, third valvula
226 0.40 mm long, sheaths 0.30 mm long; sheaths narrow, tapering apically to broadly rounded apex,
227 covered with short subdecumbent setae. Gastral integument without pronounced sculpturing,
228 covered with scattered, short, subdecumbent setae.

229

230 ***Myanmephialtites* gen. nov.**

231 *urn:lsid:zoobank.org:act:53BB71B4-1736-4FC4-8E73-CDD6120F259F*

232 *Type species: Myanmephialtites bashkuevi* sp. nov.

233 *Etymology.* The genus name is a combination of a corrupted name of the country of origin
234 (Myanmar), and *Ephialtites*, type genus of the related family *Ephialtitidae*.

235 *Diagnosis.* Stature relatively slender, with body and appendages long and narrow; antennae 28 or
236 29-segmented, with first flagellomere elongate. Hind wing vein *2A* present. Posterior propodeal

237 foramen much wider than metasomal base. Metatibial spurs long. Femoral segments more than
238 twice as long as high.

239

240 *Myanmephialtites bashkuevi* sp. nov.

241 [urn:lsid:zoobank.org:act:A1211E5A-7FBA-4EB4-83D9-35F6B16B4DD9](https://zoobank.org/urn:lsid:zoobank.org:act:A1211E5A-7FBA-4EB4-83D9-35F6B16B4DD9)

242 (Figs. 4–5)

243

244 *Holotype*. PIN no. 5608/55, sex unknown; specimen approximating the amber surface, with right
245 half of head and apical portion of fore wings missing, destroyed during trimming of the amber
246 piece; housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
247 (PIN).

248 *Horizon and locality*. Upper Cretaceous, upper Albian–lower Cenomanian (ca. 99 Ma); in amber
249 from Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar.

250 *Etymology*. The specific epithet is a patronym honoring Mr. Alexei Bashkuev who donated the fossil
251 to the PIN collection.

252 *Diagnosis*. As for the genus, by monotypy.

253 *Description*. Body length 5.2 mm, wing length as preserved 3.2 mm, estimated total wing length 4.7
254 mm. Preserved fragment of head with 5 visible teeth on frons / vertex; mandibles small, elongate,
255 symmetrically pointed apical as preserved (dentition obliterate due to integument degradation).

256 *Antenna* elongate, with 28–29 segments (apparently different in two antennae), pedicel slightly
257 thinner than scape and thicker than flagellum; flagellar segments subequal in width, all more than
258 twice as long as broad, gradually slightly decreasing in length toward apex, except
259 disproportionally long first flagellomere, subapical and apical segments shortest.

260 *Mesosomal structures* poorly visible by preservation except propodeum which is, in lateral view,
261 only slightly convex dorsally and without posterior face; instead, posterior propodeum entirely
262 open to form a wide articulatory foramen which is much wider than metasomal base, as is

263 described for some Ephialtinae (see Koshitsyn and Zhang, 2010, Li et al., 2013), dorsal posterior
264 propodeal margin extending backward above metasomal base.

265 Fore wing (Fig. 5B), as preserved, much similar to that of *Ohlhoffia robusta*; costal cell much
266 narrow, both veins C and R incrassate distally; pterostigma not much elongate, with 2r-rs
267 originating near its midlength; 1-RS distant from pterostigma for less than its length, subequal to 1-
268 M in length, angular at junction with 1-M; RS+M parallel to 1-Cu, almost as long as pterostigma;
269 2-RS long, distinctly arched basally, with no trace of 1r-rs; 2r-m meeting RS slightly distal of 2r-rs,
270 oblique, delimiting long, low, nearly triangular submarginal cell 2; 1m-cu not parallel to 1-M,
271 distinctly shorter than 2-Cu; 2m-cu joining M well before 2r-m; cu-a interstitial; first sub-discal cell
272 higher than discal one. Hind wing (Fig. 5B) with 1-RS and 1-M subequal in length, much longer
273 than subvertical r-m, both distinctly arched basally; 2-M+Cu longer than cu-a and about 0.75× as
274 long as 1-M; RS, M, Cu and A with distinct but short abscissae not reaching wing margin; 2A
275 distinct, much approximated to hind margin of wing; jugal lobe apparently not delimited; anterior
276 margin of wing with seven basal hamuli, distal hamuli not visible.

277 Legs long and thin, with particularly long trochanters (and probably with trochantelli, although
278 these are not reliably identifiable), basitarsi, and hind tibial spurs; basitarsus subequal to
279 remaining tarsomeres combined, fourth tarsomere elongate, fifth one subequal to second, third and
280 fourth combined (precise proportions unknown because of deformation); pretarsal claws small,
281 with a small preapical tooth.

282 Metasoma. Petiolar segments elongate, each more than twice as long as high, with first segment
283 slightly longer than second, and second segment barrel-shaped in lateral view. Remaining
284 mesosoma (gaster) apparently distorted, segmentation obscured by preservation; as preserved,
285 gaster roughly as long as petiolar segments combined, less than 3× as high as petiolar segments,
286 slightly higher in its apical half; genitalia not preserved.

287

288 Comment. *Myanmephialtites* gen. nov. primarily differs from *Ohlhoffia* gen. nov. in its slender
289 stature, particularly the more elongate petiolar segments, and in the antennae more segmented, the

290 hind wing vein 2A present, and the long hind tibial spurs. Both fore wings of *Myanmephialtites* gen.
291 nov. and *Ohlhoffia* gen. nov. are much similar.

292

293 ***Cretephialtites* Rasnitsyn & Ansorge, 2000**

294 *Type species: Cretephialtites pedrerae* Rasnitsyn & Ansorge, 2000: 62, figs. 3, 4 (isolated fore wing
295 only).

296

297 *Diagnosis. Fore wing as in Ohlhoffia* gen. nov. and *Myanmephialtites* gen. nov., except for the
298 costal cell which is distinctly wider. Additionally, the veins 2r-m, 3r-m, and 2m-cu lack the bullae
299 that are present in *Ohlhoffia*. Metacoxa and metafemur (known in *C. hispanicus* only) shorter and
300 thicker than in *Ohlhoffia* and *Myanmephialtites*.

301

302 *Included species. Type species, and possibly C.(?) hispanicus* (Rasnitsyn & Martínez-Delclòs,
303 2000) (= *Karataus hispanicus* Rasnitsyn & Martínez-Delclòs, 2000) (see below).

304

305 *Comment. Cretephialtites* was described based solely on an isolated fore wing from the Barremian
306 of Spain (Rasnitsyn and Ansorge, 2000) which is nearly identical to those of *Ohlhoffia* and
307 *Myanmephialtites*, except for the wider costal cell. Based on the current knowledge on stephanoid
308 wasps, this difference is considered sufficient to distinguish the fossils as separate genera.

309 Rasnitsyn and Ansorge (2000) also guessed that *Karataus hispanicus*, and possibly *Karataus*
310 *kourios* (misspelled therein as *kourius*) Sharkey, in Darling and Sharkey (1990), may belong in
311 *Cretephialtites* as well. This could be correct for *K. hispanicus*, except that it was restored with the
312 costal cell wide although the preservation of the fore wing is poor and this inference would need
313 confirmation. Otherwise, the general appearance of the fossil agrees well with that of *Ohlhoffia*
314 gen. nov. (stature robust, petiolar segments short and thick, hind trochanters long), though with a
315 hind wing vein 1-M more strongly arched. This would make possible to assign *K. hispanicus* to a

316 genus of its own, but the incomplete preservation state of the fossil tainer suggests its tentative
 317 attribution to *Cretephialtites*, as *C.(?) hispanicus* comb. nov., until new information appears.

318 *Karataus kourios* differs more profoundly from *Ohlhoffia*, and by extension the *Ohlhoffiidae*, by
 319 its ovipositor much longer and, based on additional material found since its original description
 320 (Grimaldi and Engel, 2005: fig. 11.11; Osten, 2007: fig. 11.75d, pl. 15j, 15k), by the absence of
 321 metasomal petiolar segments. *Karataus kourios* was attributed to a particular genus *Cratophialtites*
 322 *Rasnitsyn, 1999* (again misspelled as *C. koiurus*) and in our opinion would be left there in the
 323 family *Ephialtitidae*.

324

325 *Key to genera of Ohlhoffiidae:*

326

- 327 1. Fore wing with costal cell wide *Cretephialtites* Rasnitsyn & Ansorge, 2000
 328 – Fore wing with costal cell long and narrow 2
 329 2. Stature stout; tibial spurs short; first and second metasomal (petiolar) segments compact, barely
 330 longer than high, cushion-shaped; hind wing vein 2A absent *Ohlhoffia* gen.
 331 nov.
 332 – Stature slim; tibial spurs long; petiolar segments elongate, more than twice as long as high, barrel-
 333 shaped; hind wing vein 2A present *Myanmephialtites* gen. nov.

334

335 **4. Discussion**

336 *Most Stephanoidea and Orussidae share the coronal teeth or tubercles on the vertex, a*
 337 *symplesiomorphy which may be considered as a convergent response to a same constraint of*
 338 *leaving the galleries dug by their hosts. However, it seems that stephanoid wasps possess one*
 339 *single, median, anterior tooth while this character is lacking in Orussidae. The latter also possess a*
 340 *plesiomorphic wing venation (Rasnitsyn, 1978) and a “Symphyta-like” habitus which allows an*
 341 *clear distinction from the Apocrita. The specimens described above display a unique combination*
 342 *of characters that are otherwise found independently in Stephanidae or Ephialtitidae, but cannot be*

343 assigned to any of these families without altering their diagnosis. In our opinion, these taxa belong
344 to a sister family of Stephanidae. The perfect preservation of *Ohlhoffia robusta* gen. et sp. nov and
345 the wing venation of *Myanmephialtites bashkuevi* gen. et sp. nov. allow the diagnosis of typical
346 morphological characters only known from these specimens and distinctive enough to warrant the
347 description of the fossils as a family of their own. The Ohlhoffiidae differ from other stephanoid
348 families (*Aptenoperissidae*, *Ephialtitidae*, *Myanmarinidae*, and *Stephanidae*) primarily by a
349 plesiomorphic wing venation, unmodified legs (plesiomorphic character), a bipetiolate metasoma
350 (synapomorphy), and a different organization of the coronal teeth (difficult to categorize for the
351 moment).

352 We propose to place *C. pedrerae* among the new family Ohlhoffiidae based on its strikingly
353 similar wing venation, which is distinguishable from *Myanmephialtites* and *Ohlhoffia* only by its
354 broader costal cell, broader cell 3_{rm}, and the shorter distance separating the veins 2_{r-m} and 2_{m-cu}. However, *C. pedrerae* is known from an isolated fore wing (Rasnitsyn and Ansorge, 2000) so
355 the comparison remains limited, as the wing venation of *Cratephialtites kourios* (*Ephialtitidae*) is
356 also rather close. The discovery of a complete *C. pedrerae* specimen would strengthen the
357 membership of this taxa in Ohlhoffiidae and would enhance the discussion about the character
358 states as well as the paleobiogeographical implications.

360 An island endemism has been recently suggested for the Burmese amber biota (Zhang et al.,
361 2018c; Westerweel et al., 2019), providing elements for a better understanding of this highly
362 peculiar fauna. Insularity generally favors speciation and therefore the establishment of a unique
363 fauna. These assumptions are consistent with the unique stephanoid diversity observed in Burmese
364 amber and its possible affinities with the Gondwanan fauna. The Cretaceous Stephanoidea were
365 hitherto represented by 26 species, including few amber taxa (Fossilworks, available at
366 <http://fossilworks.org>, accessed 16 April 2020). Unlike the well represented ichneumonoids which
367 show a distinct increase of diversity since the Early Cretaceous, the stephanoid wasps were
368 apparently more diverse during the Cretaceous than today (Fig. 6). The group comprised only 4%
369 of the non-aculeate wasps recorded in the Early Cretaceous, reached its maximal diversity (ca.

370 1170) during the Late Cretaceous, then dropped to less than 170 today. A similar trend is observed
371 in Evanioidea and Proctotrupoidea. In contrast, ichneumonoids comprised 24% of non-aculeate
372 wasps in the Early Cretaceous, 70% during the Oligocene, and 55% today. This fossil record may
373 be biased, for example a bias over rock-imprint preservation in the Oligocene, as this period is
374 largely devoid of fossiliferous amber deposits.

375 *But this may reflect more or less accurate trends in the diversity of these parasitoid wasps, due*
376 *to their subservient life condition in peculiar habitats, correlated with the extinction or*
377 *diversification of their host. The diversity of both ichneumonoids and stephanoids in Burmese*
378 *amber is yet underestimated, but systematic descriptions of ichneumonoids have probably been*
379 *more neglected owing to the often difficult-to-place fossil taxa between extant or even extinct*
380 *subfamilies (Quicke, 2015).*

381

382 **5. Concluding remarks**

383 *The bi-segmented petiole, mobile gaster, long antennae and comparatively large, movable head*
384 *of Ohlhoffiidae are suggestive of insects parasitizing cryptic preys. This supposed behavior agrees*
385 *with the proposed taxonomic position of Ohlhoffiidae in Stephanoidea. Extant stephanid wasps are*
386 *known to develop at the expense of xylophagous beetles (van Achterberg, 2002), however using a*
387 *long ovipositor to reach the hosts deep in wood galleries. In contrast, the short ovipositor displayed*
388 *by Ohlhoffia may suggest they were parasitic on non-xylophagous insects.*

389 *The description of Ohlhoffiidae fam. nov. adds to the uniqueness of the hymenopteran Burmese*
390 *amber fauna. In Ross' (2020) latest inventory, 1173 hexapod species are listed in no less than 412*
391 *families. Among these, the order Hymenoptera comprises a significant diversity of 189 species in 53*
392 *families, encompassing 16 percent of the total hexapod diversity in Burmese amber. It is certain*
393 *that undescribed, potentially endemic taxa are yet to be discovered from this extraordinary fossil*
394 *deposit.*

395

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403 amber collection of the Museum für Naturkunde Berlin. Finally, we sincerely appreciate the input
404 from the editor and anonymous reviewers in improving our manuscript.

405

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532

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534 **Figures captions**

535

536 **Fig. 1.** *Photomicrograph of Ohlhoffia robusta gen. et sp. nov., female holotype MB.I.12345, from*
 537 *mid-Cretaceous Burmese amber. Habitus in left lateral view. Scale bar: 2 mm.*

538

539 **Fig. 2.** *Photomicrographs of Ohlhoffia robusta gen. et sp. nov., female holotype MB.I.12345, from*
 540 *mid-Cretaceous Burmese amber. A, Mesosoma and petiolar segments in left lateral view. B, Head*
 541 *in left lateral view. C, Metasoma in left lateral view. D, Detail of head dorsum in right lateral view.*
 542 *E, Head in frontal view. Scale bars: 0.5 mm (C), 0.2 mm (A, B, E), 0.1 mm (D).*

543

544 **Fig. 3.** *Line drawings of Ohlhoffia robusta gen. et sp. nov., female holotype MB.I.12345, from mid-*
 545 *Cretaceous Burmese amber. A, Habitus in left lateral view. B, Head in lateral right view. C, Wings*
 546 *with indication of the vein nomenclature used herein. Scale bars: 2 mm (A), 0.5 mm (C), 0.2 mm*
 547 *(B).*

548

549 **Fig. 4.** *Photomicrograph of Myanmephialtites bashkuevi gen. et sp. nov., holotype PIN no. 5608/55,*
 550 *from mid-Cretaceous Burmese amber. Habitus in right lateral view. Scale bar: 1 mm.*

551

552 **Fig. 5.** *Myanmephialtites bashkuevi gen. et sp. nov., holotype PIN no. 5608/55, from mid-*
 553 *Cretaceous Burmese amber. Interpretation of general appearance and wing venation.*
 554 *Abbreviations: ct, circumocellar teeth; cx₁, cx₂, cx₃, pro-, meso- and metacoxa; f₁, f₂, f₃, pro-, meso-*
 555 *and metafemur; ha – hamuli; md, mandible; N₁, N₂, pro- and mesonotum; ppd, propodeum; scl₁,*
 556 *scl₂, meso- and metascutellum; sp, tibial spurs; t₁, t₂, metasomal petiolar tergites; ta₁, ta₂, ta₃, pro-,*
 557 *meso- and metatarsus; ti₁, ti₂, ti₃, pro-, meso- and metatibia. Scale bar: 1 mm.*

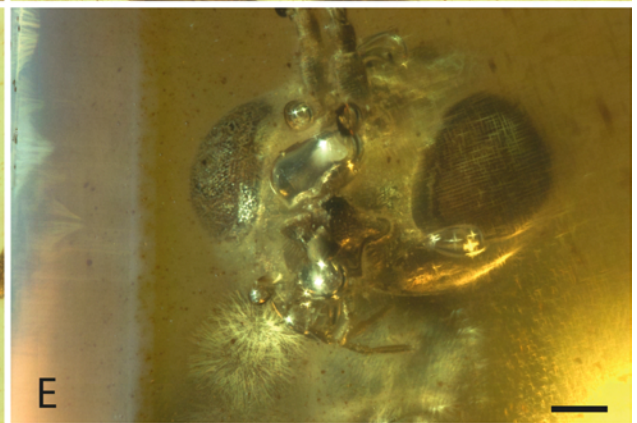
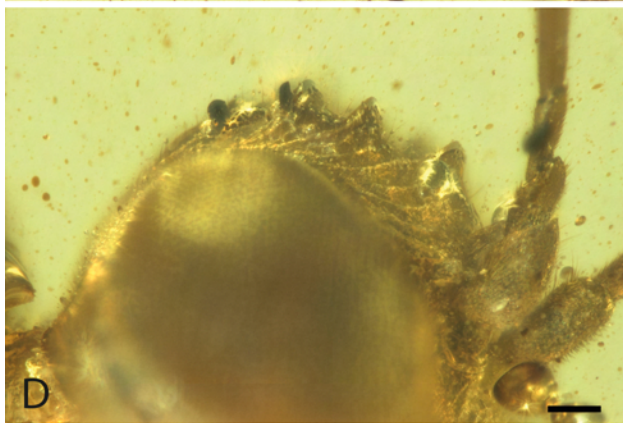
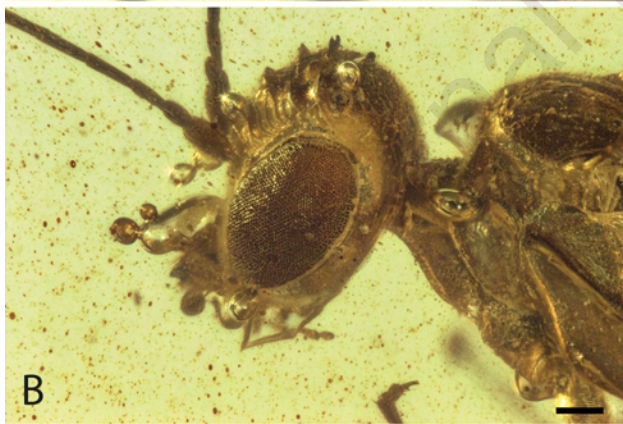
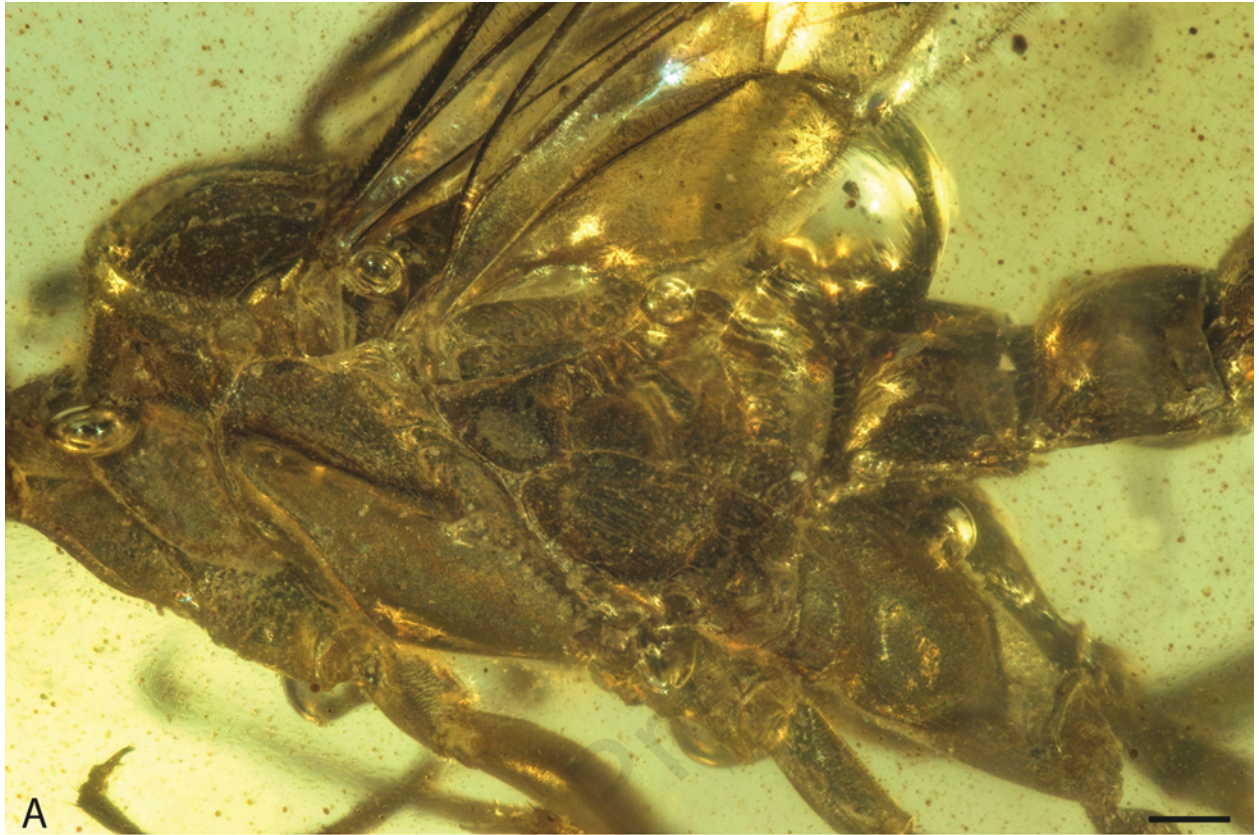
558

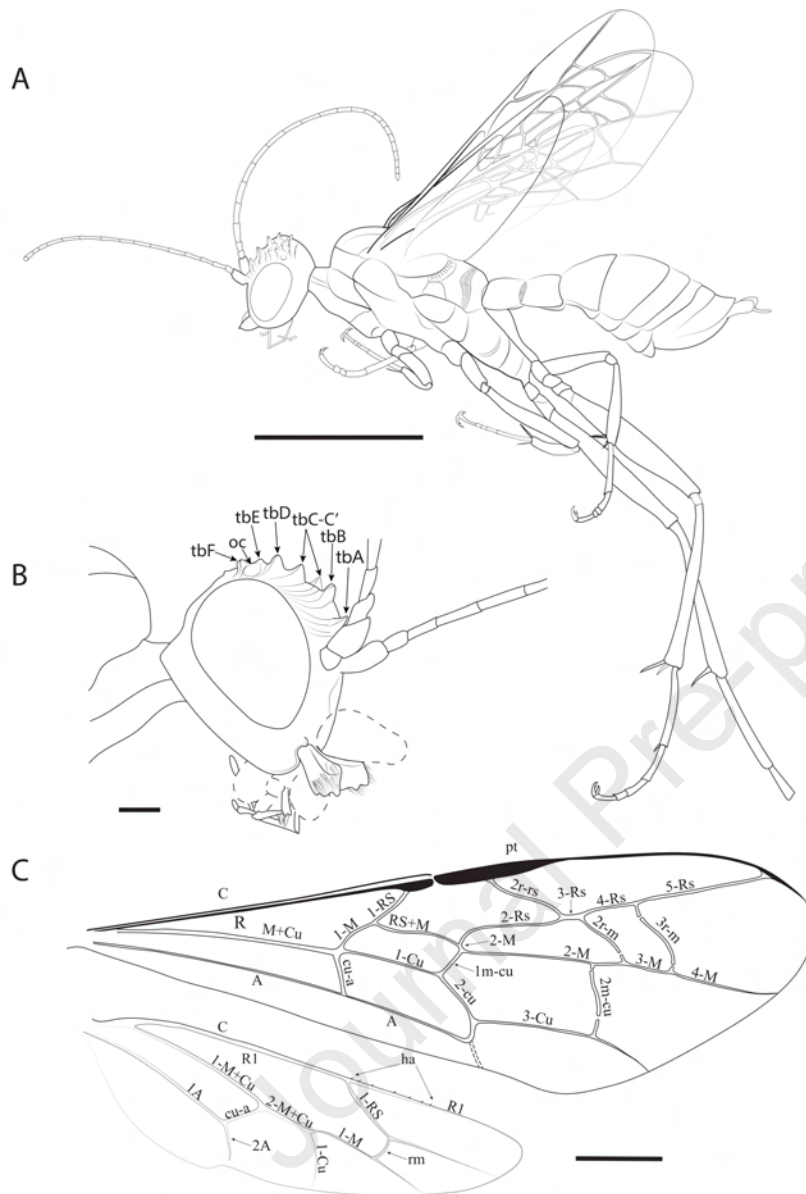
559 **Fig. 6.** *Relative proportions of non-aculeate superfamilies as recorded by geological epochs from*
 560 *the Early Cretaceous to Recent, highlighting the current dominance of Ichneumonoidea. Data*

561 computed from the Jostu taxon count request at <http://jostuworks.org/> and the species list of extant
562 taxa at <https://hol.osu.edu> (both accessed 16 April 2020).

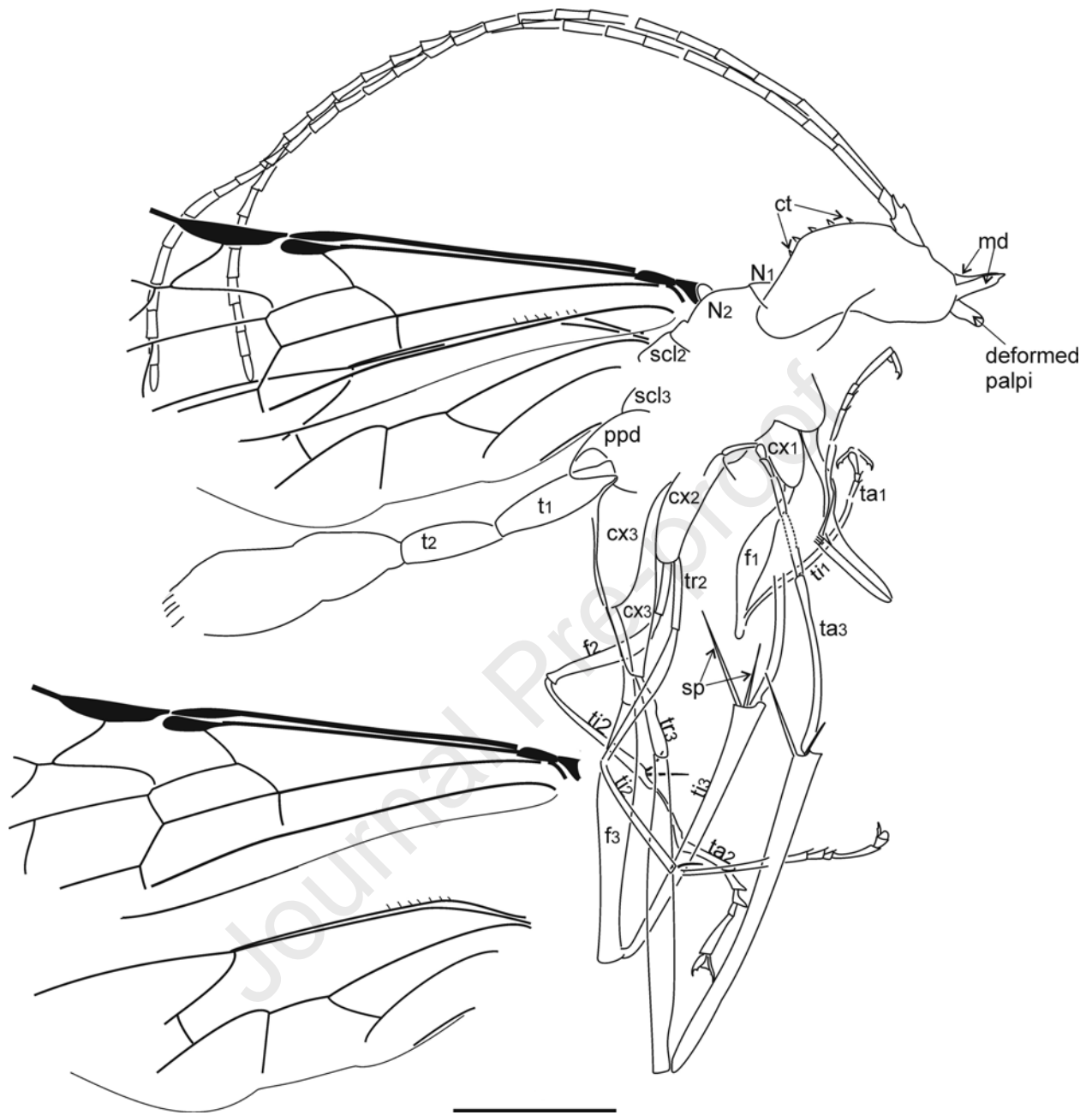
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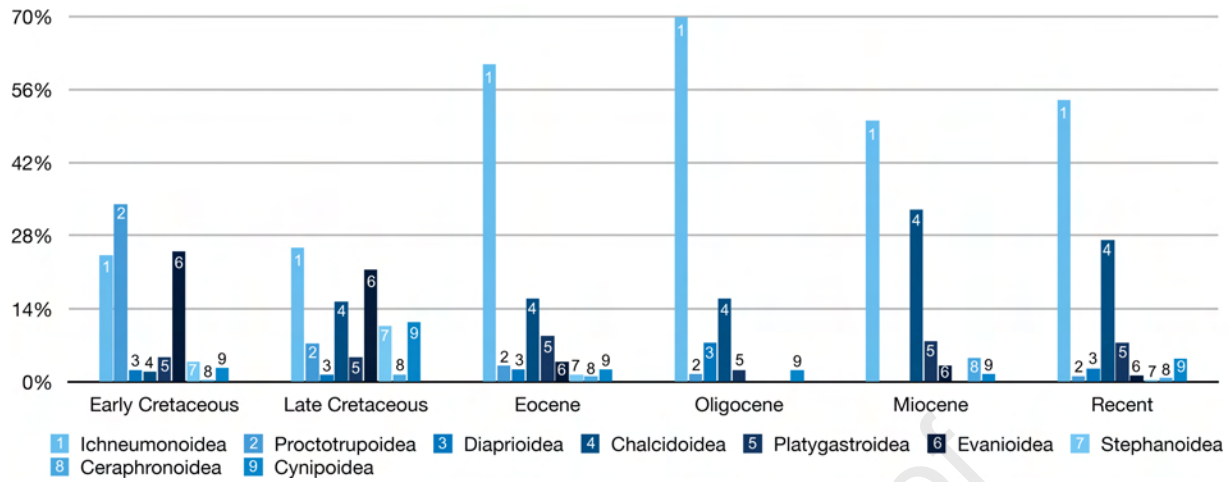












Declaration of interests

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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