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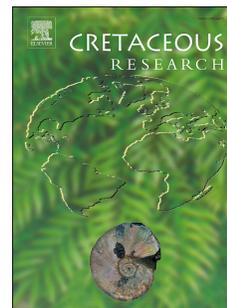


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1 **New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera:**
2 **Diaprioidea)**

3
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16
17 **Abstract**

18
19 The Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea), containing five species
20 in four genera, showed a wide distribution from the upper Barremian to the Turonian. We
21 describe two new representatives of the family from the upper Albian San Just outcrop in the
22 eastern Iberian Peninsula that correspond to *Diameneura marveni* gen. et sp. nov. Santer and
23 Álvarez-Parra and to a female member of *Mymaropsis turolensis* Engel and Ortega-Blanco,
24 2013. The forewing venation of *Diameneura marveni* gen. et sp. nov. is interpreted, allowing
25 an appropriate comparison for future descriptions. Furthermore, we provide a diagnosis for

26 *Mymaropsis baabdaensis* since no diagnosis was proposed in the initial paper. We indicate the
27 taphonomic characteristics of the newly described specimens, discuss the interrelationships of
28 the family, and provide new insights about the sexual dimorphism and palaeobiology of
29 spathiopterygids.

30

31 **Keywords:** Albian, amber, palaeobiology, parasitoidism, wasps

32

33 1. Introduction

34

35 Hymenoptera is a diverse insect order containing more than 153,000 living species that
36 play a panoply of ecological roles in the environment, such as herbivory, pollination, predation,
37 and parasitoidism (Peters et al., 2017). It has shown outstanding diversity since the Triassic,
38 with more than 3,607 extinct species described to date (Fossilworks, available at
39 <http://fossilworks.org>, accessed 13 December 2021). Moreover, its members are common
40 bioinclusions in amber deposits worldwide (e.g., Zhang et al., 2018). The Cretaceous shows an
41 impressive diversity of these insects thank to the specimens found in Burmese amber. Among
42 this diversity, several extinct hymenopteran families are restricted to the Cretaceous, such as
43 Serphitidae, Apteroperissidae, and Ohlhoftiidae (Ortega-Blanco et al., 2011a; Rasnitsyn et al.,
44 2017; Jouault et al., 2021c). Their studies are crucial to understand the diversification and
45 palaeobiology of hymenopterans during the early evolution of the Recent ecosystems.

46 Spathiopterygidae is a poorly known Cretaceous family of tiny wasps. It currently
47 includes four genera and five species identified from deposits of Lebanon, Spain, Myanmar,
48 and the USA, spanning from the upper Barremian to the Turonian (Engel et al., 2013, 2015;
49 Krogmann et al., 2016). *Cretapria tsukadai* Fujiyama, 1994, from the Aptian Choshi amber,
50 could also belong to this family (Rasnitsyn and Öhm-Kühnle, 2020). Interestingly, these wasps

51 appear to be rare, mostly being only represented by the holotype specimens. Therefore, their
52 intraspecific variability and sexual dimorphism are unclear. Until now, only one female
53 specimen has been described (Krogmann et al., 2016). The study of these wasps is important to
54 gain further knowledge on their hypothesised parasitoid lifestyle (Engel et al., 2015). It is
55 expected that this known palaeodiversity will be increased through the description of new
56 specimens, as some from the Cenomanian Burmese amber are currently pending investigation
57 (Zhang et al., 2018). It is likely that additional specimens are also present in more Cretaceous
58 amber deposits, such as in French and Burmese ambers (Corentin Jouault pers. comm.).

59 Spathiopterygidae is currently included in the superfamily Diaprioidea (Engel et al., 2013)
60 and in the infraorder Proctotrupomorpha alongside several other groups of parasitoid wasps
61 (Sharkey, 2007; Sharkey et al., 2012; Peters et al., 2017). The superfamily Diaprioidea was
62 originally proposed to include the extant families Diapriidae, Monomachidae, and
63 Maamingidae (Dowton and Austin, 2001: fig. 2; Sharkey, 2007). Later, the family Ismaridae
64 was added after it was raised from the rank of diapriid subfamily to that of family (Sharkey et
65 al., 2012). The reduced wing venation of Diapriidae, Maamingidae, and Spathiopterygidae
66 suggests a grouping of these families, when considering the relative complete venation of
67 Monomachidae as a plesiomorphic state character (Engel et al., 2013). The sister group of
68 Spathiopterygidae could be Maamingidae (Engel et al., 2013), a monogeneric family that
69 includes only two species from New Zealand (Early et al., 2001a), but no cladistic analyses
70 prove that. Recently, in the revision of Proctotrupomorpha by Rasnitsyn and Öhm-Kühnle
71 (2020), a new clade called Microprocta was proposed to comprise the groups Chalcidoidea,
72 Diaprioidea, Platygastroidea, and Bipetiolarida (embracing Serphitoidea and
73 Mymarommatoidea). Furthermore, the families Monomachidae and Maamingidae were
74 excluded from Diaprioidea, Diapriidae being the putative sister group of Spathiopterygidae
75 (Rasnitsyn and Öhm-Kühnle, 2020).

76 Here, we describe a new genus and species belonging to Spathiopterygidae and the first
77 known female of *Mymaropsis turolensis*. Both specimens were identified in amber pieces from
78 the upper Albian San Just amber-bearing outcrop (eastern Iberian Peninsula). The new genus
79 and species correspond to the fifth genus and sixth species known for this enigmatic Cretaceous
80 family of tiny wasps. We discuss its phylogenetic position within the family and provide new
81 comments about the presumable palaeobiology of the spathiopterygids. Furthermore, we
82 provide the first diagnosis for *Mymaropsis baabdaensis* originally described from the
83 Barremian Lebanese amber.

84

85 **2. Geological setting**

86

87 The San Just amber-bearing outcrop (Fig. 1) is located near Utrillas (Teruel Province,
88 Spain) in the Aliaga Sub-basin within the Maestrazgo Basin in the Aragonese Branch of the
89 Iberian Chain (Salas and Guimerà, 1996). There are more than 30 amber-bearing outcrops in
90 the Maestrazgo Basin, although only four of them have yielded bioinclusions to date (Álvarez-
91 Parra et al., 2021): Ariño, San Just, Arroyo de la Pascueta, and La Hoya. The stratigraphic
92 section of San Just belongs to the middle member (Regachuelo Member) of the Escucha
93 Formation (Peñalver et al., 2007). The age of onset of the Escucha Formation was first
94 established as late Aptian–early Albian based on palynological data (Peyrot et al., 2007),
95 although a chronostratigraphic study supported by ammonoid biostratigraphy and strontium
96 isotope stratigraphy suggested early Albian as the oldest age (Bover-Arnal et al., 2016). The
97 San Just amber is found in a layer of grey-black marls containing high amounts of organic
98 matter, charcoal, and fusinite (Peñalver et al., 2007). The San Just locality has been dated
99 middle–earliest late Albian based on the palynological assemblage (Villanueva-Amadoz et al.,
100 2010), although a new, extensive palynological study has constrained the dating to the late

101 Albian based on unpublished data. The amber could be parautochthonous in a depositional
102 environment that has been proposed to have been a freshwater swamp plain (Peñalver et al.,
103 2007; Villanueva-Amadoz et al., 2010).

104 San Just is the amber-bearing outcrop with the highest number of bioinclusions in the
105 Maestrazgo Basin, including coprolites, Araneae orbwebs, fungi, plants, arachnids, 12 insect
106 orders, and dinosaur feathers (Peñalver et al. 2006, 2007; Peñalver and Delclòs, 2010). It is the
107 type locality of 25 arthropod species (including the new species described herein).
108 Hymenopterans are one of the most abundant insect orders in San Just amber, but only eight
109 species have been identified so far belonging to the families Alavarommatidae, Evaniidae,
110 Gallorommatidae, Serphitidae, Spathiopterygidae, and Stigmaphronidae.

111

112 3. Material and methods

113

114 The studied material corresponds to the bioinclusions of two amber pieces from the San
115 Just amber-bearing outcrop (Teruel, Aragon, Spain) obtained during fieldwork in 2007. The
116 pieces were cut, polished, and embedded in epoxy resin following the methodology of Corral
117 et al. (1999). This is important for the stabilisation and protection of the amber pieces. An
118 Olympus CX41 compound microscope with an attached camera lucida and the digital camera
119 sCMEX-20 was used to make the drawings and take the photographs of the specimens.
120 Photographs were taken with ImageFocusAlpha version 1.3.7.12967.20180920. The figures
121 were prepared using Photoshop CS6. The 3D reconstruction and animation were performed
122 with Blender 2.91.2. The anatomical nomenclature follows the work of Engel et al. (2013). The
123 diagnosis for *Mymaropsis baabdaensis* has been made following the description provided in
124 work of Krogmann et al. (2016). The forewing venation nomenclature corresponds to: Sc+R =

125 subcostal and radial; B = basal; R = radial; Rs = radial sector; M = medial; Rs+M = radial sector
126 and medial; M+Cu = medial and cubital; Cu = cubital.

127 The specimens are housed at the Museo Aragonés de Paleontología (Fundación Conjunto
128 Paleontológico de Teruel-Dinópolis) in Teruel, Spain. Regarding the fossil notation, CPT is the
129 official number at the museum and SJ-07 is the field notation for the excavation in 2007
130 (administrative permission code: 171/2007).

131 This manuscript has been registered in ZooBank under the number
132 urn:lsid:zoobank.org:pub:6B175995-DBB6-4AE8-B2E4-839ADC05168C.

133

134 4. Results

135

136 4.1. Systematic palaeontology

137

138 Order Hymenoptera Linnaeus, 1758

139 Superfamily Diaprioidea Haliday, 1833

140 **Family Spathiopterygidae** Engel and Ortega-Blanco, 2013 (in Engel et al., 2013)

141

142 Type genus: *Spathiopteryx* Engel and Ortega-Blanco, 2013 (in Engel et al., 2013).

143 Other genera: *Mymaropsis* Engel and Ortega-Blanco, 2013 (in Engel et al., 2013),

144 *Spathopria* Engel, Ortega-Blanco and Grimaldi, 2013 (in Engel et al., 2013), *Diaspathion* Engel

145 and Huang, 2015 (in Engel et al., 2015), and *Diameneura* gen. nov. More information provided

146 in Table 1.

147

148 Genus *Diameneura* gen. nov. Santer and Álvarez-Parra

149

150 This new genus has been registered in ZooBank under the number
151 urn:lsid:zoobank.org:act:F092F27C-BF78-41D3-91ED-8FC7B7E6E20A.

152

153 Type species: *Diameneura marveni* sp. nov., by present designation and monotypy.

154

155 *Etymology.* The new generic name is composed of the Greek terms ‘*diamesos*’ (meaning
156 ‘median’) and ‘*neura*’ (meaning ‘venations’), referring to the fact that the forewing has
157 longitudinal veins as well as a sclerotised part of the margin. Gender feminine.

158 *Diagnosis.* Compound eyes not bulging, with number of ommatidia over 120 each;
159 polygonal rugulose microsculpture present on back of head and mesoscutum; forewing
160 membrane wrinkled; margin densely covered with stiff setae; visible venation, but mainly
161 nebulous; setae disposition on membrane not homogeneous, with positive gradient from base
162 to apex; highly sclerotised mid-basal section of costal margin (thick parastigma); sclerotised
163 M+Cu covered with rough, stiff setae; Rs+M not contacting M+Cu; Rs not contacting Rs+M;
164 Rs well defined and well distant from R.

165

166 ***Diameneura marveni*** sp. nov. Santer and Álvarez-Parra

167 Figs. 2, 3, S1

168

169 This new species has been registered in ZooBank under the number
170 urn:lsid:zoobank.org:act:6ADB8802-C684-467A-9596-C71E926F59E7.

171

172 *Material.* Holotype only, CPT-4095 (SJ-07-41), sex unknown, from San Just amber.
173 Housed at Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-

174 Dinópolis) in Teruel, Spain. Specimen preserved in a milky amber piece prepared in an epoxy
175 prism of 23×15 mm.

176 *Locality and horizon.* San Just amber-bearing outcrop, Teruel, Spain; Escucha Formation,
177 upper Albian (Peñalver et al., 2007).

178 *Etymology.* The specific epithet *marveni* is a patronym honouring Nigel Marven, a British
179 wildlife TV presenter known for his appearances in several palaeontology documentaries; and
180 is to be treated as a noun in a genitive case.

181 *Diagnosis.* Same as that for the genus (see above).

182 *Description.* Integument black to dark brown, sex unknown (Fig. 2A–D). Head globular-
183 ovoid, 0.19 mm long and 0.30 mm wide; three ocelli visible; compound eyes not bulging and
184 occupying large portion of head lateral surface, with number of dorsally visible ommatidia over
185 120 each and distance between eyes 0.13 mm wide; antennae 0.96 mm long, densely covered
186 by small bubbles; scape about twice as long as pedicel and slightly curved; elongate pedicel not
187 globular, 1.5 x longer than wide, with a rimmed distal margin; flagellomeres covered with
188 curved setae, distal flagellomere tapering toward apex; antennomeres lengths: scape 0.11 mm
189 and pedicel 0.06 mm, with only two distal flagellomeres completely visible (0.08 mm and 0.11
190 mm long, respectively). Mesosoma with bulging mesoscutum 0.21 mm long and 0.24 mm wide.
191 Polygonal rugulose microsculpture present on back of head and mesoscutum (Fig. 2E); notauli
192 if present not visible or only anteriorly. Forewings surpassing metasoma (Fig. 2C, D), whitish,
193 1.05 mm long and 0.43 mm wide; membrane wrinkled, and moderately covered with setae, with
194 a positive gradient from base to apex of wing; margin densely covered with stiff fringe setae;
195 highly sclerotised mid-basal section of costal margin (thick parastigma) (Fig. 2F); Sc+R present
196 in anterior part near wing base; sclerotised M+Cu at base of wings, covered with rough, stiff
197 setae; diverging into B and Cu at 0.11 mm from wing base; R reaching margin at 0.62 mm from
198 wing base; Rs+M horizontal not contacting with M+Cu; Rs not contacting Rs+M; Rs well

199 defined and well distant from R; Rs reaching wing margin at 0.88 mm from wing base; M
200 reaching wing margin at 0.84 mm from wing base; Cu present, parallel to M, reaching wing
201 margin at 0.44 mm from wing base; anal vein difficult to discern, if present; several secondary
202 folds present on membrane based on rows of setae and relief of membrane. Hind wings not
203 visible, although possibly present, maybe covered by forewings. Legs partly visible in ventral
204 view, but encompassed by a complete coat of air (Fig. S1). Metasoma and genitalia not visible.

205 *Discussion.* The specimen CPT-4095 fits in the family Spathiopterygidae based on its
206 general habitus, which is very similar to those of the other genera in this family. Many of the
207 diagnostic characters for the family listed by Engel et al. (2013) are visible in the specimen,
208 viz., head slightly wider than long, circular compound eyes with coarse ommatidia, thin
209 antennae longer than the body length, scape longer than the remaining antennomeres,
210 flagellomeres not expanded nor flattened and longer than wide, forewings with fringe setae not
211 greatly elongated, membrane with scattered short setae, reduced venation represented by
212 nebulous or spectral lines on the membrane, pterostigma absent, Rs+M bifurcating before the
213 middle part of the wing, Rs parallel to R and the anterior wing margin, M directed towards the
214 apico-posterior part of the wing, and Cu parallel to M. Other key characteristics of the
215 spathiopterygid venation would be M+Cu fork (junction of B and Cu) shifted far basal, all veins
216 distal of that fork lost as tubular, and presence of diverging folds often nested and partially of
217 secondary nature (Alexandr P. Rasnitsyn pers. comm.). Several diagnostic characters of the
218 family are poorly visible in the studied specimen due to its preservation, as it can be only seen
219 from the dorsal view. We assign the specimen to a new genus and species within the family
220 based on the diagnostic characteristics that differentiate it from the other genera. *Diameneura*
221 gen. nov. has more than 40 ommatidia per eye, like *Mymaropsis* and *Spathopria*, and unlike
222 *Spathiopteryx* and *Diaspathion*. Forewings with a marginal fringe of short setae are also present
223 in *Spathiopteryx* and *Mymaropsis*, but not in *Spathopria*. *Diameneura* gen. nov. shares with

224 *Mymaropsis* the sclerotised mid-basal section of the forewing margin (thick parastigma), unlike
225 in *Spathiopteryx*, *Spathopria*, and *Diaspathion*. The wrinkled membrane of *Diameneura* gen.
226 nov. is also present in *Spathopria* and *Diaspathion*, but not in *Spathiopteryx* and *Mymaropsis*.
227 The forewing membrane of *Diameneura* gen. nov. is less setose than that of *Mymaropsis*. The
228 specimen CPT-4095 shows unique characters in the family, such as the gradient of setae on the
229 forewing membrane and the polygonal rugulose microsculpture present on back of head and
230 mesoscutum. An interpretation of the forewing venation of *Diameneura marveni* gen. et sp. nov.
231 is proposed (Fig. 2D). Forewing venation is similar to that of *Mymaropsis*, although somewhat
232 more sclerotised, with Rs+M not contacting M+Cu, Rs well defined and well distant from R,
233 and Rs not contacting Rs+M (these venation characteristics are absent or dubious in
234 *Mymaropsis*). Vein Rs is either absent or appressed to R in *Mymaropsis* (Engel et al. 2013). The
235 new genus *Diameneura* might be closely related to *Mymaropsis*. We consider that CPT-4095
236 merits its determination as a new genus based on key differences with *Mymaropsis*: polygonal
237 rugulose microsculpture on back of head and mesoscutum (vs. head and mesoscutum punctured
238 in *Mymaropsis*), forewing membrane wrinkled (vs. smooth in *Mymaropsis*), and forewings
239 moderately covered by setae with positive gradient from base to apex (vs. densely and
240 homogeneously setose in *Mymaropsis*). Hind wings are not visible, but they cannot be
241 considered absent, as they might be covered by the forewings. The presence vs. absence of hind
242 wings is an unstable character in the family, as they are present in *Spathiopteryx* and
243 *Mymaropsis*, but absent in *Spathopria* and *Diaspathion*.

244

245 Genus *Mymaropsis* Engel and Ortega-Blanco, 2013 (in Engel et al., 2013)

246

247 Type species: *Mymaropsis turolensis* Engel and Ortega-Blanco, 2013 (in Engel et al.,
248 2013).

249 Other species: *Mymaropsis baabdaensis* Krogmann, Azar, Rajaei and Nel, 2016.

250

251 *Original diagnosis* (from Engel et al., 2013: 6–7). ‘Head closely punctured, punctures not
252 particularly coarse. Frontal shelf reduced but still present; toruli facing upward. Compound eyes
253 not bulging (not as in *S. alavarommopsis*), with an apparent normal proportion of ommatidia.
254 Pedicel with apicalmost margin rimmed; flagellomeres subequal in length and shape although
255 II–IV slightly longer than remainder. Pronotum with fine vertical striate microsculpture.
256 Propleuron laterally concave. Mesoscutum punctured; notauli faintly impressed, converging but
257 not meeting posteriorly. Forewing membrane smooth, densely covered by short setae, with
258 reduced venation distinct as weakly sclerotized lines, and with same veins present as in
259 *Spathiopteryx*. Hind wing retaining a small portion of membrane with three distal marginal
260 hamuli and a longer seta on apicalmost margin of membrane. Metasoma extremely short,
261 shorter than mesosoma; second metasomal tergum largest, dorsally covering portions of
262 subsequent terga.’

263 *Remarks.* Females of *Mymaropsis* are larger in size than males. The character
264 ‘flagellomeres subequal in length and shape although II–IV slightly longer than remainder’
265 proposed in the original diagnosis should be modified to ‘flagellomeres F1–F4 longer than the
266 remainder except for F12’, based on the observations of the new specimens. Females of
267 *Mymaropsis turolensis* do not show forewings densely covered with setae, a character plausible
268 due to the sexual dimorphism of the species, while females of *Mymaropsis baabdaensis* show
269 forewings densely covered with setae. Females show a basitarsus longer than the remaining
270 tarsomeres. The character ‘metasoma extremely short, shorter than mesosoma’ should be
271 removed from the diagnosis, based on the observations of the new specimens, as the metasoma
272 of the previously described specimen of *M. turolensis* seems to be incomplete (Engel et al.,
273 2013: fig. 2).

274

275 *Mymaropsis turolensis* Engel and Ortega-Blanco, 2013 (in Engel et al., 2013)

276 Fig. 4

277

278 *Material.* CPT-4097 (SJ-07-43), female, from San Just amber. Housed at Museo Aragonés
279 de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis) in Teruel, Spain.
280 Complete specimen preserved in an amber piece prepared in an epoxy prism of 24 × 14 mm.

281 *Original diagnosis* (from Engel et al., 2013). Same as that of the original diagnosis of the
282 genus *Mymaropsis* (see above).

283 *Emended diagnosis.* Scape not ventrally expanded; pedicel almost globular (thinner than
284 in *Mymaropsis baabdaensis*); flagellomeres with a similar width; forewing densely covered
285 with setae in males and moderately covered with setae in females.

286 *Description of new female specimen.* Body 1.40 mm long (until the ovipositor tip) and
287 completely preserved in transparent amber (Fig. 4A, B); integument black to dark brown
288 without fine hairs. Head globular-ovoid, 0.19 mm long and 0.32 mm wide; head plus mesosoma
289 0.60 mm long; compound eyes not bulging and occupying large portion of head lateral surface,
290 with number of ommatidia over 40; ocelli not visible; scape about twice as long as pedicel and
291 slightly curved; pedicel elongated, with a rimmed distal margin; 12 flagellomeres covered with
292 setae; last eight flagellomeres with more straight, distinct setae almost perpendicular to
293 flagellomeres; distal flagellomere elongated and tapering toward apex; length:width of each
294 antennomere, considering the mean of both antennae, from proximal to distal (in mm): scape
295 0.11:0.32, pedicel 0.69:0.26, F1 0.10:0.16, F2 0.81:0.18, F3 0.86:0.16, F4 0.81:0.18, F5
296 0.59:0.18, F6 0.61:0.22, F7 0.75:0.24, F8 0.76:0.21, F9 0.75:0.27, F10 0.70:0.22, F11 0.71:0.22,
297 and F12 0.10:0.26; mouthparts not clearly discernible, hindered by small bubbles. Mesosoma
298 0.33 mm long and 0.21 mm wide, poorly visible from dorsal view; undetermined structure

299 present left to mesosoma, possibly corresponding to a broken part of mesoscutum. Forewings
300 smooth, 1.21 mm long and 0.52 mm wide; margin covered with rough, stiff setae; highly
301 sclerotised mid-basal section of costal margin; membrane moderately covered with setae (not
302 as dense as in the holotype of *Mymaropsis turolensis* described by Engel et al., 2013); pattern
303 of venation unclear. Possible left hind wing visible (Fig. 4C), very reduced, hamuli not visible.
304 Legs well-preserved; trochanters almost 2/3 length of femora; small rounded trochantellus
305 present; femora and tibiae of fore- and mid-legs covered with a few small setae; femur and tibia
306 of hind-leg densely covered with long, stiff setae; one distal spur on inner side of tibiae, with
307 that of the pro-tibia being curved and 0.05 mm long and those of the meso- and metatibiae being
308 nearly straight and 0.03 mm long; five tarsomeres; basitarsus longer than remaining tarsomeres;
309 lengths of tarsomeres from proximal to distal, forelegs: I 0.12 mm, II 0.05 mm, III 0.04 mm,
310 IV 0.03 mm, and V 0.06 mm; midlegs: I 0.13 mm, II 0.05 mm, III 0.04 mm, IV 0.03 mm, and
311 V 0.05 mm; and hindlegs: I 0.19 mm, II 0.07 mm, III 0.06 mm, IV 0.04 mm, and V 0.06 mm;
312 distal tarsomeres with simple pretarsal claws; arolium large. Metasoma 0.77 mm long, 0.30 mm
313 wide; nine visible sclerites; length of exposed part of ovipositor 0.063 mm (Fig. 4D).

314 *Remarks.* The specimen CPT-4097 shows most of the diagnostic characters for the genus
315 *Mymaropsis*, such as the compound eyes not bulging with around 40 ommatidia, the pedicel
316 presenting a rimmed distal margin, the forewing membrane being smooth with a marginal fringe
317 of setae, and the venation reduced with weakly sclerotised parts of the forewings (Engel et al.,
318 2013). Other diagnostic characters are not clearly visible in the specimen due to its preservation.
319 The specimen is assigned to *Mymaropsis turolensis* based on the similarity of its habitus with
320 that of the holotype. The adscription to *Mymaropsis baabdaensis* is discarded based on
321 differences in the general dimensions (e.g., body and forewing lengths), the shape of the pedicel
322 (globular and wider in *M. baabdaensis*) and flagellomeres (wider in *M. baabdaensis*), and the
323 dense covering of setae on the forewing in the female of *M. baabdaensis*. The differences

324 between the studied specimen and the holotype of *M. turolensis* are as follows: general size
325 (approximately 1.5 times larger than the holotype); flagellomeres F1–F4 longer than the
326 remainder, except for F12, vs. flagellomeres F2–F4; thin flagellomeres vs. slightly wider
327 flagellomeres; last eight flagellomeres bearing more setae than the remainder vs. more setae in
328 the last five flagellomeres; and forewings moderately covered with setae vs. densely covered
329 forewings. Although the genitalia are not visible in the holotype of *M. turolensis*, Engel et al.
330 (2013) supposed that it is a male. Therefore, these minor differences could be explained by
331 sexual dimorphism and intraspecific variability within *M. turolensis* instead of attributing the
332 specimen to a new species. The basitarsi are longer than the remaining tarsomeres in the female
333 of *M. turolensis* and *M. baabdaensis*, but not in the holotype of *M. turolensis*. Thus, this
334 character can also be attributed to sexual dimorphism. The metasoma of the new specimen is
335 similar in shape to that of *M. baabdaensis*, both females. Therefore, it could be a female
336 character of the genus.

337

338 *Mymaropsis baabdaensis* Krogmann, Azar, Rajaei and Nel, 2016

339

340 *Material.* Holotype specimen 855, female, from the upper Barremian Hammana-Mdeyrij
341 amber. Housed at the Natural History Museum of the Lebanese University (Faculty of Science
342 II) in Fanar, Lebanon.

343 *Diagnosis.* Scape slightly expanded ventrally; pedicel globular (wider than in
344 *Mymaropsis turolensis*); flagellomeres F5–F12 about twice as wide as remaining ones;
345 forewing densely covered with setae in females.

346 *Remarks.* Based on the lack of an original diagnosis for *Mymaropsis baabdaensis* in
347 Krogmann et al. (2016) and according to the requirements of article 13.1.1 of the International
348 Code of Zoological Nomenclature (ICZN, 1999), we propose here a diagnosis to allow the name

349 to be valid for the described species. The general size of the holotype specimen of *M.*
 350 *baabdaensis* is larger than that of the male of *Mymaropsis turolensis*, but smaller than that of
 351 the female of the latter. These differences are also present in forewing length (wing length
 352 generally suffer less from improper preservation than body length): 0.85 mm (*M. turolensis*
 353 male), 1.21 mm (*M. turolensis* female), 1.05 mm (*M. baabdaensis* female) (Engel et al., 2013;
 354 Krogmann et al., 2016). The discovery and description of male specimens of *M. baabdaensis*
 355 would be quite useful to better understand the characters attributable to sexual dimorphism.
 356 Interestingly, the habitus of *M. baabdaensis* and *M. turolensis* is similar despite the time (more
 357 than 20 Ma; late Barremian to late Albian) and geographical distance between them.

358

359 4.2. Key to the genera and species of *Spathiopterygidae*

360

361 Characters between [] can be difficult to observe. Thus, they are considered to be of less
 362 importance than the others.

363

364 1. Forewing with a well-defined marginal fringe of setae... 2

365 —. Forewing without a marginal fringe of setae... 5

366 2. Compound eye bulging with few ommatidia; forewing slightly sclerotised on basal veins;
 367 thin parastigma [hind wing present as a veinal stub, without any remnants of a membrane;
 368 notauli meeting posteriorly]... *Spathiopteryx alavarommopsis*

369 —. Compound eye with numerous ommatidia; forewing sclerotised on basal veins; thick
 370 parastigma... 3

371 3. Forewing wrinkled, with visible venation and a positive gradient of setae towards the apex;
 372 less sclerotised M+Cu, highly sclerotised parastigma... *Diameneura marveni* gen. et sp. nov.

373 —. Forewing smooth, with unclear venation, M vein not clearly defined and setae distribution
374 on the membrane homogeneous; highly sclerotised M+Cu, less sclerotised parastigma; [hind
375 wing present with a small membranous portion; notauli not meeting posteriorly]... 4

376 4. Scape slightly expanded ventrally; pedicel globular; flagellomeres F5–F12 around twice as
377 wide as the remainder... *Mymaropsis baabdaensis*

378 —. Scape not ventrally expanded; pedicel almost globular; flagellomeres with similar widths...
379 *Mymaropsis turolensis*

380 5. Head coarsely punctured; antennae short, not longer than the total body length; metasoma
381 globose, about as long as the mesosoma; [hind wing absent]... *Spathopria sayrevillensis*

382 —. Head imbricate; antennae elongated, longer than the total body length; metasoma ovoid,
383 longer than the mesosoma; [hind wing absent]... *Diaspathion ortegai*

384

385 5. Discussion

386

387 5.1. Taphonomy

388

389 The specimens from San Just amber studied here show different preservation. The
390 holotype of *Diameneura marveni* gen. et sp. nov. (CPT-4095) is preserved in a milky amber
391 piece, allowing good visualisation only from the dorsal view (Fig. 2A), while the *Mymaropsis*
392 *turolensis* female (CPT-4097) is preserved in a transparent amber piece (Fig. 4A). Interestingly,
393 some parts of the holotype of *Diameneura marveni* gen. et sp. nov. (e.g., the antennae) are
394 covered by small bubbles, probably phloem sap drops (Lozano et al., 2020). These small
395 bubbles could be due to wasp movement in the fluid resin before its death. Its legs are
396 encompassed by a coat of air (Fig. S1). Usually, the bubbles around fossil insects preserved in
397 amber have been linked to the escape of decay gases during necrolysis in resins or to bacterial

398 activity (Martínez-Delclòs et al., 2004). Amber pieces with bioinclusions are related to aerial
399 resin produced by the branches or trunks of resiniferous trees, and the different internal aspect
400 might depend on the conditions of resin production such as stressful situations caused by
401 palaeofires (Martínez-Delclòs et al., 2004). Internal dark marks in the amber piece including on
402 the *M. turolensis* female (Fig. 4A) correspond to surfaces of desiccation in aerial conditions
403 between different flows of the original resin.

404

405 5.2. Interrelationships in Spathiopterygidae

406

407 The six Spathiopterygidae species had a wide distribution from the upper Barremian to
408 the Turonian (Table 1). Several character states of *Mymaropsis* seem to be plesiomorphic, such
409 as the more developed forewing venation and the presence of hind wings with a membrane, as
410 noted by Engel et al. (2015) and Krogmann et al. (2016). Therefore, *Mymaropsis* would be the
411 most ‘basal’ member of the family. The other representatives show reductions in several
412 structures related to putative apomorphic character states. However, the hind wings, which are
413 extremely reduced in this family, could be challenging to observe in fossil specimens. Therefore,
414 the character of the presence/absence of hind wings in each spathiopterygid species should be
415 treated carefully in phylogenetic analyses. A general trend of reduction and simplification in
416 morphology (e.g., miniaturisation and reduction of wing venation) among several
417 hymenopteran lineages was proposed by Rasnitsyn (1969, 1980). This trend has been recently
418 supported in some families by description of new taxa from Burmese amber (Li et al., 2015;
419 Jouault et al., 2021a,b), and the spathiopterygids could be another example of this kind of
420 evolutionary trend.

421 Engel et al. (2015) summarised the interrelationships of the family as [*Mymaropsis*
422 (*Spathiopteryx* [*Diaspathion* + *Spathopria*])]. Based on current knowledge, this seems to be

423 correct. Nonetheless, the description of new specimens of spathiopterygids is necessary (even
424 corresponding to the known species) to better understand the plesiomorphic and apomorphic
425 conditions of each character. *Diameneura* gen. nov. shows morphological similarities with the
426 basal *Mymaropsis* (such as the forewings with a marginal fringe of short setae and sclerotised
427 mid-basal section of the costal margin) and the derived representatives *Spathopria* and
428 *Diaspathion* (such as the wrinkled forewing membrane). Furthermore, it has unique characters
429 within the family, such as the gradient of setae on the forewing membrane and the polygonal
430 rugulose microsculpture present on back of head and mesoscutum. Therefore, its phylogenetic
431 position and relationships with the other genera are obscure, although it might be closely related
432 to *Mymaropsis* based on the similar anatomic characteristics. A detailed phylogenetic analysis
433 is required to resolve the interrelationships within Spathiopterygidae, as well as the
434 relationships with the other families within Diaprioidea.

435

436 5.3. Sexual dimorphism and palaeobiology of Spathiopterygidae

437

438 Spathiopterygidae is currently represented by seven specimens from six species obtained
439 from Cretaceous ambers, although only two of them are female (Table 1). Therefore, there is
440 little information on sexual dimorphism and intraspecific variability within the family. Female
441 hymenopterans are usually larger than males (Stubblefield and Seger, 1994). This sexual size
442 dimorphism is also present in spathiopterygids based on the comparisons between the male and
443 female specimens of *Mymaropsis turolensis* (Fig. S2). Furthermore, there are other characters
444 that could be related to sexual dimorphism in *M. turolensis*, such as the width of the
445 flagellomeres (thinner in females), the setae on the flagellomeres (F5–F12 with more setae in
446 females vs. F8–F12 in males), and the setae covering the forewings (moderately in females vs.
447 densely in males). The presence of abundant setae (acting as sensillae) on flagellomeres is

448 possibly an adaptation to sense and identify prey for the gravid female searching a host.
449 Interestingly, the diapiiid *Trichopria drosophilae* Perkins, 1910 has the most developed
450 sensillae for host selection situated on the apical flagellomeres of the females (Romani et al.,
451 2002), which maybe suggests a similar use of the sensillae in Spathiopterygidae. Females of
452 both *M. turolensis* and *M. baabdaensis* show a similar morphology of the metasoma, probably
453 related to the life habit of female parasitoid wasps that need a host to lay eggs. Basitarsi longer
454 than the remaining tarsomeres in females of both species maybe facilitated the attaching to the
455 host previously to the egg laying.

456 The putative extant sister group of Spathiopterygidae is Maamingidae (Engel et al., 2013),
457 which is found today only in New Zealand (Early et al., 2001a), contrast with the wide
458 distribution of spathiopterygids during the Cretaceous. *Maaminga rangi* Early, Masner,
459 Naumann and Austin, 2001 inhabits *Agathis australis* (Araucariaceae) forests. *Maaminga*
460 *marrisi* Early, Masner, Naumann and Austin, 2001 ‘is a leaf litter inhabitant of bushy scrub in
461 exposed sites, from near the shoreline to montane shrubs and snow tussock’ (Early et al., 2001a:
462 348–349). Even if the resin-producing trees of Spanish amber were araucarians related to
463 *Agathis*, the diversity of the habitats of the extant Maamingidae and the putative sister grouping
464 would stop us from making inferences from the biological data of these extant wasps for the
465 Spathiopterygidae. An alternative sister group of Spathiopterygidae would be Diapriidae
466 (Rasnitsyn and Öhm-Kühnle, 2020), with a worldwide distribution today (Masner, 1993).

467 The extant Diapriidae, Monomachidae, and Ismaridae are known to be parasitoid wasps
468 (Masner, 1993; Perioto et al., 2016), and the Maamingidae are likely to have a similar life habits
469 based on their morphology (Early et al., 2001a, b). More generally, this is also the case for the
470 whole group Microprocta. Therefore, it is highly probable that spathiopterygids were also
471 parasitoids, based on a simple phylogenetic inference (Nel, 1997). The Diapriidae are
472 parasitoids of several insect groups (Masner, 1993), such as diverse families of dipterans (e.g.,

473 Mycetophilidae, Sciaridae, Syrphidae, and Calliphoridae), or secondarily change their hosts to
474 beetles (Staphylinidae and Psephenidae) or ants (Formicidae). The biology of Monomachidae
475 is poorly known, although some species are parasitoids of Stratiomyidae (Diptera) (Masner,
476 1993; Johnson and Musetti, 2012). The Ismaridae are known to be hyperparasitoids of
477 planthoppers (Hemiptera: Cicadellidae) via the larvae of Dryinidae (Hymenoptera) (Masner,
478 1976, 1993). The hosts of the Maamingidae remain unknown (Early et al., 2001a, 2001b),
479 although the species *Maaminga marrisi* could be a parasitoid of Phoridae (Diptera) based on
480 their abundance in the same habitat (Early et al., 2001a). The hosts of spathiopterygids could
481 also have been some dipteran families, such as other families within Diaprioidea. However, this
482 is not yet known as the morphological characters of the specimens have not shed light on this
483 topic. Furthermore, all the specimens of the family have been found in amber pieces without
484 the syninclusions that could indicate the putative host taxa. New descriptions of
485 spathiopterygids and a detailed study and comparison of the female genitalia with that of other
486 hymenopteran families might help to resolve this question. It is important to note that
487 hymenopterans were the main driver of the Mid-Mesozoic Parasitoid Revolution (MMPR)
488 described by Labandeira and Li (2021). Spanish amber, based on its chronological age, would
489 be included in the final extension of Phase 2 of the MMPR after the diversification events that
490 established six of the seven major parasitoid groups (Labandeira and Li, 2021). In Phase 3 after
491 the MMPR, starting during the Cenomanian, the number of hymenopteran families within
492 Proctotupomorpha and Aculeata greatly increased in diversity, and the insect parasitoid fauna
493 was finally consolidated into food webs (Labandeira and Li, 2021). Interestingly, the latter
494 authors suggested that spathiopterygids could have been endoparasitoids attacking the host at
495 its egg stage.

496 An interesting characteristic of Spathiopterygidae is the bizarre reduction of the hind
497 wings. In the case of *Mymaropsis*, the hind wings retain a small portion of the membrane and

498 hamuli. In *Spathiopteryx*, they are reduced to a stalk without a membrane, while in *Spathopria*
499 and *Diaspathion*, they are completely absent. Furthermore, as Engel et al. (2015) noted, they
500 seem to represent a transitional series that correlate with age, with the absence of hind wings
501 being a derived character of the younger representatives of the family. Nonetheless, as we
502 indicate above, the hind wings could be difficult to observe due to preservation artefacts or
503 other body parts covering them. Hind wings might have been present in *Diameneura marveni*
504 gen. et sp. nov. considering its geological provenance (upper Albian). Hind wing reduction is
505 also present in some other hymenopteran groups (e.g., Ortega-Blanco et al., 2011b), although a
506 complete loss of hind wings is extremely unusual. Interestingly, the bizarre ceraphronoid family
507 Aptenoperissidae known from Burmese amber is wingless (Rasnitsyn et al., 2017). Recently, a
508 new Cretaceous monospecific family within Hymenoptera was described as showing
509 morphological diptery (Rasnitsyn et al., 2019). The case of the spathiopterygids is even more
510 exceptional, as diptery is only shared by two of the species, but not by all the members of the
511 family. Morphological diptery is uncommon in active flying insects (Rasnitsyn et al., 2019),
512 which clearly affected the flight mode of these bizarre insects.

513

514 6. Conclusions

515

516 The family Spathiopterygidae now contains six species in five genera thank to the
517 description of *Diameneura marveni* gen. et sp. nov. that increases the known palaeodiversity of
518 the family. The forewing venation of *Diameneura marveni* gen. et sp. nov. has been interpreted
519 based on sclerotisation, nebulous veins, rows of setae, and reliefs of the membrane, providing
520 a new framework for comparison with new undescribed specimens. The study of the sexual
521 dimorphism of the family has been addressed from the description of the first known female of
522 *Mymaropsis turolensis*, revealing characters that can be interpreted as differences between the

523 sexes of the same species. The genus *Mymaropsis* would be the most basal member of the
524 family as it retains plesiomorphic state characters, although a phylogenetic analysis is necessary
525 to resolve the interrelationships of the family. As previously proposed, it is plausible that
526 Spathiopterygidae belongs to Diaprioidea since it shares morphological similarities with
527 Mymarommatoidea, Myanmarinidae, and Mymaridae, such as the peduncular forewing with
528 nebulous venation and the reduced hind wings, could be explained as convergent evolution, as
529 these families probably shared similar parasitoid biology. Despite the new information provided
530 here, there are anatomical (presence vs. absence of hind wings) and phylogenetical
531 (interrelationships of the family and with other families) uncertainties. The putative sister group,
532 Maamingidae, is also not very well known. Key questions might be resolved after the
533 monographic study of the new specimens from Burmese amber.

534

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536

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549

550 **CRedit author statement**

551

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717

718 **Table caption**

719

720 **Table 1.** Checklist of the known genera and species of Spathiopterygidae, with the known sex,
721 age, and provenance indicated. In bold: new genus and species described herein. The
722 information about the resin-producing tree and Burmese amber is from McCoy et al. (2021)
723 and Ross et al. (2010), respectively.

724

725 **Figure captions**

726

727 **Figure 1.** Geographical and geological location of the upper Albian San Just amber-bearing
728 outcrop (Teruel Province, Spain); modified from Canerot et al. (1977) and Martín Fernández
729 and Canerot (1977). Scale bars = 100 km (Iberian Peninsula), 2 km (geological map).

730

731 **Figure 2.** *Diameneura marveni* gen. et sp. nov. (Hymenoptera: Spathiopterygidae), sex
732 unknown, late Albian, San Just (Teruel Province, Spain), holotype CPT-4095 (SJ-07-41): A, B)
733 photograph and drawing from dorsal view, both at the same scale; C, D) venation and covering
734 of setae in the right forewing; E) polygonal microsculpture on the back of the head and
735 mesoscutum, with the ocelli indicated by the arrowheads; F) arrowheads indicate the
736 sclerotisation of the mid-basal section of the costal margins of forewings (parastigma); arrows:
737 indicate the veins Sc+R, B, M+Cu, Rs+M, and Cu. Scale bars = 0.5 mm (A, B), 0.2 mm (C, D),
738 0.1 mm (E, F).

739

740 **Figure 3.** Artistic 3D reconstruction of *Diameneura marveni* gen. et sp. nov. (Hymenoptera:
741 Spathiopterygidae). Unknown parts of the body taken from other species in the family; presence

742 of hind wings speculative. Forewing 1.05 mm long. Author: Maxime Santer. Animation of the
743 supposed living behaviour in Video 1.

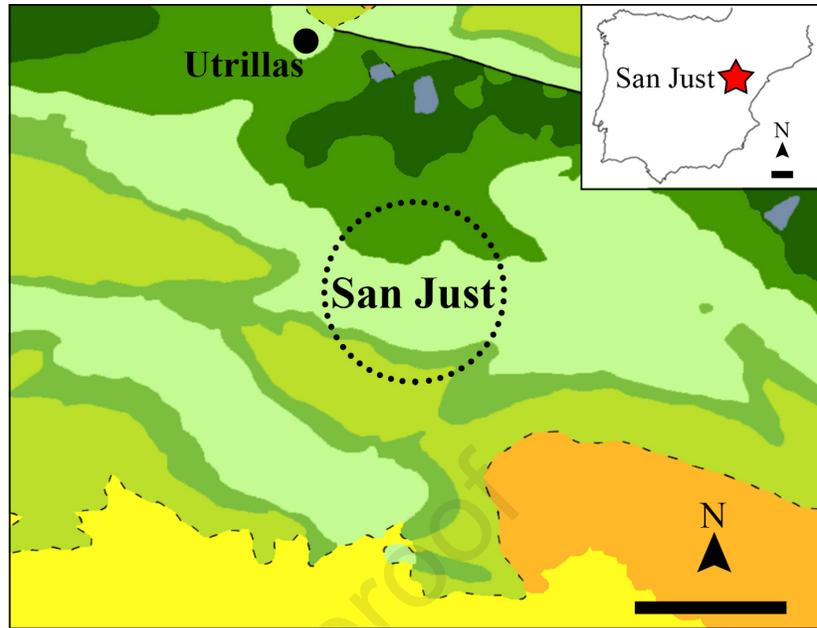
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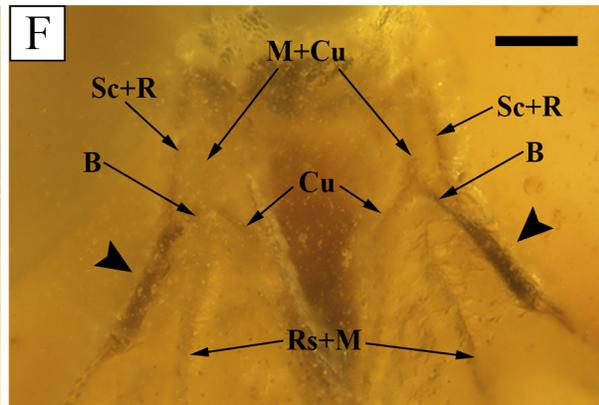
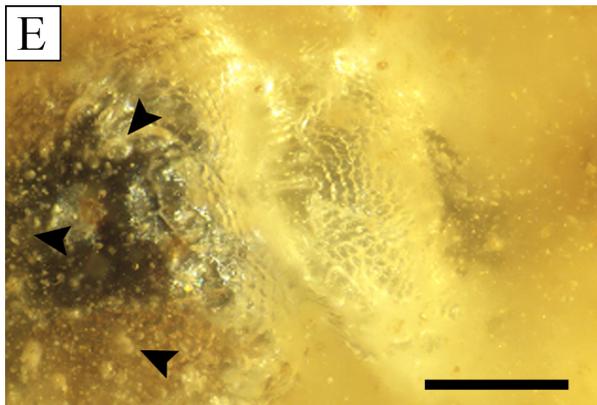
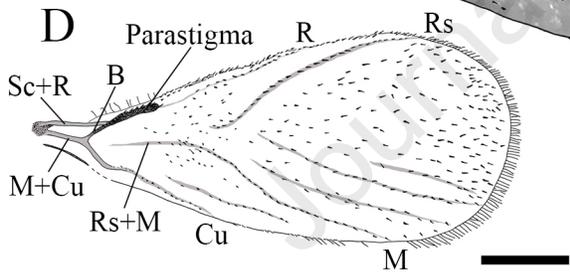
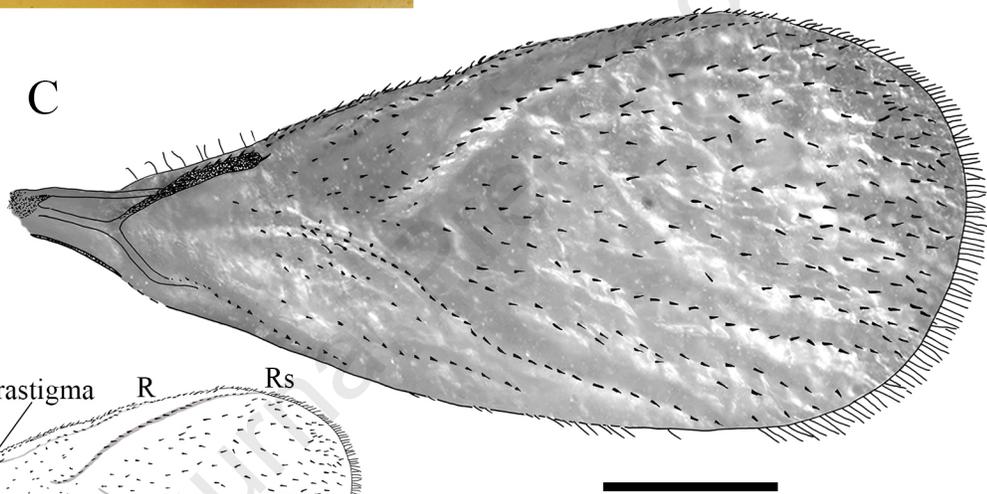
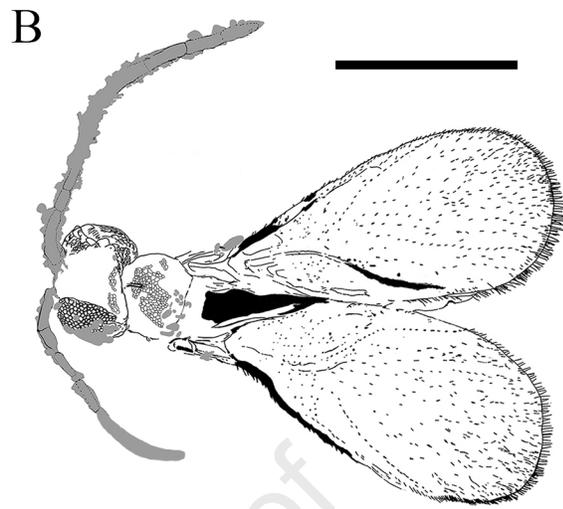
745 **Figure 4.** *Mymaropsis turolensis* Engel and Ortega-Blanco, 2013 (Hymenoptera:
746 Spathiopterygidae), female, late Albian, San Just (Teruel Province, Spain), specimen CPT-4097
747 (SJ-07-43): A, B) photograph and drawing in ventral view, both at the same scale; C) mesosoma
748 from dorsal view; with the arrow indicating the possible left hind wing; D) ovipositor in ventral
749 view; with the arrow indicating the tip of the ovipositor. Scale bars = 0.5 mm (A, B), 0.1 mm
750 (C, D).

Genus and species	Known sex	Age	Provenance	Resin-producing tree	Reference
<i>Spathopria sayrevillensis</i> Engel, Ortega-Blanco and Grimaldi, 2013	♂	Turonian	Sayreville, USA	Cupressaceae	Engel et al. (2013)
<i>Diaspathion ortegai</i> Engel and Huang, 2015	♂	early Cenomanian	Hukawng Valley, Myanmar	Araucariaceae or Dipterocarpaceae	Engel et al. (2015)
<i>Spathiopteryx alavarommopsis</i> Engel and Ortega-Blanco, 2013	♂	late Albian	Peñacerrada I, Spain	Araucariaceae	Engel et al. (2013)
<i>Diameneura marveni</i> gen. et sp. nov. Santer and Álvarez-Parra	Unknown	late Albian	San Just, Spain	Cheirolepidiaceae	This paper
<i>Mymaropsis turolensis</i> Engel and Ortega-Blanco, 2013	♂?, ♀	late Albian	San Just, Spain	Cheirolepidiaceae	Engel et al. (2013); this paper
<i>Mymaropsis baabdaensis</i> Krogmann, Azar, Rajaei and Nel, 2016	♀	late Barremian	Hammana-Mdeyrij, Lebanon	Conifers (Araucariaceae, Cheirolepidiaceae or Podocarpaceae)	Krogmann et al. (2016); this paper

Legend

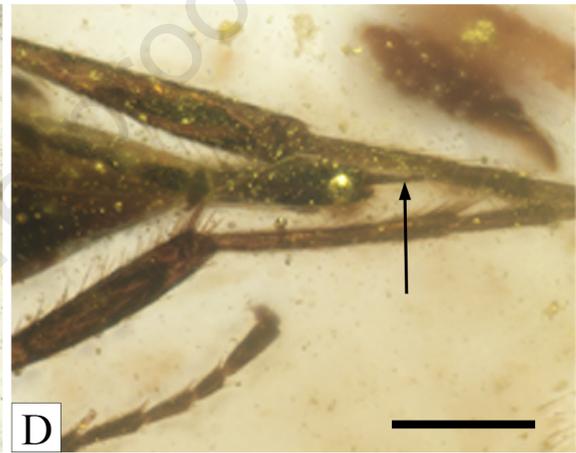
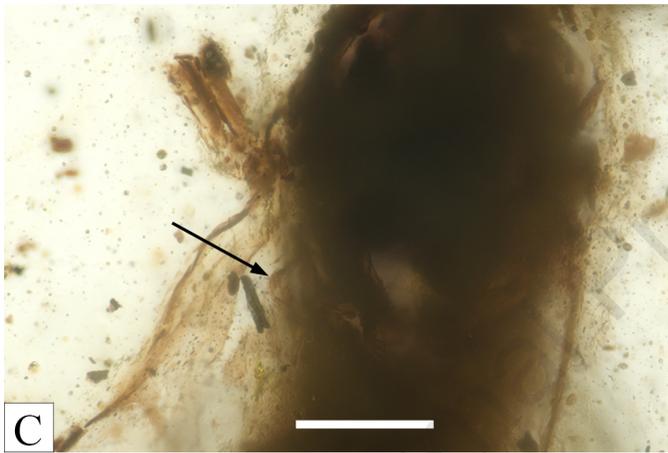
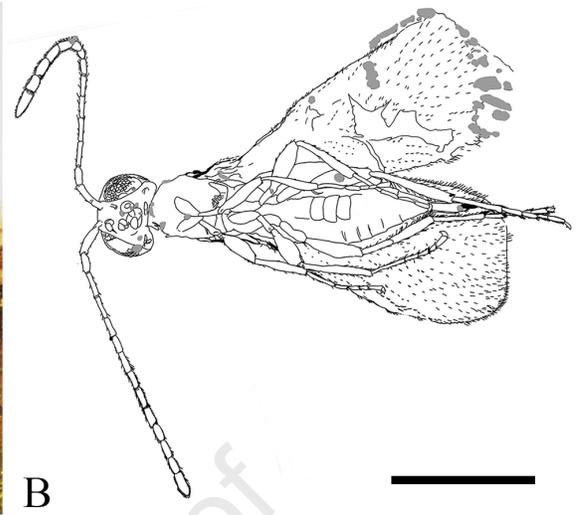
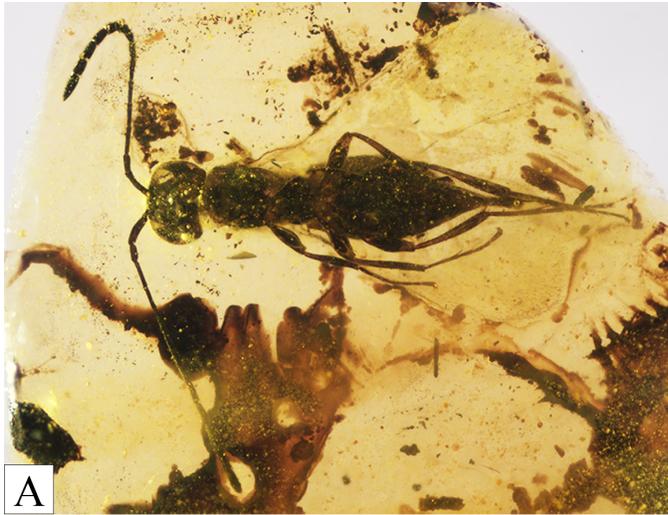
- Fault
- Discontinuity
-  Oligocene–Miocene
-  Oligocene
-  Upper Cretaceous
-  Albian–Cenomanian
-  Albian
-  Aptian–Albian
-  Lower Cretaceous
-  Jurassic







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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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