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The wasp family Spathiopterygidae in mid-Cretaceous amber from Myanmar (Hymenoptera: Diaprioidea)



Famille des guêpes Spathiopterygidae de l'ambre du Crétacé moyen de Birmanie (Hymenoptera : Diaprioidea)

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ARTICLE INFO

Article history:

Received 7 July 2014

Accepted after revision 2 December 2014

Available online 15 January 2015

Handled by Annalisa Ferretti

Keywords:

Insecta

Euhymenoptera

Spathiopterygidae

Burmese

Taxonomy

Mesozoic

Mots clés :

Insectes

Euhymenoptera

ABSTRACT

The extinct parasitoid wasp family Spathiopterygidae is recorded for the first time from the mid-Cretaceous amber deposits of northern Myanmar, often referred to as Burmese amber. The family was previously known only from three species in Spanish (Albian) and New Jersey (Turonian) ambers, representing an otherwise western Eurasia/eastern North America distribution. The discovery of a new genus and species, *Diaspathion ortegai* Engel and Huang, gen. et sp. nov., reveals a novel combination of traits seemingly intermediary between the Albian and Turonian taxa. Comparisons are made between the known species and a revised key to genera is provided, along with some general remarks about challenges facing the study of fossil parasitoid wasps.

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R É S U M É

La famille des Spathiopterygidae, guêpes parasitoïdes qui n'existent plus, a été enregistrée pour la première fois dans les dépôts d'ambre du Crétacé moyen du Nord de la Birmanie, souvent appelés « ambre birman ». La famille n'était préalablement connue qu'à partir de trois

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espèces dans l'ambre espagnol (Albien) et dans l'ambre du New Jersey (Turonien), représentant une distribution autre que celle de l'Europe occidentale et de l'Est de l'Amérique du Nord. La découverte des nouveaux genre et espèce *Diaspathion ortegai* Engel et Huang gen. et sp. nov. révèle une nouvelle combinaison de traits semblant intermédiaires entre les taxons albien et turonien. Des comparaisons sont effectuées entre les espèces connues et une clé révisée est fournie pour les genres, avec des remarques générales sur les défis offerts par l'étude des guêpes parasitoïdes fossiles.

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1. Introduction

In the various Mesozoic ambers of the world, there are a few lineages of minute parasitoid wasps that are hallmarks of the Cretaceous and although each has living relatives in the modern era, they are wholly unique in their own rights. Each family, with one exception, is known only in fossiliferous resins, largely given that their diminutive proportions require high preservational fidelity in order to adequately recognize their features. Some of the more widely known examples are the Serphitidae, Alavarommatidae, and Gallorommatidae, all belonging to the Bipetiolarida of the Proctotrupomorpha and closely allied to the Mymarommatidae (Brues, 1937; Kozlov and Rasnitsyn, 1979; McKellar and Engel, 2011a; Ortega-Blanco et al., 2011a,b). The latter two families are placed in the same superfamily with mymarommatids and appear to represent step-wise branches in the evolution of this clade (Gibson et al., 2007), while the former is presently classified in a separate but sister superfamily (Grimaldi and Engel, 2005; McKellar and Engel, 2011a). Another remarkable example is those species of the Stigmaphronidae and Radiophronidae (Ceraphronoidea), which analogously represent an apparent gradual branching from the lineage producing the Megaspilidae and Ceraphronidae (Ortega-Blanco et al., 2011c). With a few minor exceptions, these families are known from deposits spanning from the Early into the Late Cretaceous. Alongside these more familiar groups, another family of tiny wasps, this time of the Diaprioidea, is the recently discovered Spathiopterygidae (Engel et al., 2013). Spathiopterygids are apparently related to the enigmatic living Maamingidae, today known only from New Zealand (Early et al., 2001, 2002). As is the case for all of these extinct families, their biologies remain unknown. The mymarommatoid families Alavarommatidae and Gallorommatidae were likely egg parasitoids, as has been hypothesized for Mymarommatidae (Yoshimoto, 1984). Given the diversity of possible hosts among living megaspilids and ceraphronids it is impossible to even remotely hypothesize possible victims of stigmaphronids and radiophronids, although their particularly high diversity among the Spanish fauna might suggest that their hosts are among the more common of inclusions therein, such as Diptera (Ortega-Blanco et al., 2011c), but we are aware that simple frequent occurrence does not represent evidence of biological association. Ascertaining the hosts of spathiopterygids is even more challenging given the complete absence of biological data for their living relatives among the Maamingidae.

Species of Serphitidae are broadly distributed across the Cretaceous, with species in Spanish, Burmese, New Jersey, Canadian, Siberian, and French ambers (Brues, 1937; Engel, unpubl. data; Engel and Perrichot, 2014; Engel et al., 2011; Kozlov and Rasnitsyn, 1979; McKellar and Engel, 2011a, 2012; Ortega-Blanco et al., 2011a); Gallorommatidae are known from Myanmar, New Jersey, and France (Engel, unpubl. data; Engel and Grimaldi, 2007; Ortega-Blanco et al., 2011b; Schlüter, 1978); Stigmaphronidae are documented in Spanish, Burmese, New Jersey, Canadian, Siberian, and Alaskan resins (Engel and Grimaldi, 2009; McKellar and Engel, 2011b, 2012; Muesebeck, 1963; Ortega-Blanco et al., 2011c), and some Berriasian- to Aptian-aged compressions from Siberia and Mongolia, respectively (Rasnitsyn, 1991); while Alavarommatidae and Radiophronidae are presently recorded only from Spain (Ortega-Blanco et al., 2010, 2011b). Fossils of the living families Mymarommatidae, Megaspilidae, and Ceraphronidae are known largely from the Tertiary (Alekseev, 1995; Brues, 1940; Engel, 2013; Gibson et al., 2007; Ortega-Blanco et al., 2011b; Peñalver and Engel, 2006; Szabó and Oehlke, 1986), with a few Late Cretaceous records of megaspilids (Alekseev and Rasnitsyn, 1981; Engel, unpubl. data; McKellar and Engel, 2011b; Perrichot, pers. comm.). The recently discovered Spathiopterygidae were hitherto known from Spanish and New Jersey ambers (Aguilar et al., 2013; Engel et al., 2013), (Table 1) but herein we report on the discovery of the family from the mid-Cretaceous deposits of northern Myanmar.

2. Material and methods

During sorting of extensive samples of amber from the mid-Cretaceous (Albian–Cenomanian: Grimaldi et al., 2002; Shi et al., 2012) deposits of northern Myanmar, a single individual of the family was recovered. The inclusion was discovered in a deep reddish-orange piece of amber and initially was obscured from the left side of the wasp. The wasp was separated carefully from the remaining inclusions by trimming with a fine water-fed saw and the resulting chip was finely polished close to the specimen, so that it could be examined under both compound and stereomicroscopes (Figs. 1 and 2a). The individual is exceedingly well preserved and despite various particulates in the amber, is not generally obscured from view. There are minor fracture planes around the apices of the wings (which at first give them a fringed appearance), but these do not detract from observing the structures. The right antenna, particularly the more apical flagellomeres, has separated from the amber slightly along an internal



Fig. 1. (Color online.) Holotype male (NIGP160526) of *Diaspathion ortegai* Engel and Huang, n. gen. et sp. in mid-Cretaceous amber from Myanmar; specimen length: 0.84 mm: **a**: right lateral habitus; **b**: detail of head in lateral, posterior-oblique aspect; **c**: detail of right antenna.

Fig. 1. (Couleur en ligne.) Holotype mâle (NIGP160526) de *Diaspathion ortegai* Engel et Huang, n. gen. et sp. dans l'ambre du Crétacé moyen de Birmanie; longueur du spécimen : 0,84 mm : **a** : habitus latéral droit ; **b** : détail de la tête sous son aspect latéral, postérieur-oblique ; **c** : détail de l'antenne droite.

fracture within the amber, and thereby results in an altered view of the feature. The body does have various small bubbles or micro-bubble froths in places that obscure the integument, but these are relatively minor. The only major detriment in preservation is a prominent fracture plane in the amber near the wasp that obscures portions of the left lateral, ventral oblique view (Fig. 2a). The format and terminology for the descriptions follow those used by Engel et al. (2013), and these authors also provide a general account of spathiopterygid relationships and morphology for the family. The description is provided to further document diversity within the family and to expand our knowledge of potential patterns of relationships (Grimaldi and Engel, 2007). Photomicrographs were prepared using a Canon EOS

7D digital camera attached to an Infinity K-2 long-distance microscope lens.

3. Systematic paleontology

Family Spathiopterygidae Engel and Ortega-Blanco

Diagnosis (refer to Engel et al., 2013, for complete description of family): Compound eyes of moderate size, circular, with coarse ommatidia; ocelli present; occipital carina absent. Antennal toruli widely separated from clypeus, positioned on weakly protrudent antennal shelf, not overhung by frontal lamella; frons without depressions or grooves; antenna slender, 14-segmented, anellus absent, without placoid sensilla, with distinct curved

Table 1

Spathiopterygid diversity in Cretaceous amber. All species are presently known from males only.

Tableau 1

Diversité des Spathiopterygides dans l'ambre du Crétacé. Toutes les espèces sont actuellement connues uniquement à partir de mâles.

Taxon	Locality	Age
<i>Spathiopteryx alavarammopsis</i> Engel and Ortega-Blanco	Peñacerrada, Spain	Albian
<i>Mymaropsis turolensis</i> Engel and Ortega-Blanco	San Just, Spain	Albian
<i>Diaspathion ortegai</i> , Engel and Huang, gen. et sp. nov.	Hukawng, Myanmar	Albian–Cenomanian
<i>Spathopria sayrevillensis</i> Engel et al.	New Jersey, USA	Turonian

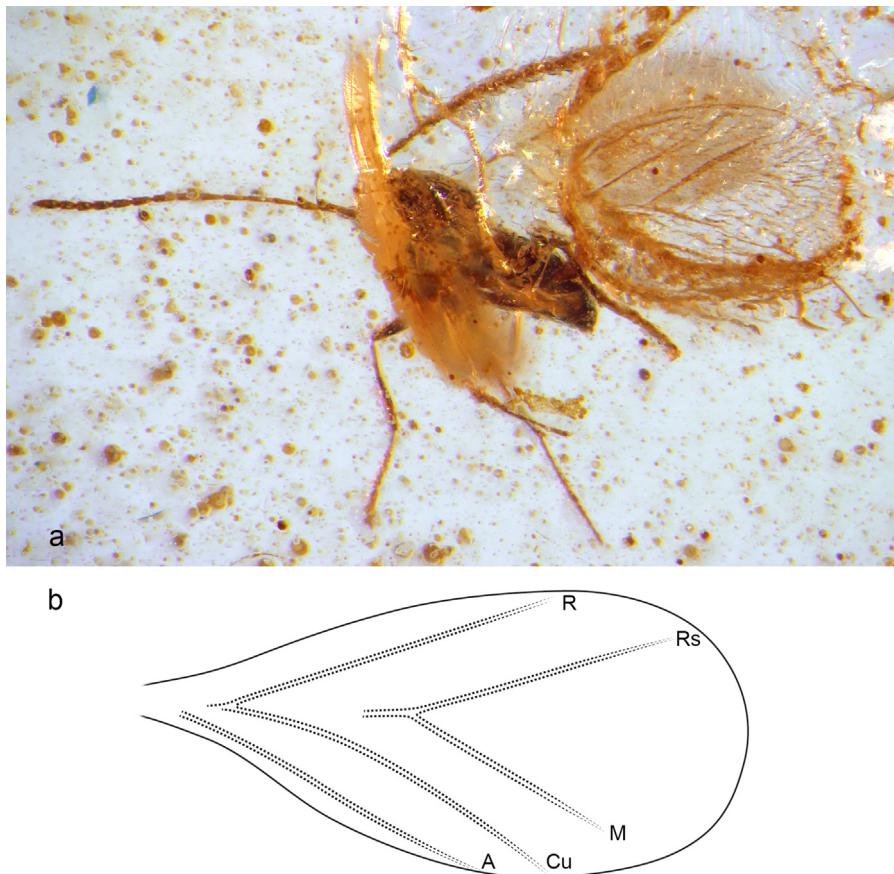


Fig. 2. (Color on line.) Holotype male (NIGP160526) of *Diaspathion ortegai* Engel and Huang, n. gen. et sp. in mid-Cretaceous amber from Myanmar: **a**: left lateral, ventral oblique habitus; specimen length 0.84 mm; **b**: forewing venation; wing length: 0.94 mm.

Fig. 2. (Couleur en ligne.) Holotype mâle (NIGP160526) de *Diaspathion ortegai* Engel et Huang, n. gen. et sp. du Crétacé moyen de Myanmar : **a** : habitus en vue latérale gauche, ventrale-oblique ; longueur du spécimen : 0,84 mm ; **b** : réseau de veines de l'aile antérieure ; longueur de l'aile : 0,94 mm.

trichoid sensilla apically on flagellomeres. Mesosoma higher than wide; pronotum with posterolateral corner nearly reaching tegula, posterior margin deeply concave, lateral surface fused to mesopleuron; prepectus absent. Mesoscutum with percurrent or indistinct notauli, lateral borders slightly converging posteriorly, transscutal sulcus complete; mesoscutellum about as long as wide, axilla not produced. Legs long with respect to body length; tibial spur formula 1-1-1; pretarsal claws simple, arolium large. Forewing distinctly larger than body, extending well beyond metasomal apex, spatulate, with or without well-defined marginal fringe, when present fringe setae not greatly elongate; venation represented by weakly nebulous or largely spectral lines on membrane, membrane with scattered short setae, hyaline, smooth to reticulate or wrinkled, pterostigma absent; venation greatly reduced, without C, single basal stem branching into spectral trace of A running to posterior wing margin and anteriorly with R running to anterior wing margin; Cu branching shortly after A, diverging to posterior margin of wing; Rs + M not contacting directly with Cu. Hind wing reduced or absent. Metasoma inserted low on mesosoma, between metacoxae; terga laterally covering lateral margins of sternae;

without visible syntergites or synsternites; first metasomal segment reduced to small petiole and mostly obscured; second and third metasomal segments largest, the latter larger.

Diaspathion Engel and Huang, gen. nov.

Type species: *Diaspathion ortegai* Engel and Huang, new species.

Diagnosis: Head imbricate and impunctate. Compound eyes slightly bulging, with a reduced number of coarse ommatidia (ca. 40). Scape longer than compound eye; pedicel not rimmed; flagellomeres I–IV much longer than wide, thin, distinctly longer than remaining flagellomeres. Mesoscutum imbricate, with notauli slightly impressed, percurrent, converging posteriorly. Pronotum laterally with weak, transverse striation. Forewing membrane distinctly roughened and wrinkled, without marginal fringe of setae; venation as described for family (Engel et al., 2013). Hind wing completely absent. Metasoma about as long as remainder of body.

Etymology: The new generic name is composed of the Greek terms *dia* (meaning, “between”) and the diminutive of *spathe* (meaning, “paddle”). The gender of the name is neuter.

Diaspathion ortegai Engel and Huang, sp. nov.

Figs. 1 and 2

Diagnosis: As for the genus (*vide supra*).

Description: ♂: Total length 0.84 mm; forewing length 0.94 mm; integument reddish brown, lighter on antennae and legs. Head imbricate and impunctate, more weakly so in malar area; malar area well developed, about as long as compound eye; occipital carina absent; ocelli small, well separated from compound eyes; compound eyes prominent, berry-like in appearance (Fig. 1b), composed of around 40 coarse ommatidia. Antenna arising upward from a distinct but not prominent frontal shelf, with sparse, minute, fine setae, and such setae becoming longer and more numerous on successively more apical flagellomeres; scape relatively straight (Fig. 1c); pedicel about one-half scape length; flagellomeres I–IV thinner than pedicel (Fig. 1c); flagellomeres I and II shorter than scape and slightly longer than pedicel; flagellomeres III and IV about as long as pedicel; remaining flagellomeres shorter than pedicel, except apicalmost flagellomere, which is about as long as pedicel. Mesosoma imbricate, more finely and weakly so on mesopleura. Forewing membrane roughened (Figs. 1a and 2a), not covered by setae or microtrichia, marginal setae absent; venation spectral but distinct, pattern of veins (R, Rs, M, a portion of Rs + M, Cu, and A present, Fig. 2b), as described for family (Engel et al., 2013). Legs elongate, with sparsely scattered, minute, fine setae; tibia without inner row of setae; probasitarsus much shorter than remainder of protarsus, meso- and metabasitarsomeres just slightly shorter than remainder of corresponding tarsomeres. Metasoma faintly imbricate, about as long as combined lengths of prosoma and mesosoma.

♀: Unknown.

Holotype: ♂, NIGP160526, Albian–Cenomanian boundary, Hukawng Valley, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Etymology: The specific epithet is a patronym for our dear friend and colleague, Dr. Jaime Ortega-Blanco, authority on fossil Hymenoptera from the Universitat de

Barcelona and formerly of the University of Kansas. Jaime was the first to hypothesize spathiopterygids in Burmese amber and we are delighted to validate his speculation.

4. Discussion

It is both exciting and expected to discover a spathiopterygid in Burmese amber. Given the broad geographical and temporal distribution of the previous records, it is unsurprising to find an individual in a deposit of more intermediary age. The Burmese species also extends the distribution of this family, expanding the known range into southern Eurasia and along the northern shores of the Tethys Ocean. Given these points, these minute wasps should be carefully sought in other Mesozoic sites such as those in France, North Carolina, Canada, Siberia, Alaska, and even Lebanon, albeit some are slightly outside of the known temporal range, but not dramatically so. Indeed, given their size and ease with which they ‘disappear’ among flow lines or reflective fractures, they may already have been collected among samples from these localities and perhaps have understandably been overlooked. Alternatively, to the uninitiated they may have also been passed over, because at a quick glance the wings are not distinctively ‘hymenopteran’ and could superficially suggest the wings of a male aleyroid or coccoid hemipteran.

The new genus is fascinating in that it, at least in some features, seems to bridge the morphological disparity between the Spanish and New Jersey taxa. Admittedly, there is a relatively minor diversity known thus far and few characters from which to work, but it would appear that *Mymaropsis* is the most basal member of the family based on its more developed hind wing. In this genus, the hind wing is certainly reduced and vestigial but is still present with some minor membranous area. In *Spathiopteryx*, the hind wing is reduced to a simple veinal stub, without a membrane of any kind (Engel et al., 2013), and in *Spathopria* and *Diaspathion*, the hind wing is clearly absent. Interestingly, this small transition series also correlates with geological age, with the two younger taxa being apparently more closely related based on an apomorphic loss of the hind wing. Naturally, a larger suite of character data is needed and hopefully more taxa will be discovered for a more extensive exploration of relationships within the family. Nonetheless, for the time being it seems safe to conclude, based on the aforementioned transition series, that familial relationships may be summarized as [*Mymaropsis* (*Spathiopteryx* [*Diaspathion* + *Spathopria*])] in advance of a cladistic analysis.

Documenting these tiny wasps certainly represents a major advance in understanding the diversity of parasitoids during various stages of the Late Mesozoic and refines our knowledge of relationships and the evolution of biological traits (Grimaldi and Engel, 2007). Nonetheless, one of the long-standing challenges will be to more fully understand the biology and ecology of these wasps, and this will be enhanced greatly by the discovery of females. Today parasitoids are critical in virtually all terrestrial ecosystems, as they regulate and influence populations of their hosts, which in turn impacts downstream taxa such as particular floral species, and are integral to host-parasite

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 3
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*
- 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*
3. Head coarsely punctured; antenna comparatively short, not longer than total body length; metasoma globose, about as long as mesosoma (Turonian: New Jersey) *Spathopria*
- Head imbricate; antenna more elongate, longer than total body length; metasoma ovoid, longer than mesosoma (Albian–Cenomanian: Myanmar) *Diaspathion*, gen. nov.

(updated from Engel et al., 2013)

coevolution. Naturally, fossils representing crown groups with known biology are easily understood, but the more important revelations will come from knowledge of host-parasite relationships among those extinct clades more basal among the diversifications of particular superfamilies, perhaps spanning important host shifts or biological transformations (e.g., transitions to specializing in egg parasitoidism and the concomitant anatomical and physiological changes). Discovering the particular biology of these taxa will require either rare or uniquely preserved material, such as syninclusions with some indication of behavior, or novel methods of inference. Either way, overcoming this tremendous difficulty will reap broad-reaching rewards for understanding the phases of parasitoid evolution.

Acknowledgements

We are thankful to Ryan C. McKellar and Vincent Perrichot for their helpful comments on an early draft of the manuscript. HDY would like to thank the National Basic Research Program of China (2012CB821903), Outstanding Youth Foundation of Jiangsu Province (BK 2012049), and the National Natural Science Foundation of China (91114201) for financial support. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum, and to the team project, “Biodiversity: Origin, Structure, Evolution and Geology” granted to DA by the Lebanese University.

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