

## A New Lineage of Enigmatic Diaprioid Wasps in Cretaceous Amber (Hymenoptera: Diaprioidea)

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### ABSTRACT

A new family of microhymenopteran wasps is described and figured from three new species discovered in Cretaceous amber of Spain (Albian) and New Jersey (Turonian). Spathiopterygidae Engel and Ortega-Blanco, new family, is allied to the Diapriidae and Maamingidae (Proctotrupomorpha: Diaprioidea), sharing with these families putatively derived features relative to Monomachidae. The family contains three genera and three species, all new: *Spathiopteryx alvarommopsis* Engel and Ortega-Blanco, new genus and species, and *Myamaropsis turolensis* Engel and Ortega-Blanco, new genus and species, both from the Early Cretaceous (Albian) of Spain, and *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new genus and species, from the Late Cretaceous (Turonian) of New Jersey. *Spathopria sayrevillensis* is reconstructed using x-ray synchrotron microtomography. In addition, a peculiar new genus and species, *Iberopria perialla* Engel, Ortega-Blanco, and Delclòs, of stem-group Diapriidae is described from Spanish

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amber. The distinctive features and character combinations of these taxa are discussed in connection with possible relationships to the surviving lineages of diaprioids.

## INTRODUCTION

The superfamily Diaprioidea comprises three extant families of relatively peculiar parasitoid wasps—Monomachidae, Diapriidae, and Maamingidae. The Monomachidae is a putatively archaic group of diapiroids. Two genera are recognized, *Chasca* Johnson and Musetti with two species in Chile and Peru, and *Monomachus* Klug (with *Tetraconus* Szépligeti from southeastern Brazil as a junior synonym: vide Johnson and Musetti, 2012). Within *Monomachus* there are 21 species scattered across Australia and New Guinea, while the majority are from southern Mexico to Argentina and Chile (Musetti and Johnson, 2004). Monomachids are also among the largest of diapiroids, ranging from 1–2 cm in total length, and are parasitoids of Chiromyzinae (Diptera: Stratiomyidae), ovipositing into the egg of the host and emerging from the mature larva or puparium (Riek, 1970; Naumann, 1985, 1991). Johnson and Musetti (2012) have provided a phylogenetic framework for the family. The Maamingidae was only recently discovered and consists of a single genus with two species occurring in New Zealand (Early et al., 2001, 2002). One of the species, *Maaminga rangi* Early et al., is polymorphic, with brachypterous and fully winged forms (Early et al., 2001). Unfortunately, nothing has yet been discovered of maamingid biology. Lastly, the Diapriidae (including the Ismaridae as a subfamily alongside Ambositrinae, Belytinae, and Diapriinae) is the most diverse family with about 4000 species, although this is certainly a mere fraction of the total global diversity (e.g., Masner and García, 2002). Diapriidae occur worldwide and the family is varied in its biology, although most species, where known, are parasitoids of fly puparia, which is likely the groundplan biology for the family, as well as that of the superfamily. Significant taxonomic and phylogenetic work remains to be conducted throughout the Diaprioidea. Not surprisingly, the fossil record of these families is scarce. To date no fossils are known of Maamingidae and Monomachidae, and diapiroids are largely known from a few amber inclusions in Cretaceous deposits from France and Japan (Fujiyama, 1994; Perrichot and Nel, 2008; Lak and Nel, 2009) and from mid-Eocene Baltic amber (e.g., Maneval, 1938; Szabó and Oehlke, 1986; Buhl, 1999, 2002). Specimens are also known from the Eocene amber of China (Hong, 2002), but these require verification of their taxonomic assignments. Perrichot and Nel (2008) have provided a checklist of the described amber species, along with those compression fossils currently assigned to the family.

Over the last 15 years a series of Cretaceous diapiroids have gradually come to light, three of which cannot be classified into any of the families as currently circumscribed (figs. 1–5). Two of these specimens come from the Albian amber deposits of Spain and the last from the Turonian amber of New Jersey. Herein we provide a description of these peculiar wasps in order to bring them to the attention of those studying amber insect inclusions, as well as to the community of hymenopterists. In addition, we provide some brief comments on the possible affinities of these taxa relative to other diapiroid wasps and accompany these with descriptions of two definitive diapiroids from the Albian deposits of Spain.

## MATERIAL AND METHODS

Two individuals of the new family were found in two geological units within the northeastern Iberian Peninsula, the Basque-Cantabrian Chain and the Iberian Chain. These units date from the Albian and coincide with the late syn-rift cycle (latest Oxfordian to middle Albian rifting cycle 2) and with the development of some important basins into the Iberian Plate, such as the Maestrat Basin and Basque-Cantabrian Basin (Salas et al., 2001). Both Peñacerrada (Basque-Cantabrian Basin) and San Just (Maestrat Basin) ambers are included in the Escucha Formation, associated with coal or organic-rich sediments. The precise age of these deposits is controversial; the Escucha Formation is diachronous. Recently, a middle Albian age was proposed for the San Just outcrop on the basis of angiosperm pollen (Villanueva-Amadoz et al., 2010), and it was included in the El Regachuelo Member. The Peñacerrada outcrops have yielded a diverse palynomorph assemblage consisting of spores, gymnosperm, and angiosperm pollen grains, in addition to dinoflagellate cysts and acritarchs, suggesting an Early Albian age (Alonso et al., 2000; Barrón et al., 2001). The fauna found as bioinclusions suggests a similar age, and a lot of genera are shared between both outcrops (Peñalver and Delclòs, 2010), as well as many of the same species across a variety of insect orders (Arillo et al., 2008; Ortega-Blanco et al., 2011a). Both localities are associated with deltaic environments, with the Maestrat Basin dominated by freshwater and the Basque-Cantabrian Basin influenced by marine water. The amber-bearing deposit of San Just is the product of desiccated ponds associated with fluvial environments or freshwater swamps, while the Peñacerrada deposit is linked to marine environments formed under a subtropical, seasonal, wet-dry climate (Peñalver et al., 2007; Peñalver and Delclòs, 2010).

A single individual was discovered in Late Cretaceous (Turonian) amber from Sayreville, New Jersey. The geology of the Sayreville site has been comprehensively discussed by Grimaldi et al. (2000). The New Jersey specimen was found in a densely turbid piece of amber, obscuring most details of the individual. Accordingly, the specimen was subjected to synchrotron x-ray computerized microtomography. The piece was scanned at the European Synchrotron Radiation Facility (ESRF) in Grenoble, France, using a propagation phase contrast microtomography protocol (PPC-SR $\mu$ CT), as described in Tafforeau et al. (2006) and Soriano et al. (2010). The scan was made in ID19 beamline, with a monochromatic beam using a RuB4C multilayer with a set energy of 20 keV. The tomography consisted of 2000 projections acquired through a 180° rotation and 0.3 seconds of exposure time. The images were acquired at 1.4  $\mu$  of voxel size and a propagation distance of 25 mm. All microtomographic data, including original and segmented slices, segmentation files, pictures, animations, and stereolithographic models will be made available eventually at the ESRF paleontological online database under development (<http://paleo.esrf.eu>).

Light microscopy of all specimens was undertaken with Olympus BX41 and SZX12 stereomicroscopes, and imaged with Olympus U-DA and Cannon 7D digital camera systems.

Abbreviations for institutional repositories are: **AMNH**, Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York, New York; **MCNA**, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; and **CPT**, Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain.

## SYSTEMATIC PALEONTOLOGY

## Superfamily Diaprioidea Haliday

**Spathiopterygidae** Engel and Ortega-Blanco, new family

TYPE GENUS: *Spathiopteryx* Engel and Ortega-Blanco, new genus.

DIAGNOSIS: **Male.** Head hypognathous, slightly wider than long, without posterior bel-  
lowslike structure. Mandibles endodont and overlapping, bidentate; maxillary palpus appar-  
ently 2 segmented; labial palpus apparently 3 segmented; malar space wide; labrum short,  
with rounded apex; clypeus short, wider than long, about as long as mandibular width;  
epistomal sulcus well impressed. Compound eyes of moderate size, circular, with coarse  
ommatidia (raspberrylike); ocelli present; occipital carina absent. Antennal toruli at about  
midface level, widely separated from clypeus, positioned on weakly protrudent antennal  
shelf, not overhung by frontal lamella; frons without depressions or grooves for reception of  
scape. Antenna large with respect to body length, slender, 14-segmented, anellus absent,  
without placoid sensilla, but with distinct curved trichoid sensilla apically on flagellomeres  
(visible only in *Spathiopteryx* and *Mymaropsis*); scape longer than remaining antennomeres,  
not greatly elongate; flagellomeres without carinae, without sex segment, each longer than  
wide, none expanded or flattened. Mesosoma higher than wide; pronotum without acute  
reentrant declivity, posterolateral corner nearly reaching tegula, posterior margin deeply con-  
cave, lateral surface of pronotum clearly fused to mesopleuron; prepectus absent. Mesoscu-  
tum somewhat vaulted, with percurrent or indistinct notauli, lateral borders slightly  
converging posteriorly, parapsidal lines apparently absent, transscutal sulcus complete, rela-  
tively straight; mesoscutellum about as long as wide, axilla not produced. Metanotum reduced  
to thin, transverse strip, much shorter than basal area of propodeum. Mesopleuron higher  
than long, expanded ventrally. Propodeum short, smooth, without carinae or areolae. Legs  
very large with respect to body length; procoxae well separated from mesocoxae, mesocoxae  
close to metacoxae; trochantellus present on all legs; femora slightly dilated medially; tibial  
spur formula 1-1-1, protibial spur slightly curved, with simple apex; metatibia not greatly  
swollen; tarsi pentamerous, basitarsus longest tarsomere; pretarsal claws simple, arolium  
large. Forewing larger than body, extending well beyond metasomal apex, spatulate, with or  
without well-defined marginal fringe (present in *Spathiopteryx* and *Mymaropsis*, absent in  
*Spathopria*) (figs. 1–6), fringe setae not greatly elongate; venation represented by weakly  
nebulous or largely spectral lines on membrane (figs. 1–3, 6, 7), membrane with scattered  
short setae over surface, hyaline, smooth in *Spathiopteryx* and *Mymaropsis* and reticulate in  
*Spathopria*, pterostigma absent; venation reduced (figs. 6, 7), without C (i.e., open costal  
cell), single basal stem branching into spectral trace of A, A running to posterior wing mar-  
gin before midlength; Cu branching shortly after divergence from A, diverging to posterior  
margin of wing and running parallel to A and M; Rs+M not contacting directly with Cu,  
diverging before middle of wing; Rs diverging to wing apex parallel to R and anterior wing  
margin and M trace extending posteriorly to apico-posterior apex of wing. Hind wing  
reduced to absent (very reduced but present in *Mymaropsis*, reduced to veinal stub in *Spa-  
thiopteryx*, absent in *Spathopria*). Metasoma inserted low on mesosoma, between metacoxae;

terga extend laterally to cover sterna laterally; no syntergites or synsternites visible; first metasomal segment reduced to form small petiole, largely obscured by second metasomal segment; second (abdominal III) and third (abdominal IV) metasomal segments largest, third (abdominal IV) larger than second, remaining segments distinctly shorter; aedeagus with blunt apex, parameres apparently separate from aedeagus.

**INCLUDED TAXA:** Three genera are currently included in the family—*Spathiopteryx* and *Mymaropsis* from the Early Cretaceous of Spain, and *Spathopria* from the Late Cretaceous of New Jersey. It is possible that exploration of other Cretaceous ambers will eventually reveal further spathiopterygid species extending the distribution of the family across the period and around the globe, much like the families Stigmaphronidae (Engel and Grimaldi, 2009; Ortega-Blanco et al., 2011b; McKellar and Engel, 2011a) and Serphitidae (Brues, 1937; Kozlov and Rasnitsyn, 1979; Ortega-Blanco et al., 2011c; Engel et al., 2011; McKellar and Engel, 2011b). However, given that the deposits of New Jersey and Spain were relatively close through the earlier part of the Cretaceous it is equally plausible that the family was more restricted in distribution. If so, then Cretaceous deposits most likely to harbor spathiopterygids might be those in Canada, Alabama, and France, with progressively more distant ones in Lebanon, Ethiopia, Alaska, Siberia, and Myanmar.

#### Key to Genera of Spathiopterygidae

1. Hind wing reduced but present; forewing with well-defined marginal fringe of setae, membrane smooth ..... 2
- Hind wing absent; forewing without marginal fringe of setae, membrane distinctly roughened and wrinkled (Turonian: New Jersey) ..... *Spathopria*, n. gen.
2. Hind wing present as veinal stub, without remnant of membrane; notauli meeting posteriorly; metasoma about as long as remainder of body; compound eye bulging with few ommatidia (Albian: Peñacerrada, Spain) ..... *Spathiopteryx*, n. gen.
- Hind wing with small membranous portion; notauli not meeting posteriorly; metasoma short, shorter than mesosoma; compound eye with numerous ommatidia (Albian: San Just, Spain) ..... *Mymaropsis*, n. gen.

#### *Spathiopteryx* Engel and Ortega-Blanco, new genus

**TYPE SPECIES:** *Spathiopteryx alavarommopsis* Engel and Ortega-Blanco, new species.

**DIAGNOSIS:** Head closely punctured, punctures not particularly coarse. Compound eyes bulging, with a reduced number of coarse ommatidia (around 40). Flagellomeres I–IV slightly more elongate and thin than flagellomeres V–XII. Pronotum with distinct, strong, transverse striation. Mesoscutum with notauli well impressed, percurrent, distinctly converging posteriorly, meeting at very acute angle, integument otherwise strongly imbricate. Forewing membrane smooth, with scattered, rough, short setae, with distinct marginal fringe of short setae; venation distinguishable thanks to gaps in rough setal pattern, otherwise venation nebulous to spectral. Hind wing present as veinal stub, without a relic of membrane. Metasoma about as long as remainder of body.

ETYMOLOGY: The new genus-group name is a combination of the Greek terms *spathe* (“paddle”) and *pteryx* (“wing”). The name is feminine.

*Spathiopteryx alavarommopsis* Engel and Ortega-Blanco, new species

Figures 1, 6A, 7A, 7B

DIAGNOSIS: As for the genus.

DESCRIPTION: **Male.** Total length 0.85 mm; forewing length 1.08 mm; integument black to dark brown. Head punctured; occipital carina absent but distinct arista demarcating where dorsal and occipital surfaces would separate. Ocelli small; compound eyes composed of around 40 large ommatidia. Antenna arising upward from a distinct but not very prominent frontal shelf, with moderately long curved setae; apical flagellomeres with a distinct curved seta almost perpendicular to individual flagellomeres; scape slightly curved; pedicel around one-half length of scape; flagellomeres shorter than scape and longer than pedicel. Forewing membrane smooth, scarcely setose, setae mainly concentrated on wing margins and outlining venation, thereby making venation pattern more distinguishable: R, Rs, M, a portion of Rs+M, Cu, and A present. Hind wings present merely as stalk, without remnants of membrane visible. Legs elongate (around body length) and setose, setation concentrated apically on each podite; tibia with stiff, apical, inner row of setae; probasitarsus much shorter than remainder of tarsus, meso- and metabasitarsomeres just slightly shorter than remainder of corresponding tarsomeres. Metasomal sterna largely obscured by lateral portions of greatly enlarged terga which wrap around ventrally.

HOLOTYPE: Male; MCNA 12603; labeled as Early Cretaceous (Albian); Peñacerrada [Peñacerrada I = Moraza, Burgos], Álava, Spain. Deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

ETYMOLOGY: The specific epithet is a combination of the generic name *Alavaromma* (type genus of Alavarommatidae, also in Spanish amber: Ortega-Blanco et al., 2011a) and the Greek suffix *opsis* (“sight, appearance,” thus “looking like”) and refers to the superficial similarities between these two taxa, particularly in some details of wing form, despite their relatively distant relationship among proctotrupomorphan wasps.

*Mymaropsis* Engel and Ortega-Blanco, new genus

TYPE SPECIES: *Mymaropsis turolensis* Engel and Ortega-Blanco, new species.

DIAGNOSIS: 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.

ETYMOLOGY: The new genus-group name is a combination of *mymar-* (a reference to the chalcidoid family Mymaridae in which the hind wings are similarly reduced) and the Greek suffix *opsis* (meaning, “sight, appearance,” thus “looking like”). The name is feminine.

*Mymaropsis turolensis* Engel and Ortega-Blanco, new species

Figures 2, 6B, 7D, 7E

DIAGNOSIS: As for the genus.

DESCRIPTION: Total length 0.63 mm; forewing length 0.85 mm; integument black to dark brown. Head globular-ovoid. Compound eyes occupying large portion of head, with an unclear number of ommatidia but certainly more than 40 (unlike *S. alavarommopsis*). Maxillary and labial apical palpomeres with two distinct apical setae. Antenna arising upward from prominent toruli and from weakly developed frontal shelf; flagellomeres covered by moderately long, curved setae; last five flagellomeres with more straight, distinct seta, almost perpendicular to flagellomere; scape short and slightly curved; pedicel almost globular, with rimmed distal margin. Forewing with highly sclerotized midbasal sector of anterior margin, also covered by rough, stiff setae or spicules; forewing membrane moderate to densely covered by setae, clearly more dense than in other two spathiopterygid species and more homogeneous; pattern of venation pattern less clear. Hind wing very reduced, with three distal hamuli. Legs highly setose, every seta arising from small prominence, mainly on femora and tibiae; trochanter almost 2/3 of femur length; small, rounded trochantellus present; basitarsi almost as long as remainder of tarsomeres; pretarsal claws simple; arolium large. Metasoma with imbricate or punctured sculpture (difficult to discern), shorter than mesosoma; first tergum half as long as second tergum; second tergum largest, almost covering all of remaining terga; genitalia not visible.

HOLOTYPE: CPT 4077; labeled as Early Cretaceous (Albian); San Just, Teruel, Spain. Deposited in the Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain.

ETYMOLOGY: The specific epithet *turolensis* refers to Teruel, the Spanish province containing the outcrop where the specimen was found.

*Spathopria* Engel, Ortega-Blanco, and Grimaldi, new genus

TYPE SPECIES: *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new species.

DIAGNOSIS: Head with strong, coarse, contiguous punctures, appearing almost areolate. Flagellomeres I–IV distinctly longer than wide, distinctly longer than remaining flagellomeres; pedicel not rimmed. Pronotum with strong transverse striation. Mesoscutum with notauli indistinct among strong longitudinal striations, punctured between striae. Forewing membrane distinctly roughened and wrinkled, without scattered short setae, without marginal fringe of setae. Hind wing completely absent. Metasoma about as long as mesosoma.

ETYMOLOGY: The generic name is a combination of the Greek terms *spathe* (“paddle”) and the root of *Diapria*, commonly employed among diapiroid wasps [Greek, *dia*, “between,” and *prio*, “to saw”; while it is often asserted that the root *pria* means “little wasp” in Latin, this is apparently an error, and Latreille’s (1796) usage of the name seems to refer to his understanding of the ovipositor, “Tarière dans la femelle, droite, renfermée entre deux pièces, cachée” (our emphasis)]. The name is feminine.

***Spathopria sayrevillensis*** Engel, Ortega-Blanco, and Grimaldi, new species

Figures 3–5, 6C, 7C

DIAGNOSIS: As for the genus.

DESCRIPTION: **Male.** Total length 0.80 mm; forewing length 0.95 mm; integument black to dark brown. Head globular-ovoid, slightly wider than long, with coarsely punctured sculpture. Compound eyes occupying around half lateral view of head, with unclear number of ommatidia but apparently more than 40 (unlike *S. alavarommopsis*). Ocelli small (smaller than in *M. turolensis*), placed between compound eyes, very indistinct due to similar size and shape of head sculpture, but slightly ovoid, placed in shallow depression instead of on protuberance as in *M. turolensis*. Antenna arising upward from prominent toruli but from faintly developed frontal shelf; flagellomeres not setose, without regular setae or distinct perpendicular setae; scape very short and curved; pedicel as long as wide, less than one-half length of scape. Forewing with roughened and wrinkled membrane, not covered by setae, marginal setae absent; venation spectral but distinct. Legs almost galbrous; trochanter curved, less than half length of femur; apparently small, rounded trochantellus present; basitarsi almost as long as remainder of tarsomere; pretarsal claws simple; arolium large. Metasoma with sculpture unclear, about as long as mesosoma (similar to several mymaromatoids); terga unclear due to preservation but apparently tergum 2 largest and overlapping succeeding terga; genitalia not visible.

HOLOTYPE: Male; AMNH NJ-145; New Jersey, Middlesex County, Sayreville, White Oaks pit, Late Cretaceous (Turonian); deposited in the amber fossil collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet refers to the borough of Sayreville, located along the Raritan River, in New Jersey.

Family Diapriidae Haliday

***Iberopria*** Engel, Ortega-Blanco, and Delclòs, new genus

TYPE SPECIES: *Iberopria perialla* Engel, Ortega-Blanco, and Delclòs, new species.

DIAGNOSIS: **Male.** Mandibles short, apparently bidentate. Compound eyes prominent, sub-circular; ommatidia small. Antenna 14 segmented; scape elongate, nearly as long as head height (figs. 7A, 8A), inserted high above clypeus, toruli situated on prominent antennal shelf, opening upward, torular level in upper part of compound eye; frons without depression or groove for reception of scape. Pronotum not prominently developed; epomium not developed; meso-scutum weakly convex. Metatibia with row of stout setae running along inner margin. Fore-



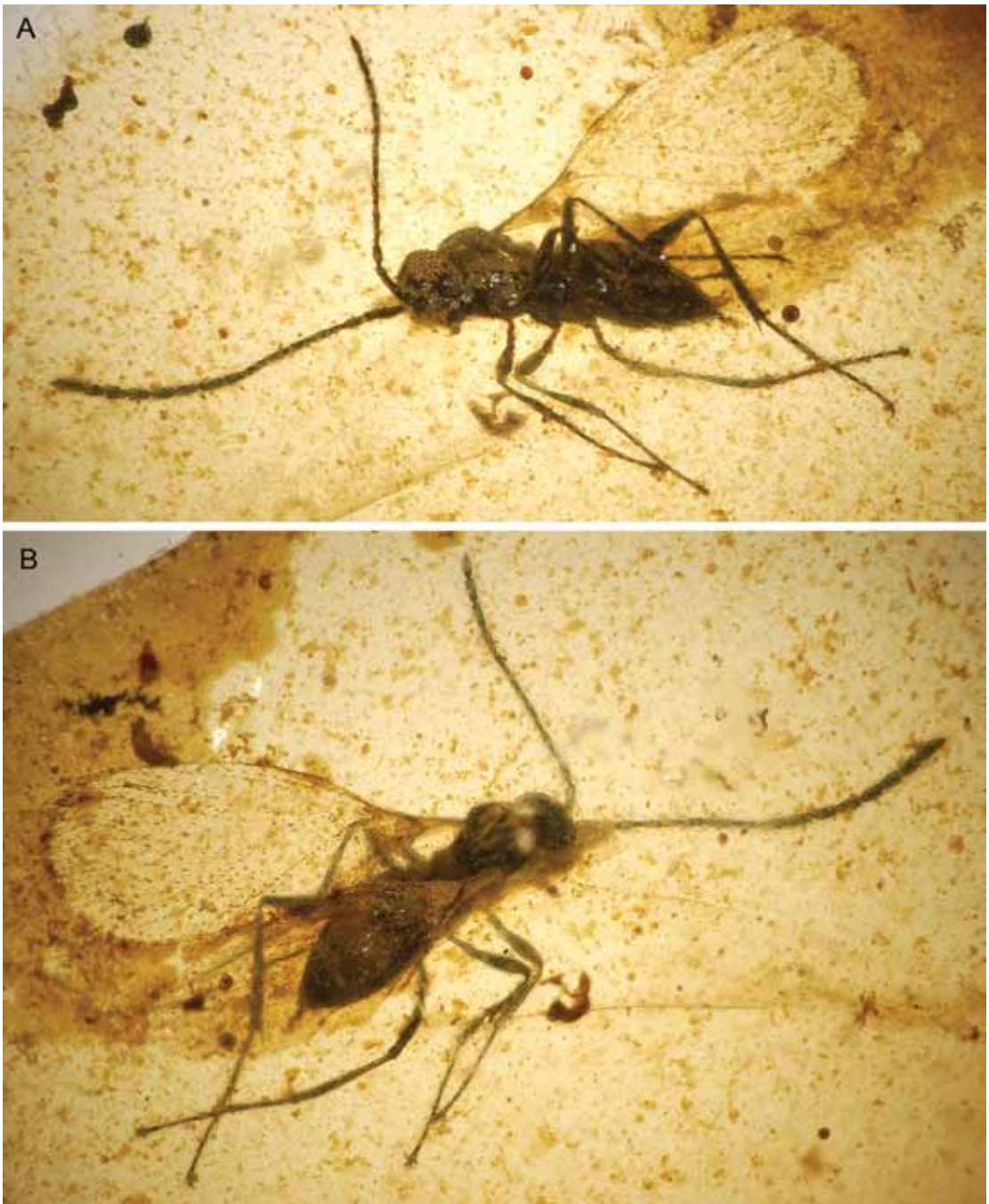


FIGURE 1. Photomicrographs of holotype male of *Spathiopteryx alavarrowmopsis* Engel and Ortega-Blanco, new genus and species (MCNA 12603), in Spanish amber (from Peñacerrada outcrop). Note that the left antenna is broken at the amber surface, leaving only 10 antennomeres preserved. **A.** Ventral oblique view. **B.** Dorsal oblique view.



FIGURE 2. Photomicrograph of holotype of *Mymaropsis turolensis* Engel and Ortega-Blanco, new genus and species (CPT 4077), in Spanish amber (from San Just outcrop). **A.** Ventral oblique view. **B.** Lateral oblique view. **C.** Dorsal oblique view.



FIGURE 3. Photomicrograph of holotype male of *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new genus and species (AMNH NJ-145), in New Jersey amber.

wing without marginal cell (figs. 8B, 9); submarginal vein long, with short, thickened marginal vein, stigmal vein about as long as marginal vein, expanded at apex; basal vein present, tubular; M+Cu present, tubular; stub of free abscissa Cu present, tubular; distal abscissae Rs and M apparently absent (fig. 9); membrane with scattered, fine setae, hyaline; with fringe of short, fine setae; hind wing with tracheate marginal vein, bearing three hamuli apically; M+Cu present as nebulous vein, diverging apically to form M meeting marginal vein, and Cu extending to posterior wing margin. First metasomal segment petiolate, broadly tubular, about longer than high, with longitudinal striae; gaster distinctly broader than petiole; metasomal terga II and III (= abdominal terga III and IV) largest segments, tergum II not greatly enlarged relative to tergum III; remaining terga progressively and slightly shorter than tergum III.

**ETYMOLOGY:** The generic name is a combination of the of “Iberian,” in reference to the Iberian Peninsula, where the type originates, and the root of *Diapria*, type genus of Diapriidae, commonly employed among diaprioid wasps. The name is feminine.



FIGURE 4. Microtomographic reconstruction of holotype of *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new genus and species (AMNH NJ-145), in New Jersey amber. A. Dorsal view. B. Right lateral view.



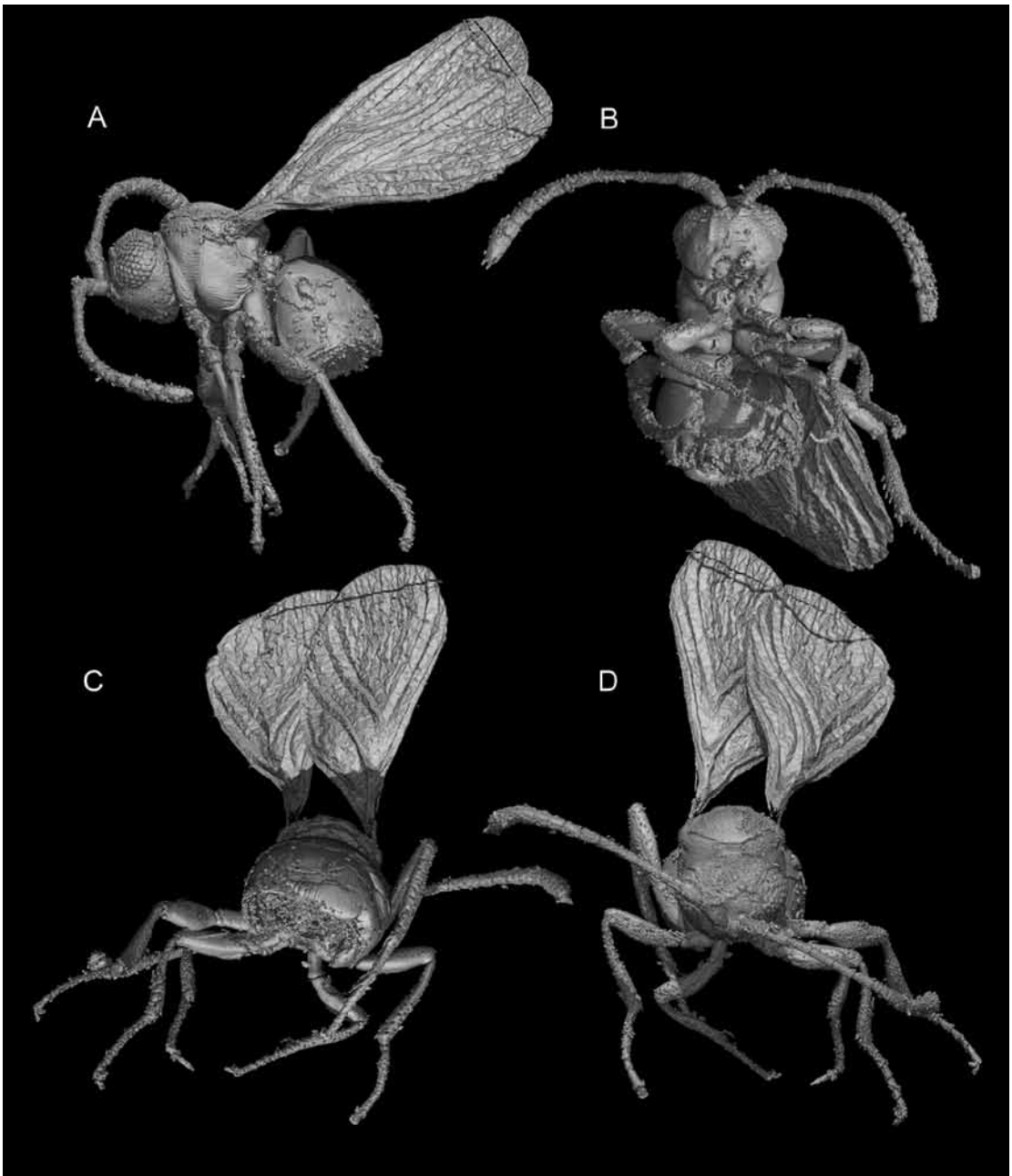


FIGURE 5. Microtomographic reconstruction of holotype of *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new genus and species (AMNH NJ-145), in New Jersey amber. A. Left lateral view. B. Ventral view. C. Caudal view. D. Frontal view.

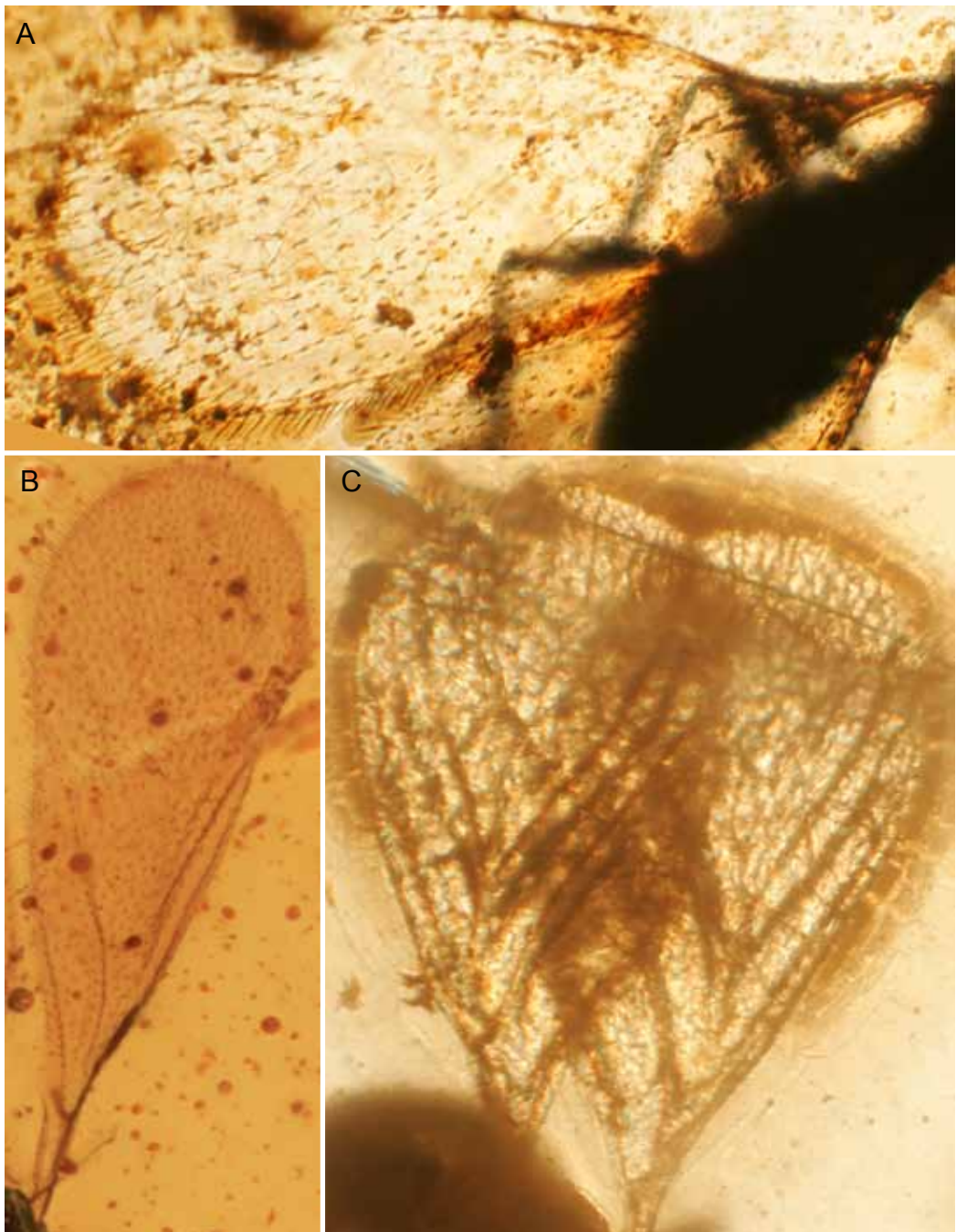


FIGURE 6. Wing-venation patterns of spathiopterygids. **A.** *Spathiopteryx alavarommopsis* Engel and Ortega-Blanco, new genus and species (MCNA 12603). **B.** *Mymaropsis turolensis* Engel and Ortega-Blanco, new genus and species (CPT 4077). **C.** *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new genus and species (AMNH NJ-145).

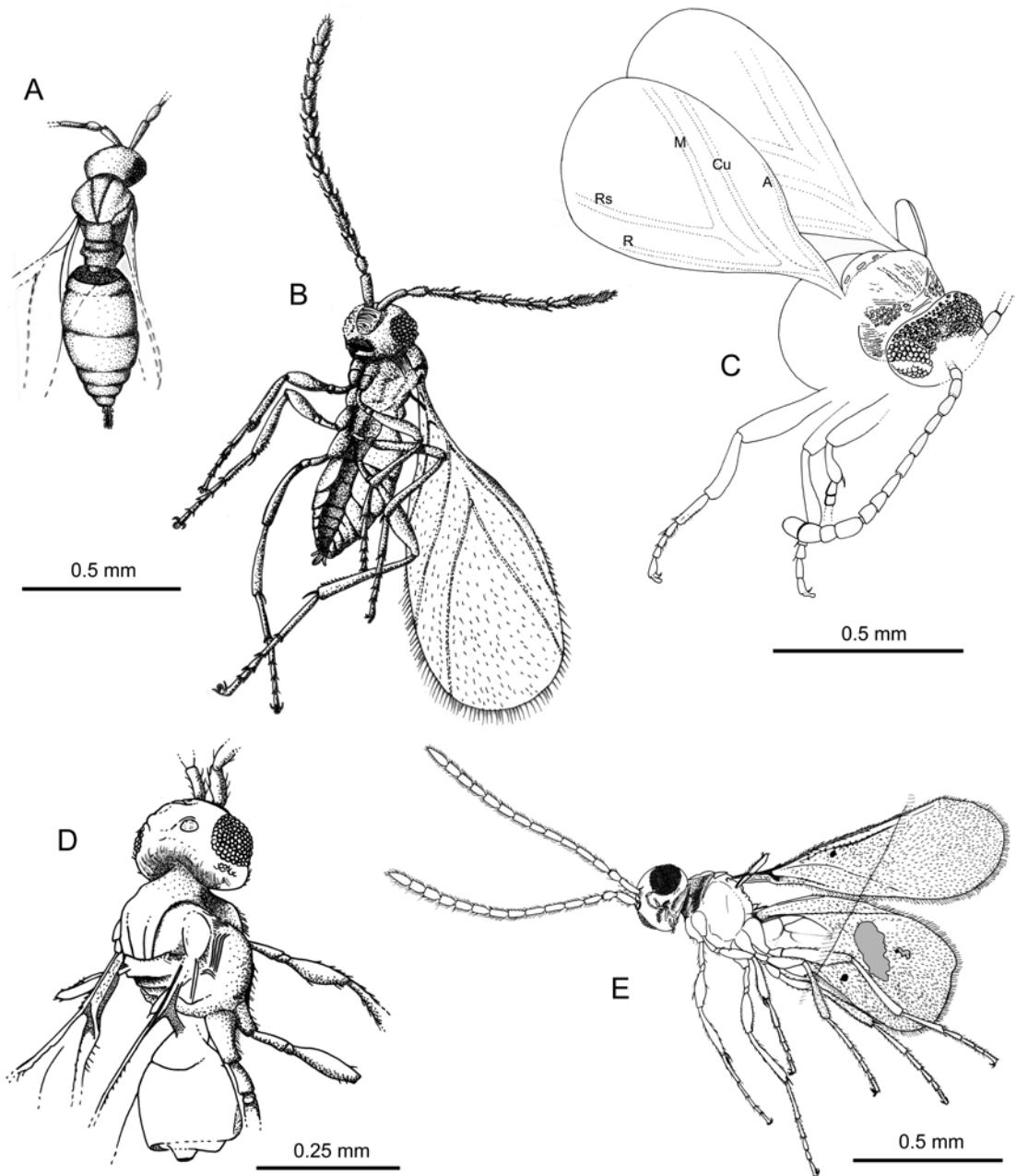


FIGURE 7. Line drawings of spathiopterygids. **A.** Dorsal detail of *Spathiopteryx alavarommopsis* Engel and Ortega-Blanco, new genus and species (MCNA 12603). **B.** Ventral view of *S. alavarommopsis* (to the same scale as A). **C.** Visible details of *Spathopria sayrevillensis* Engel, Ortega-Blanco, and Grimaldi, new genus and species (AMNH NJ-145). **D.** Dorsal details of *Mymaropsis turolensis* Engel and Ortega-Blanco, new genus and species (CPT 4077). **E.** Ventral oblique of *M. turolensis*.



FIGURE 8. Photomicrographs of Spanish amber diapiiids. **A.** Holotype of *Iberopria perialla* Engel, Ortega-Blanco, and Delclòs, new genus and species (MCNA 9896). **B.** Detail of wings of *I. perialla*. **C.** Fragmentary diapiiid (MCNA 9543).



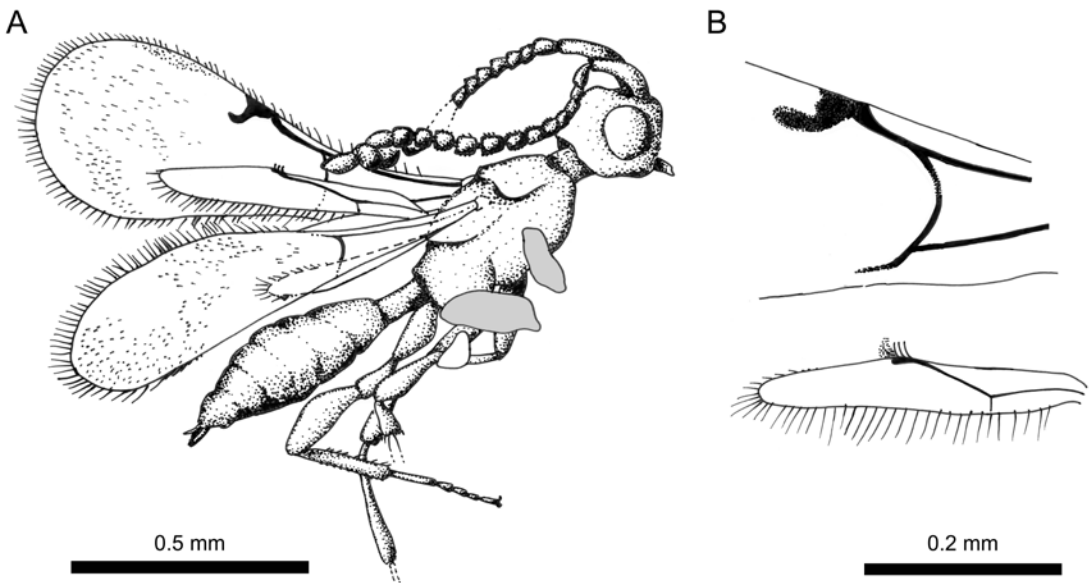


FIGURE 9. Line drawing of *Iberopria perialla* Engel, Ortega-Blanco, and Delclòs new genus and species (MCNA 9896). A. Lateral view. B. Details of fore- and hind-wing venation.

*Iberopria perialla* Engel, Ortega-Blanco, and Delclòs, new species

Figures 8A, 8B, 9

DIAGNOSIS: As for the genus.

DESCRIPTION: **Male.** As for the genus, with the addition of the following minor metrics: total length 1.19 mm; forewing length 0.91 mm; integument dark brown.

HOLOTYPE: Male; MCNA 9896; labeled as Early Cretaceous (Albian); Peñacerrada [Peñacerrada I = Moraza, Burgos], Álava, Spain. Deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain. Specimen well preserved, but the amber piece is quite disturbed with much debris and turbid matrix.

ETYMOLOGY: The specific epithet is the Greek word, *periallos*, meaning “before all others.”

Genus and species indeterminate

Figure 8C

MATERIAL: Sex indeterminate; MCNA 9543; labeled as Early Cretaceous (Albian); Peñacerrada [Peñacerrada I = Moraza, Burgos], Álava, Spain. Deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

COMMENTS: While this specimen is distinctly a diapriid as evidenced by the elongate scape, antennae widely separated from the clypeus, antennal toruli situated on a prominent shelf, 5-segmented maxillary palpi, and the lack of striae laterally on the pronotum. Unfortunately, the metasoma is not preserved at all (fig. 8C), meaning it is impossible to determine whether the individual possessed an enlarged second metasomal segment, or exhibited the plesiomorphic condition like *Iberopria*. In addition, only small basal fragments are preserved for both sets of wings, leaving

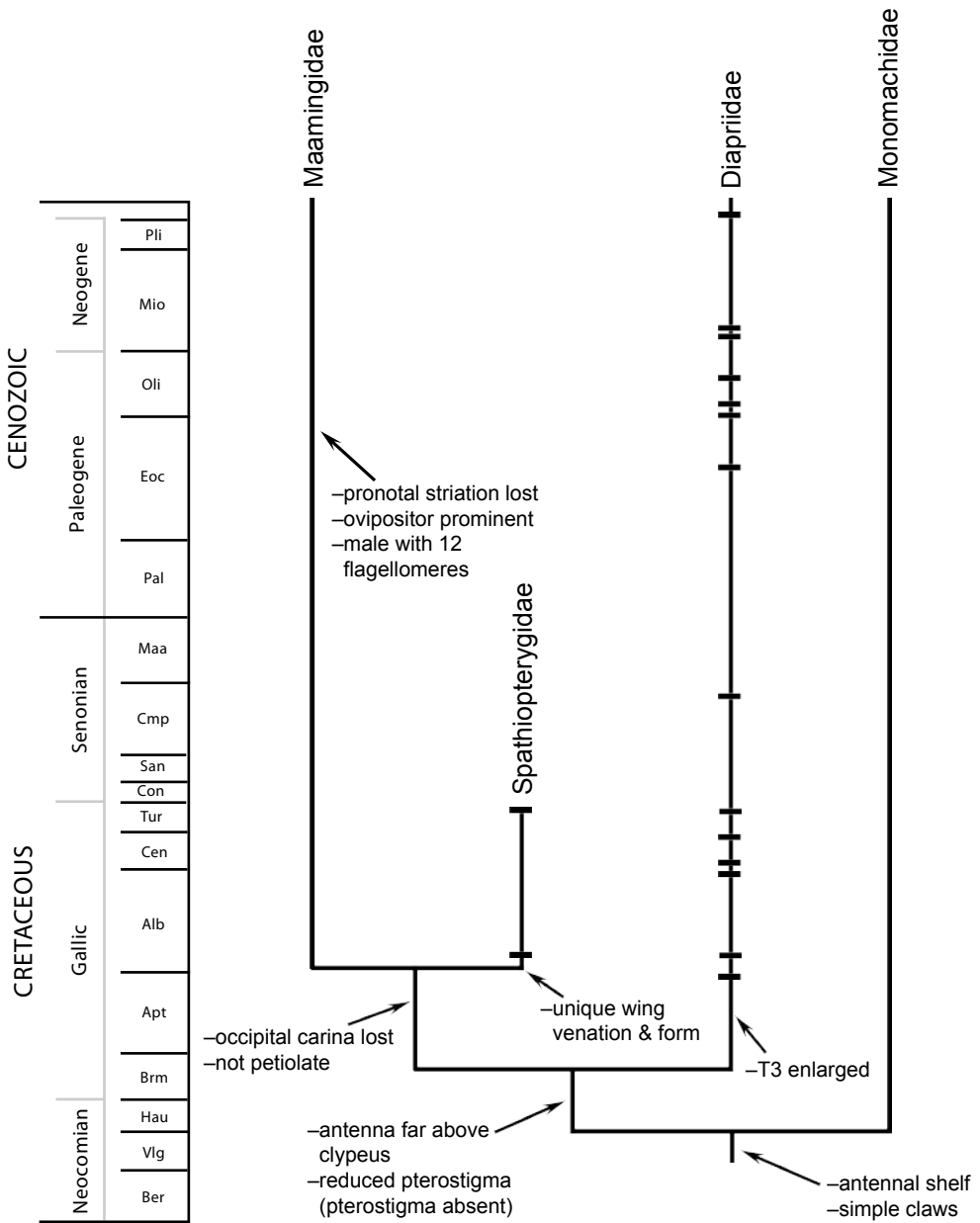


FIGURE 10. Hypothesis of relationships among families of Diaprioidea, with significant putative apomorphies indicated for clades and fossil records mapped (black bars).

the venation almost entirely unknown. The individual is 0.7 mm in preserved length (in life clearly longer), with 14 antennal segments (thereby it could have been either a female or male as the number of antennomeres is somewhat variable among diapriids).

## DISCUSSION

It is fascinating to discover a group of species so uniquely modified and yet simultaneously exhibiting so many traits that in isolation are reminiscent of different families already familiar. The wings of spathiopterygids are immediately reminiscent of *Alavaromma*, a primitive lineage of mymarommatoid wasps in Early Cretaceous amber of Spain (Ortega-Blanco et al., 2011a). The spatulate form of spathiopterygid forewings is overall very similar to Mymarommatoida including the reduced venation, albeit still distinct as nebulous or spectral traces rather than completely absent as in the latter lineage. Like *Alavaromma*, which is presumably basal among the Mymarommatoida, the marginal fringe of setae is well developed but short in comparison to the stiff, elongate setae more typical of the superfamily. Even more remarkable are the wings of *Spathopria*, in which the membrane is roughened, loosely approximating the reticulate membrane of Gallorommatidae and Mymarommatidae (Gibson et al., 2007). Despite these superficial similarities, the taxa discussed herein lack critical features of Mymarommatoida or closely related groups such as Serphitoidea and Chalcidoidea. Most importantly, the reduced first metasomatic segment that is not developed into a tubular petiole, alongside a tubular second metasomatic segment (i.e., not bipetiolate) excludes these fossils from the Mymarommatoida and Serphitoidea. In addition, the lack of a developed prepectus and the absence of placoid sensilla on the antenna further exclude the spathiopterygids from the Chalcidoidea. Instead, the insertion of the antennae on a defined antennal shelf (albeit more weak than in diapriids or maamingids, yet more distinct than in monomachids) and the presence of curved trichoid sensilla apically on the flagellomeres indicate an affinity with the diaprioids (Early et al., 2001; Sharkey, 2007).

*Iberopria* is an interesting discovery in that like crown-group diapriids the genus has a prominent antennal shelf, with antennal toruli widely separated from the clypeus; an elongate scape; lacks striations laterally on the pronotum; and the genus has a reduced wing venation with a reduced, linear “pterostigma” (reduced relative to Monomachidae). Unlike Diapriidae s.s., however, the genus does not have the second metasomal segment (third abdominal) greatly enlarged, being much larger than all of the other segments. Other Cretaceous diapriids have been documented, but all of these share with modern members the enlarged second metasomal segment (e.g., Fujiyama, 1994; Perrichot and Nel, 2008; Lak and Nel, 2009). Thus, *Iberopria* is of considerable interest as it appears to represent a stem group to other Diapriidae, and thereby helps to polarize apomorphies for this distinctive family.

Among the families of the formerly conceived Proctotrupeoidea s.l. (e.g., Naumann and Masner, 1985), studies have repeatedly united the Diapriidae, Monomachidae, and Maamingidae into a natural group (e.g., Dowton et al., 1997; Dowton and Austin, 2001; Castro and Dowton, 2006; Sharkey, 2007; Davis et al., 2010; Sharkey et al., 2012). The superfamily Diapri-

oidea (as this clade is now called) is supported by the presence of the antennal shelf, which is more prominent in the Diapriidae, Maamingidae, and the fossils described herein, but nonetheless present in Monomachidae although not as strongly developed (Naumann, 1985; Musetti and Johnson, 2004). Relationships among these families remain in flux, and so we provide herein an exploratory evaluation of some characters which might support a particular topology and placement for Spathiopterygidae, noting that much cladistic work remains to be undertaken. It is difficult to determine whether the relatively complete venation of Monomachidae is a plesiomorphic feature for the family or it is a reversal. Naturally, determination of such polarity depends on the overall placement of Diaprioidea among the proctotrupoidean superfamilies. If this clade is more derived among the superfamilies, and thereby more separated from those taxa with similarly enriched venation in the Proctotrupoidea s.s. (i.e., if groups such as Platygastroidea, Cynipoidea, or others are more basal relative to diaprioids), then one would consider the common ancestor of diaprioids to have had a more reduced venation. If this is the case, then the venation of Monomachidae would be an apomorphic reversal, perhaps resulting from their larger body size. However, other families in which miniaturization and loss of venation had taken place initially followed by subsequent enlargement in more modern clades did not result in the reacquisition of such venation (e.g., Pelecinidae: Johnson, 1998; Johnson and Musetti, 1999; Engel, 2002; Engel and Grimaldi, 2006). Thus, for the time being we consider that the monomachid venation is primitive for the clade, and thus the reduced venation seen in Diapriidae, Maamingidae, and Spathiopterygidae would suggest a relationship among these three taxa (fig. 10). The presence of an occipital carina and well-developed prominent petioles in Diapriidae and Monomachidae would accordingly be considered primitive, with the converse conditions of a very reduced petiole (metasomatic segment 1), loss of the occipital carina, and reduced maxillary palpus with only two palpomeres potentially uniting Maamingidae and Spathiopterygidae. This is merely a tentative scenario of possible relationships among these groups that will require extensive testing. Given the rather gross phenotypic differences between the lineages of Diaprioidea, it is greatly hoped that additional Early Cretaceous fossils will be recovered and brought to bear on the question of relationships, breaking up some of the otherwise apparently long branches separating each of these groups.

#### ACKNOWLEDGMENTS

We are grateful to two anonymous reviewers for their encouraging comments and constructive criticisms for the initial manuscript. Partial support for this work was provided by U.S. National Science Foundation grants EF-0341724 and DEB-0542909 (to M.S.E.), and the Ministerio de Ciencia e Innovación of Spain (project CGL2008-00055/BTE: "The Cretaceous amber of Spain: a pluridisciplinary study," to X.D.). The participation of J.O.-B. was supported by the Ministerio de Economía y Competitividad, Fulbright España and FECYT (Fundación Española para la Ciencia y la Tecnología). We thank the curators and administrators of the Museo de Ciencias Naturales de Álava and Conjunto Paleontológico de Teruel-Dinópolis for

the loan of the Spanish amber specimens described herein. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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