

## New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea)

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### ABSTRACT

The Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea), containing five species in four genera, showed a wide distribution from the upper Barremian to the Turonian. We describe two new representatives of the family from the upper Albian San Just outcrop in the eastern Iberian Peninsula that correspond to *Diameneura marveni* gen. et sp. nov. Santer and Álvarez-Parra and to a female member of *Mymaropsis turolensis* Engel and Ortega-Blanco, 2013. The forewing venation of *Diameneura marveni* gen. et sp. nov. is interpreted, allowing an appropriate comparison for future descriptions. Furthermore, we provide a diagnosis for *Mymaropsis baabdaensis* since no diagnosis was proposed in the initial paper. We indicate the taphonomic characteristics of the newly described specimens, discuss the interrelationships of the family, and provide new insights about the sexual dimorphism and palaeobiology of spathiopterygids.

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### 1. Introduction

Hymenoptera is a diverse insect order containing more than 153,000 living species that play a panoply of ecological roles in the environment, such as herbivory, pollination, predation, and parasitoidism (Peters et al., 2017). It has shown outstanding diversity since the Triassic, with more than 3607 extinct species described to date (Fossilworks, available at <http://fossilworks.org>, accessed 13 December 2021). Moreover, its members are common bioinclusions in amber deposits worldwide (e.g., Zhang et al., 2018). The Cretaceous shows an impressive diversity of these insects thanks to the specimens found in Burmese amber. Among this diversity, several extinct hymenopteran families are restricted to the Cretaceous, such as Serphitidae, Aptenoperissidae, and Ohlhoffiidae (Ortega-Blanco et al., 2011a; Rasnitsyn et al., 2017; Jouault et al., 2021c). Their studies are crucial to understand the diversification and

palaeobiology of hymenopterans during the early evolution of the Recent ecosystems.

Spathiopterygidae is a poorly known Cretaceous family of tiny wasps. It currently includes four genera and five species identified from deposits of Lebanon, Spain, Myanmar, and the USA, spanning from the upper Barremian to the Turonian (Engel et al., 2013, 2015; Krogmann et al., 2016). *Cretapria tsukadai* Fujiyama, 1994, from the Aptian Choshi amber, could also belong to this family (Rasnitsyn and Öhm-Kühnle, 2020). Interestingly, these wasps appear to be rare, mostly being only represented by the holotype specimens. Therefore, their intraspecific variability and sexual dimorphism are unclear. Until now, only one female specimen has been described (Krogmann et al., 2016). The study of these wasps is important to gain further knowledge on their hypothesised parasitoid lifestyle (Engel et al., 2015). It is expected that this known palaeodiversity will be increased through the description of new specimens, as some from the Cenomanian Burmese amber are currently pending investigation (Zhang et al., 2018). It is likely that additional specimens are also present in more Cretaceous amber deposits, such as in French and Burmese ambers (Corentin Jouault pers. comm.).

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

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

## 2. Geological setting

The San Just amber-bearing outcrop (Fig. 1) is located near Utrillas (Teruel Province, Spain) in the Aliaga Sub-basin within the

Maestrazgo Basin in the Aragonese Branch of the Iberian Chain (Salas and Guimerà, 1996). There are more than 30 amber-bearing outcrops in the Maestrazgo Basin, although only four of them have yielded bioinclusions to date (Álvarez-Parra et al., 2021): Ariño, San Just, Arroyo de la Pascueta, and La Hoya. The stratigraphic section of San Just belongs to the middle member (Regachuelo Member) of the Escucha Formation (Peñalver et al., 2007). The age of onset of the Escucha Formation was first established as late Aptian–early Albian based on palynological data (Peyrot et al., 2007), although a chronostratigraphic study supported by ammonoid biostratigraphy and strontium isotope stratigraphy suggested early Albian as the oldest age (Bover-Arnal et al., 2016). The San Just amber is found in a layer of grey-black marls containing high amounts of organic matter, charcoal, and fusinite (Peñalver et al., 2007). The San Just locality has been dated middle–earliest late Albian based on the palynological assemblage (Villanueva-Amadoz et al., 2010), although a new, extensive palynological study has constrained the dating to the late Albian based on unpublished data. The amber could be parautochthonous in a depositional environment that has been proposed to have been a freshwater swamp plain (Peñalver et al., 2007; Villanueva-Amadoz et al., 2010).

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

## 3. Material and methods

The studied material corresponds to the bioinclusions of two amber pieces from the San Just amber-bearing outcrop (Teruel, Aragon, Spain) obtained during fieldwork in 2007. The pieces were

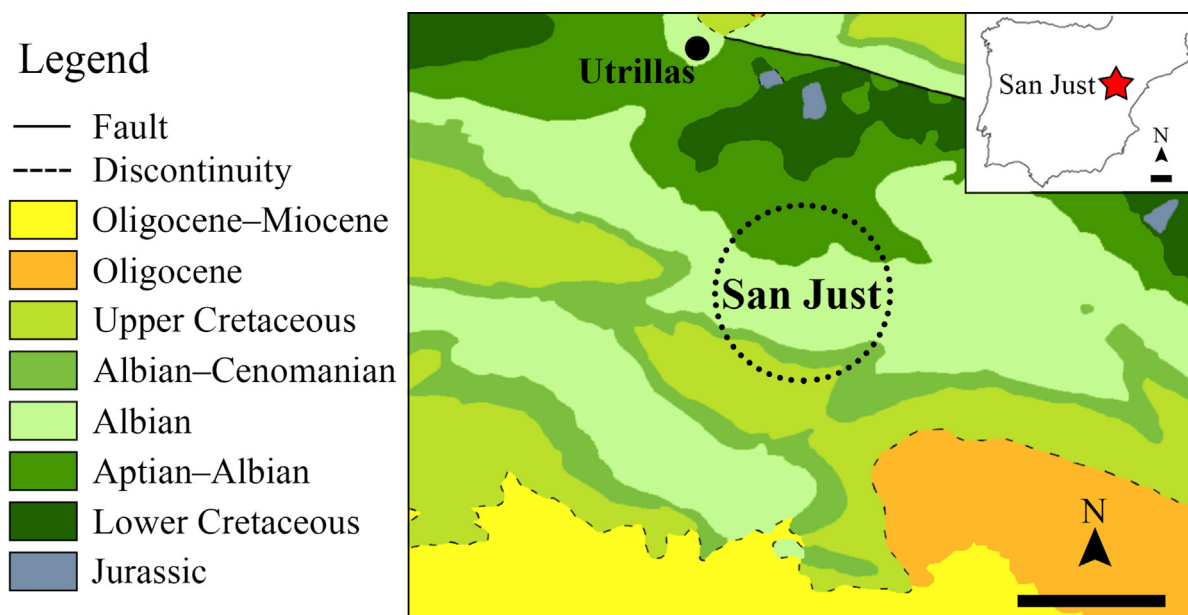


Fig. 1. Geographical and geological location of the upper Albian San Just amber-bearing outcrop (Teruel Province, Spain); modified from Canerot et al. (1977) and Martín Fernández and Canerot (1977). Scale bars = 100 km (Iberian Peninsula), 2 km (geological map).

cut, polished, and embedded in epoxy resin following the methodology of Corral et al. (1999). This is important for the stabilisation and protection of the amber pieces. An Olympus CX41 compound microscope with an attached camera lucida and the digital camera sCMEX-20 was used to make the drawings and take the photographs of the specimens. Photographs were taken with ImageFocusAlpha version 1.3.7.12967.20180920. The figures were prepared using Photoshop CS6. The 3D reconstruction and animation were performed with Blender 2.91.2. The anatomical nomenclature follows the work of Engel et al. (2013). The diagnosis for *Mymaropsis baabdaensis* has been made following the description provided in work of Krogmann et al. (2016). The forewing venation nomenclature corresponds to: Sc+R = subcostal and radial; B = basal; R = radial; Rs = radial sector; M = medial; Rs+M = radial sector and medial; M+Cu = medial and cubital; Cu = cubital.

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

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## 4. Results

### 4.1. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Superfamily Diaprioidea Haliday, 1833

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

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

Other genera: *Mymaropsis* Engel and Ortega-Blanco, 2013 (in Engel et al., 2013), *Spathopria* Engel, Ortega-Blanco and Grimaldi, 2013 (in Engel et al., 2013), *Diaspathion* Engel and Huang, 2015 (in Engel et al., 2015), and *Diameneura* gen. nov. More information provided in Table 1.

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

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

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

**Table 1**

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

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 alavarammopsis</i> Engel and Ortega-Blanco, 2013	♂	late Albian	Peñacerrada I, Spain	Araucariaceae	Engel et al. (2013)
<b><i>Diameneura marveni</i></b> 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

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

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

***Diameneura marveni*** sp. nov. Santer and Álvarez-Parra  
Figs. 2, 3, Fig. S1

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

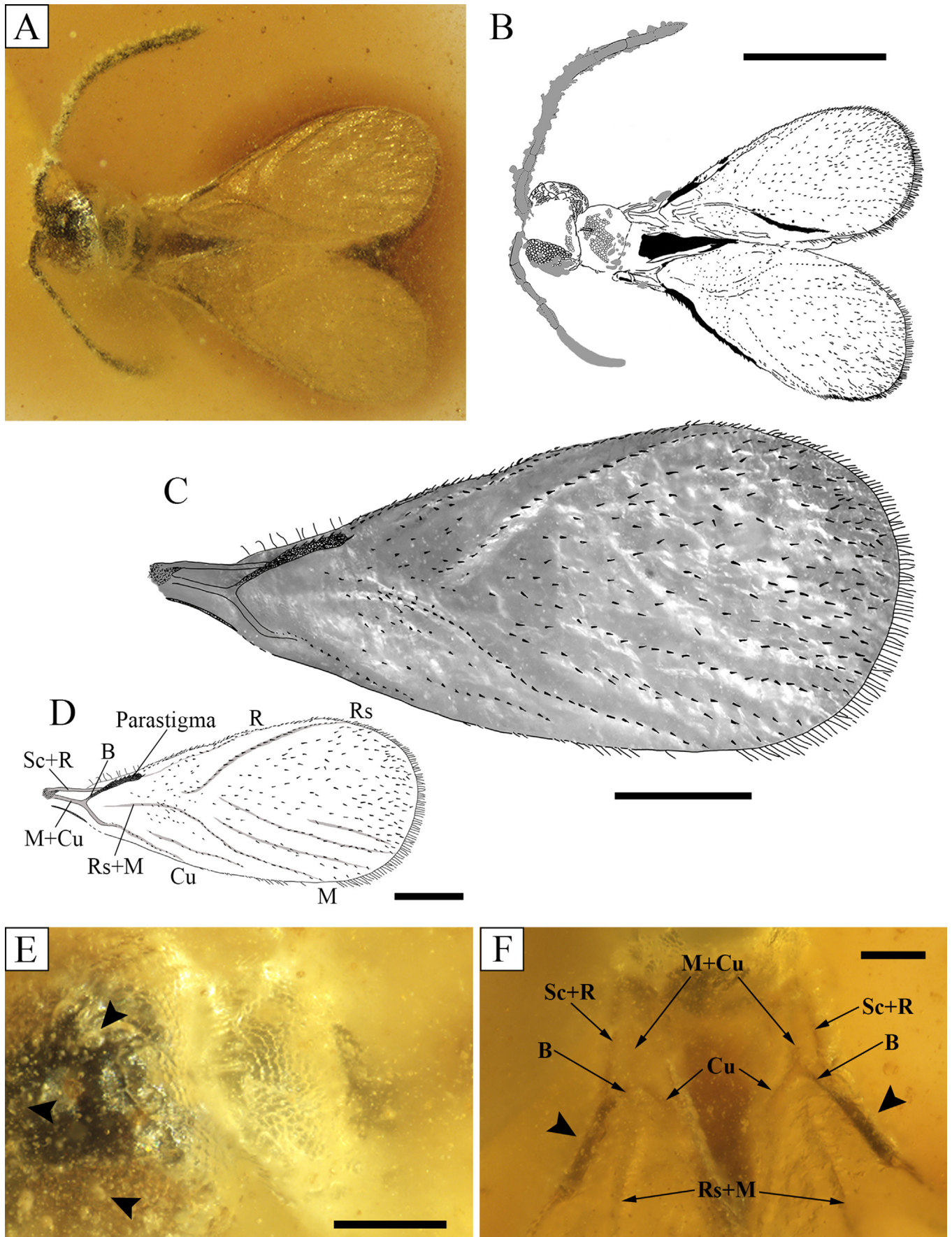
**Material.** Holotype only, CPT-4095 (SJ-07-41), sex unknown, from San Just amber. Housed at Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis) in Teruel, Spain. Specimen preserved in a milky amber piece prepared in an epoxy prism of 23 × 15 mm.

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

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

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

**Description.** Integument black to dark brown, sex unknown (Fig. 2A–D). Head globular-ovoid, 0.19 mm long and 0.30 mm wide; three ocelli visible; compound eyes not bulging and occupying large portion of head lateral surface, with number of dorsally visible ommatidia over 120 each and distance between eyes 0.13 mm wide; antennae 0.96 mm long, densely covered by small bubbles; scape about twice as long as pedicel and slightly curved; elongate pedicel not globular, 1.5 × longer than wide, with a rimmed distal margin; flagellomeres covered with curved setae, distal flagellomere tapering toward apex; antennomeres lengths: scape 0.11 mm and pedicel 0.06 mm, with only two distal flagellomeres completely visible (0.08 mm and 0.11 mm long, respectively). Mesosoma with bulging mesoscutum 0.21 mm long and 0.24 mm wide. Polygonal rugulose microsculpture present on back of head and mesoscutum (Fig. 2E); notauli if present not visible or only





**Fig. 3.** Artistic 3D reconstruction of *Diameneura marveni* gen. et sp. nov. (Hymenoptera: Spathiopterygidae). Unknown parts of the body taken from other species in the family; presence of hind wings speculative. Forewing 1.05 mm long. Author: Maxime Santer. Animation of the supposed living behaviour in [Video 1](#).

anteriorly. Forewings surpassing metasoma (Fig. 2C, D), whitish, 1.05 mm long and 0.43 mm wide; membrane wrinkled, and moderately covered with setae, with a positive gradient from base to apex of wing; margin densely covered with stiff fringe setae; highly sclerotised mid-basal section of costal margin (thick parastigma) (Fig. 2F); Sc+R present in anterior part near wing base; sclerotised M+Cu at base of wings, covered with rough, stiff setae; diverging into B and Cu at 0.11 mm from wing base; R reaching margin at 0.62 mm from wing base; Rs+M horizontal not contacting with M+Cu; Rs not contacting Rs+M; Rs well defined and well distant from R; Rs reaching wing margin at 0.88 mm from wing base; M reaching wing margin at 0.84 mm from wing base; Cu present, parallel to M, reaching wing margin at 0.44 mm from wing base; anal vein difficult to discern, if present; several secondary folds present on membrane based on rows of setae and relief of membrane. Hind wings not visible, although possibly present, maybe covered by forewings. Legs partly visible in ventral view, but encompassed by a complete coat of air (Fig. S1). Metasoma and genitalia not visible.

**Discussion.** The specimen CPT-4095 fits in the family Spathiopterygidae based on its general habitus, which is very similar to those of the other genera in this family. Many of the diagnostic characters for the family listed by Engel et al. (2013) are visible in the specimen, viz., head slightly wider than long, circular compound eyes with coarse ommatidia, thin antennae longer than the body length, scape longer than the remaining antennomeres, flagellomeres not

expanded nor flattened and longer than wide, forewings with fringe setae not greatly elongated, membrane with scattered short setae, reduced venation represented by nebulous or spectral lines on the membrane, pterostigma absent, Rs+M bifurcating before the middle part of the wing, Rs parallel to R and the anterior wing margin, M directed towards the apico-posterior part of the wing, and Cu parallel to M. Other key characteristics of the spathiopterygid venation would be M+Cu fork (junction of B and Cu) shifted far basal, all veins distal of that fork lost as tubular, and presence of diverging folds often nested and partially of secondary nature (Alexandr P. Rasnitsyn pers. comm.). Several diagnostic characters of the family are poorly visible in the studied specimen due to its preservation, as it can be only seen from the dorsal view. We assign the specimen to a new genus and species within the family based on the diagnostic characteristics that differentiate it from the other genera. *Diameneura* gen. nov. has more than 40 ommatidia per eye, like *Mymaropsis* and *Spathopria*, and unlike *Spathiopteryx* and *Diaspathion*. Forewings with a marginal fringe of short setae are also present in *Spathiopteryx* and *Mymaropsis*, but not in *Spathopria*. *Diameneura* gen. nov. shares with *Mymaropsis* the sclerotised mid-basal section of the forewing margin (thick parastigma), unlike in *Spathiopteryx*, *Spathopria*, and *Diaspathion*. The wrinkled membrane of *Diameneura* gen. nov. is also present in *Spathopria* and *Diaspathion*, but not in *Spathiopteryx* and *Mymaropsis*. The forewing membrane of *Diameneura* gen. nov. is less setose than that of *Mymaropsis*. The specimen CPT-4095 shows unique characters in

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

the family, such as the gradient of setae on the forewing membrane and the polygonal rugulose microsculpture present on back of head and mesoscutum. An interpretation of the forewing venation of *Diameneura marveni* gen. et sp. nov. is proposed (Fig. 2D). Forewing venation is similar to that of *Mymaropsis*, although somewhat more sclerotised, with Rs+M not contacting M+Cu, Rs well defined and well distant from R, and Rs not contacting Rs+M (these venation characteristics are absent or dubious in *Mymaropsis*). Vein Rs is either absent or appressed to R in *Mymaropsis* (Engel et al., 2013). The new genus *Diameneura* might be closely related to *Mymaropsis*. We consider that CPT-4095 merits its determination as a new genus based on key differences with *Mymaropsis*: polygonal rugulose microsculpture on back of head and mesoscutum (vs. head and mesoscutum punctured in *Mymaropsis*), forewing membrane wrinkled (vs. smooth in *Mymaropsis*), and forewings moderately covered by setae with positive gradient from base to apex (vs. densely and homogeneously setose in *Mymaropsis*). Hind wings are not visible, but they cannot be considered absent, as they might be covered by the forewings. The presence vs. absence of hind wings is an unstable character in the family, as they are present in *Spathiopteryx* and *Mymaropsis*, but absent in *Spathopria* and *Diaspathion*.

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

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

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

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

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

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

Fig. 4

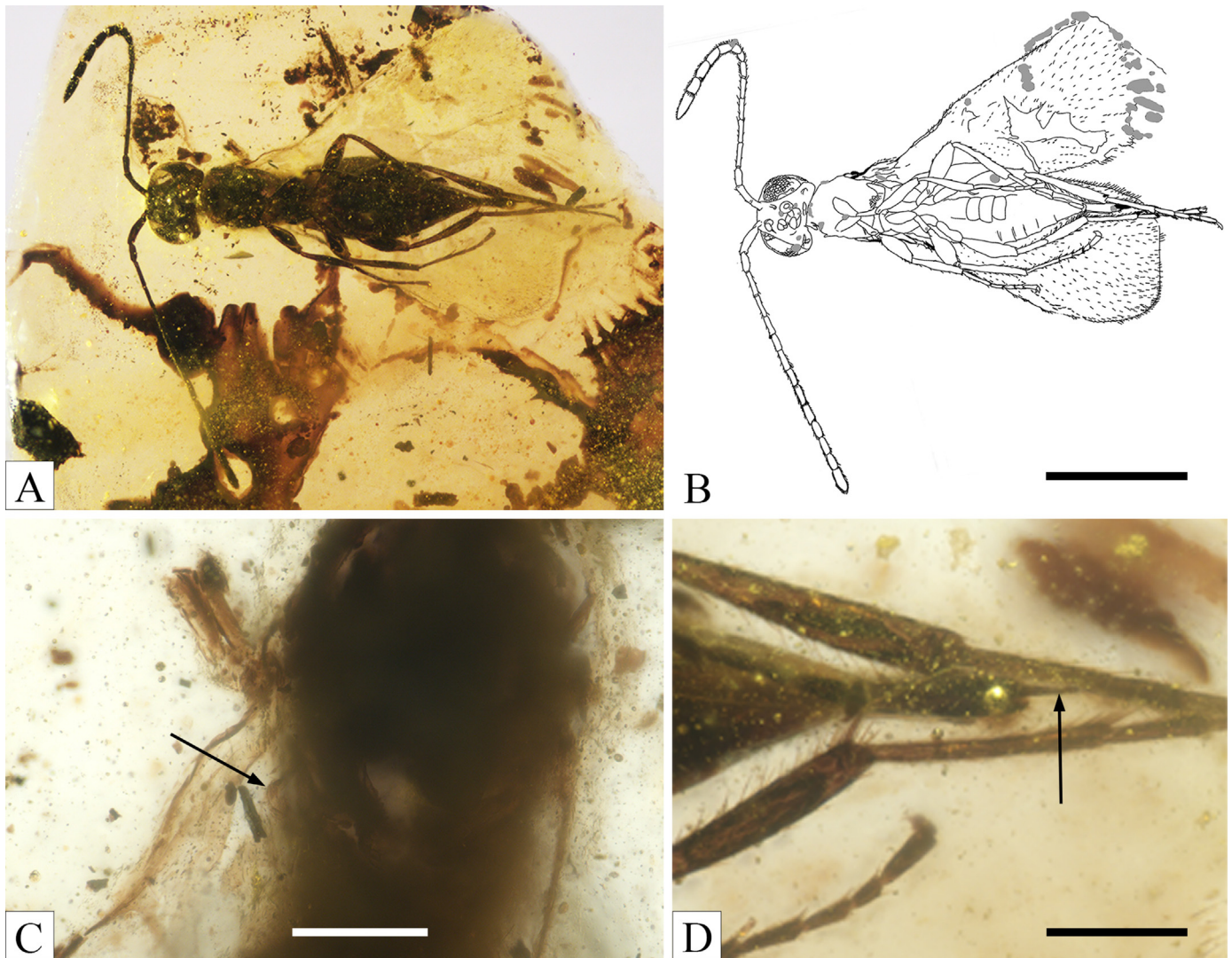
**Material.** CPT-4097 (SJ-07-43), female, from San Just amber. Housed at Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel–Dinópolis) in Teruel, Spain. Complete specimen preserved in an amber piece prepared in an epoxy prism of 24 × 14 mm.

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

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

**Description of new female specimen.** Body 1.40 mm long (until the ovipositor tip) and completely preserved in transparent amber (Fig. 4A, B); integument black to dark brown without fine hairs. Head globular-ovoid, 0.19 mm long and 0.32 mm wide; head plus mesosoma 0.60 mm long; compound eyes not bulging and occupying large portion of head lateral surface, with number of ommatidia over 40; ocelli not visible; scape about twice as long as pedicel and slightly curved; pedicel elongated, with a rimmed distal margin; 12 flagellomeres covered with setae; last eight flagellomeres with more straight, distinct setae almost perpendicular to flagellomeres; distal flagellomere elongated and tapering toward apex; length:width of each antennomere, considering the mean of both antennae, from proximal to distal (in mm): scape 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 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, and F12 0.10:0.26; mouthparts not clearly discernible, hindered by small bubbles. Mesosoma 0.33 mm long and 0.21 mm wide, poorly visible from dorsal view; undetermined structure present left to mesosoma, possibly corresponding to a broken part of mesoscutum. Forewings smooth, 1.21 mm long and 0.52 mm wide; margin covered with rough, stiff setae; highly sclerotised mid-basal section of costal margin; membrane moderately covered with setae (not as dense as in the holotype of *Mymaropsis turolensis* described by Engel et al., 2013); pattern of venation unclear. Possible left hind wing visible (Fig. 4C), very reduced, hamuli not visible. Legs well-preserved; trochanters almost 2/3 length of femora; small rounded trochantellus present; femora and tibiae of fore- and mid-legs covered with a few small setae; femur and tibia of hind-leg densely covered with long, stiff setae; one distal spur on inner side of tibiae, with that of the protibia being curved and 0.05 mm long and those of the meso- and metatibiae being nearly straight and 0.03 mm long; five tarsomeres; basitarsus longer than remaining tarsomeres; lengths of tarsomeres from proximal to distal, forelegs: I 0.12 mm, II 0.05 mm, III 0.04 mm, 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 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; distal tarsomeres with simple pretarsal claws; arolium large. Metasoma 0.77 mm long, 0.30 mm wide; nine visible sclerites; length of exposed part of ovipositor 0.063 mm (Fig. 4D).

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



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

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

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

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

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

**Remarks.** Based on the lack of an original diagnosis for *Mymaropsis baabdaensis* in Krogmann et al. (2016) and according to the requirements of article 13.1.1 of the International Code of Zoological Nomenclature (ICZN, 1999), we propose here a diagnosis to allow the name to be valid for the described species. The general size of the holotype specimen of *M. baabdaensis* is larger than that of the male of *Mymaropsis turolensis*, but smaller than that of the female of the latter. These differences are also present in forewing length (wing length generally suffer less from improper preservation than body length): 0.85 mm (*M. turolensis* male), 1.21 mm (*M. turolensis* female), 1.05 mm (*M. baabdaensis* female) (Engel et al., 2013;

Krogmann et al., 2016). The discovery and description of male specimens of *M. baabdaensis* would be quite useful to better understand the characters attributable to sexual dimorphism. Interestingly, the habitus of *M. baabdaensis* and *M. turolensis* is similar despite the time (more than 20 Ma; late Barremian to late Albian) and geographical distance between them.

#### 4.2. Key to the genera and species of Spathiopterygidae

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

1. Forewing with a well-defined marginal fringe of setae..... 2
- Forewing without a marginal fringe of setae..... 5
2. Compound eye bulging with few ommatidia; forewing slightly sclerotised on basal veins; thin parastigma [hind wing present as a veinal stub, without any remnants of a membrane; notauli meeting posteriorly]..... *Spathiopteryx alavarommopsis*
- Compound eye with numerous ommatidia; forewing sclerotised on basal veins; thick parastigma..... 3
3. Forewing wrinkled, with visible venation and a positive gradient of setae towards the apex; less sclerotised M+Cu, highly sclerotised parastigma..... *Diameneura marveni* gen. et sp. nov.
- Forewing smooth, with unclear venation, M vein not clearly defined and setae distribution on the membrane homogeneous; highly sclerotised M+Cu, less sclerotised parastigma; [hind wing present with a small membranous portion; notauli not meeting posteriorly]..... 4
4. Scape slightly expanded ventrally; pedicel globular; flagellomeres F5–F12 around twice as wide as the remainder..... *Mymaropsis baabdaensis*
- Scape not ventrally expanded; pedicel almost globular; flagellomeres with similar widths..... *Mymaropsis turolensis*
5. Head coarsely punctured; antennae short, not longer than the total body length; metasoma globose, about as long as the mesosoma; [hind wing absent]..... *Spathopria sayrevillensis*
- Head imbricate; antennae elongated, longer than the total body length; metasoma ovoid, longer than the mesosoma; [hind wing absent]..... *Diaspathion ortegai*

## 5. Discussion

### 5.1. Taphonomy

The specimens from San Just amber studied here show different preservation. The holotype of *Diameneura marveni* gen. et sp. nov. (CPT-4095) is preserved in a milky amber piece, allowing good visualisation only from the dorsal view (Fig. 2A), while the *Mymaropsis turolensis* female (CPT-4097) is preserved in a transparent amber piece (Fig. 4A). Interestingly, some parts of the holotype of *Diameneura marveni* gen. et sp. nov. (e.g., the antennae) are covered by small bubbles, probably phloem sap drops (Lozano et al., 2020). These small bubbles could be due to wasp movement in the fluid resin before its death. Its legs are encompassed by a coat of air (Fig. S1). Usually, the bubbles around fossil insects preserved in amber have been linked to the escape of decay gases during necrolysis in resins or to bacterial activity (Martínez-Delclòs et al., 2004). Amber pieces with bioinclusions are related to aerial resin produced by the branches or trunks of resiniferous trees, and the different internal aspect might depend on the conditions of resin production such as stressful situations caused by palaeofires (Martínez-Delclòs et al., 2004). Internal dark marks in the amber

piece including on the *M. turolensis* female (Fig. 4A) correspond to surfaces of desiccation in aerial conditions between different flows of the original resin.

### 5.2. Interrelationships in Spathiopterygidae

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

Engel et al. (2015) summarised the interrelationships of the family as [*Mymaropsis* (*Spathiopteryx* [*Diaspathion* + *Spathopria*])]. Based on current knowledge, this seems to be correct. Nonetheless, the description of new specimens of spathiopterygids is necessary (even corresponding to the known species) to better understand the plesiomorphic and apomorphic conditions of each character. *Diameneura* gen. nov. shows morphological similarities with the basal *Mymaropsis* (such as the forewings with a marginal fringe of short setae and sclerotised mid-basal section of the costal margin) and the derived representatives *Spathopria* and *Diaspathion* (such as the wrinkled forewing membrane). Furthermore, it has unique characters within the family, such as the gradient of setae on the forewing membrane and the polygonal rugulose microsculpture present on back of head and mesoscutum. Therefore, its phylogenetic position and relationships with the other genera are obscure, although it might be closely related to *Mymaropsis* based on the similar anatomic characteristics. A detailed phylogenetic analysis is required to resolve the interrelationships within Spathiopterygidae, as well as the relationships with the other families within Diaprioidea.

### 5.3. Sexual dimorphism and palaeobiology of Spathiopterygidae

Spathiopterygidae is currently represented by seven specimens from six species obtained from Cretaceous ambers, although only two of them are female (Table 1). Therefore, there is little information on sexual dimorphism and intraspecific variability within the family. Female hymenopterans are usually larger than males (Stubblefield and Seger, 1994). This sexual size dimorphism is also present in spathiopterygids based on the comparisons between the male and female specimens of *Mymaropsis turolensis* (Fig. S2). Furthermore, there are other characters that could be related to sexual dimorphism in *M. turolensis*, such as the width of the flagellomeres (thinner in females), the setae on the flagellomeres (F5–F12 with more setae in females vs. F8–F12 in males), and the setae covering the forewings (moderately in females vs. densely in males). The presence of abundant setae (acting as sensillae) on flagellomeres is possibly an adaptation to sense and identify prey for the gravid female searching a host. Interestingly, the diapriid *Trichopria drosophilae* Perkins, 1910 has the most developed



sensillae for host selection situated on the apical flagellomeres of the females (Romani et al., 2002), which maybe suggests a similar use of the sensillae in Spathiopterygidae. Females of both *M. turoloensis* and *M. baabdaensis* show a similar morphology of the metasoma, probably related to the life habit of female parasitoid wasps that need a host to lay eggs. Basitarsi longer than the remaining tarsomeres in females of both species maybe facilitated the attaching to the host previously to the egg laying.

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

The extant Diapriidae, Monomachidae, and Ismaridae are known to be parasitoid wasps (Masner, 1993; Perioto et al., 2016), and the Maamingidae are likely to have a similar life habits based on their morphology (Early et al., 2001a, b). More generally, this is also the case for the whole group Microprocta. Therefore, it is highly probable that spathiopterygids were also parasitoids, based on a simple phylogenetic inference (Nel, 1997). The Diapriidae are parasitoids of several insect groups (Masner, 1993), such as diverse families of dipterans (e.g., Mycetophilidae, Sciaridae, Syrphidae, and Calliphoridae), or secondarily change their hosts to beetles (Staphylinidae and Psephenidae) or ants (Formicidae). The biology of Monomachidae is poorly known, although some species are parasitoids of Stratiomyidae (Diptera) (Masner, 1993; Johnson and Musetti, 2012). The Ismaridae are known to be hyperparasitoids of planthoppers (Hemiptera: Cicadellidae) via the larvae of Dryinidae (Hymenoptera) (Masner, 1976, 1993). The hosts of the Maamingidae remain unknown (Early et al., 2001a, b), although the species *Maaminga marrisi* could be a parasitoid of Phoridae (Diptera) based on their abundance in the same habitat (Early et al., 2001a). The hosts of spathiopterygids could also have been some dipteran families, such as other families within Diaprioidea. However, this is not yet known as the morphological characters of the specimens have not shed light on this topic. Furthermore, all the specimens of the family have been found in amber pieces without the synclusions that could indicate the putative host taxa. New descriptions of spathiopterygids and a detailed study and comparison of the female genitalia with that of other hymenopteran families might help to resolve this question. It is important to note that hymenopterans were the main driver of the Mid-Mesozoic Parasitoid Revolution (MMPR) described by Labandeira and Li (2021). Spanish amber, based on its chronological age, would be included in the final extension of Phase 2 of the MMPR after the diversification events that established six of the seven major parasitoid groups (Labandeira and Li, 2021). In Phase 3 after the MMPR, starting during the Cenomanian, the number of hymenopteran families within Proctotupomorpha and Aculeata greatly increased in diversity, and the insect parasitoid fauna was finally consolidated into food webs (Labandeira and Li, 2021). Interestingly, the latter authors suggested that spathiopterygids could have been endoparasitoids attacking the host at its egg stage.

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

## 6. Conclusions

The family Spathiopterygidae now contains six species in five genera thank to the description of *Diameneura marveni* gen. et sp. nov. that increases the known palaeodiversity of the family. The forewing venation of *Diameneura marveni* gen. et sp. nov. has been interpreted based on sclerotisation, nebulous veins, rows of setae, and reliefs of the membrane, providing a new framework for comparison with new undescribed specimens. The study of the sexual dimorphism of the family has been addressed from the description of the first known female of *Mymaropsis turoloensis*, revealing characters that can be interpreted as differences between the sexes of the same species. The genus *Mymaropsis* would be the most basal member of the family as it retains plesiomorphic state characters, although a phylogenetic analysis is necessary to resolve the interrelationships of the family. As previously proposed, it is plausible that Spathiopterygidae belongs to Diaprioidea since it shares morphological similarities with Mymarommatoidea, Myanmarinidae, and Mymaridae, such as the peduncular forewing with nebulous venation and the reduced hind wings, could be explained as convergent evolution, as these families probably shared similar parasitoid biology. Despite the new information provided here, there are anatomical (presence vs. absence of hind wings) and phylogenetical (interrelationships of the family and with other families) uncertainties. The putative sister group, Maamingidae, is also not very well known. Key questions might be resolved after the monographic study of the new specimens from Burmese amber.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.105128>.