

A new genus of the family Spathiopterygidae (Hymenoptera: Diaprioidea) from mid-Cretaceous Kachin amber

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Running title: A new spathiopterygid wasp from Kachin amber

Abstract

Spathiopterygid wasps represent an enigmatic group within Proctotrupomorpha, characterized by their minute size, their peculiar forewings with reduced venation and a pattern of microtrichiae, and highly reduced or absent hind wings. This family is known exclusively from Cretaceous ambers (ranging from the Barremian to the Santonian) and shows a wide geographic distribution. Specimens of this family are rare, and most of the species are only known from their holotypes, limiting our understanding of sexual dimorphism and intraspecific variability. Here, we describe *Karaweik splendida* Álvarez-Parra & Jouault gen. et sp. nov. from mid-Cretaceous Kachin amber, bringing the known paleodiversity of Spathiopterygidae to nine species distributed in seven genera. An updated species checklist and key are provided. We discuss the different nomenclatures for forewing venation used for the family and propose the term “pseudoveins” for what appear to be spectral veins, represented by rows of microtrichiae or membrane wrinkles. The studied specimen is anatomically compared with the other representatives of the family. We also address the potential belonging of *Cretapria tsukadai* Fujiyama, 1994, from Aptian Choshi amber in Japan, to Spathiopterygidae. The new species has tooth-like structures on the posteroventral part of the head, which may be related to parasitoid behavior or wood-dwelling habit.

Furthermore, we briefly comment on the paleobiology of the family and compare the possible flight modes of spathiopterygids with those of mymarids and mymarommatids.

Keywords: Apocrita, Proctotrupomorpha, wasp, parasitoidism, Mesozoic, Burmese amber

Introduction

The family Spathiopterygidae is an enigmatic and little-known group of putatively parasitoid proctotrupomorphan wasps belonging to the superfamily Diaprioidea (Engel et al., 2013). They are characterized by their minute size, unusual wing venation—composed of nebulous or spectral veins and rows of microtrichiae—and the extreme reduction or even absence of hind wings (Engel et al., 2013; Santer et al., 2022). Currently, Diaprioidea encompass the extant families Diapriidae, Ismaridae, Maamingidae, and Monomachidae (Sharkey, 2007; Sharkey et al., 2012). The Ismaridae were traditionally considered a subfamily within Diapriidae until they were elevated to a family level based on their putative sister relationship with other diapriids (Sharkey et al., 2012). Spathiopterygidae are assigned to Diaprioidea based on the insertion of the antennae on a distinct antennal shelf and the presence of curved trichoid sensillae on the apical part of the flagellomeres (Engel et al., 2013). Furthermore, the reduced forewing venation in Diapriidae, Maamingidae, and Spathiopterygidae suggests a possible grouping of these three families, with Maamingidae being sister group of Spathiopterygidae due to shared traits such as the maxillary palps with only two palpomeres, the absence of occipital carina, and the presence of a reduced petiole (Engel et al., 2013). However, Rasnitsyn & Öhm-Kühnle (2020) excluded both Maamingidae and Monomachidae from Diaprioidea, due to the presence of a complete or at least rudimentary vein 1cu-a in the forewing. Interestingly, the Diapriidae seem to be paraphyletic, and stem to the Ismaridae, in a recent phylogenetic analysis by Blaimer et al. (2023), rising questions about the validity of Ismaridae as a separate family rather than a subfamily within Diapriidae.

Specimens of Spathiopterygidae are considered rare, despite their surprising diversity, with nine species placed into seven genera (Table 1). Eight of these species are known only from their holotypes, which limits our understanding of intraspecific variability and sexual dimorphism. Based on the known female and possible male of the species *Mymaropsis turolensis* Engel & Ortega-Blanco, 2013, the main sexual differences are the size (female about 1.5× bigger than male), characters of flagellomeres (shape, size, and setation), the density of setae on forewings, and the shape of metasoma (Santer et al., 2022). Spathiopterygidae are exclusively found in amber deposits, spanning from the Barremian to the Santonian. Undescribed specimens have also been identified from Cretaceous French and Taimyr ambers (Brazidec, 2023), indicating a broad distribution during this period. It is hypothesized that the spathiopterygids may have originated on the southern or western margins of the Tethys during the Early Cretaceous or the Late Jurassic (Brazidec, 2023). Although nothing is known about the paleobiology of Spathiopterygidae, phylogenetic

inference suggests that they might have been egg- or larval-parasitoid of dipterans, similar to some extant Diaprioidea (Santer et al., 2022). However, it is risky to infer possible behaviors for fossil hymenopteran families only based on phylogenetic relationships, considering the wide diversity of modes of life in extant hymenopterans (Nel, 1997).

No phylogenetic analysis has yet been conducted for Spathiopterygidae, leaving their relationships with the other diaprioid families and the interrelationships between genera within the family obscure. It is possible that the genus *Mymaropsis* is sister to the rest of the spathiopterygids due to the retention of plesiomorphic characters (Engel et al., 2013; Santer et al., 2022). In addition, Rasnitsyn & Öhm-Kühnle (2020) suggested that *Cretapria tsukadai* Fujiyama, 1994, from the Aptian Choshi amber (Japan), may also belong to Spathiopterygidae.

Here, we describe a new genus and species of Spathiopterygidae from mid-Cretaceous Kachin amber, further increasing the known paleodiversity of this enigmatic group of tiny wasps.

Genus and species	Known sex	Age	Provenance	References
<i>Spathiopteryx soosi</i> Szabó, Brazidec & Perrichot, 2022	♀	Santonian	Ajka-Csingervölgy, Hungary	Szabó et al. (2022)
<i>Spathopria sayrevillensis</i> Engel, Ortega-Blanco & Grimaldi, 2013	♂	Turonian	Sayreville, USA	Engel et al. (2013)
<i>Argemiones stupeflip</i> Brazidec, 2023	♂	late Albian–early Cenomanian	Hukawng Valley, Myanmar	Brazidec (2023)
<i>Diaspathion ortegai</i> Engel & Huang, 2015	♂	late Albian–early Cenomanian	Hukawng Valley, Myanmar	Engel et al. (2015)
<i>Karaweik splendida</i> Álvarez-Parra & Jouault gen. et sp. nov.	♀	late Albian–early Cenomanian	Hukawng Valley, Myanmar	This paper
<i>Spathiopteryx alavarommopsis</i> Engel & Ortega-Blanco, 2013	♂	late Albian	Peñacerrada I, Spain	Engel et al. (2013)
<i>Diameneura marveni</i> Santer & Álvarez-Parra, 2022	Unknown	late Albian	San Just, Spain	Santer et al. (2022)
<i>Mymaropsis turoloensis</i> Engel & Ortega-Blanco, 2013	♀, ♂?	late Albian	San Just, Spain	Engel et al. (2013); Santer et al. (2022)

<i>Mymaropsis baabdaensis</i> Krogmann, Azar, Rajaei & Nel, 2016	♀	late Barremian	Hammana-Mdeyrij, Lebanon	Krogmann et al. (2016); Santer et al. (2022)
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Table 1. Checklist of the known genera and species of Spathiopterygidae. Updated from Santer et al. (2022). All the species are found in Cretaceous amber.

Material and methods

The piece of amber containing the specimen derives from the deposits of Noiye Bum in the Hukawng Valley (26°29' N, 96°35' E), Kachin State, northern Myanmar (see detailed map in Grimaldi & Ross, 2017: fig. 2). Radiometric data based on zircons from volcanic clasts established an early Cenomanian age (98.79 ± 0.62 Ma) for the Kachin amber-bearing bed (Shi et al., 2012). The study of bivalve pholadid borings in Kachin amber points out a similar age for the amber-bearing bed and the amber itself, likely early Cenomanian (Smith & Ross, 2017). However, Mao et al. (2018) raised concerns on the limits of the radiometric dating of zircons, stating that the actual dating may be slightly older, and they suggested referring to the Kachin amber as mid-Cretaceous in age. Ammonites found in the same layer as the amber and within amber as bioinclusions, support a late Albian–early Cenomanian age (Cruickshank & Ko, 2003; Yu et al., 2019). More than 2,000 insect species have been described from Kachin amber so far (Ross, 2024), providing an exceptional window into the Cretaceous insect diversity. The Kachin amber pieces are considered parautochthonous, as there is no evidence suggesting long biostratigraphic transport for the original resin pieces (Mao et al., 2018). The paleoenvironment has been interpreted as a resiniferous forest in coastal or estuarine to freshwater settings under tropical climate (Smith & Ross, 2017; Mao et al., 2018; Bolotov et al., 2021).

The piece of amber containing the holotype was polished with a grinding polisher (Ameritool), with thin silicon carbide sanding paper. The specimen was examined and photographed with an Olympus BX53 compound microscope equipped with a digital camera Olympus DP74. Additional photographs were taken using a Zeiss LSM710 confocal laser scanning microscope at the Nanjing Institute of Geology and Palaeontology, at a 488 nm Argon laser excitation line (Fu et al., 2021). All images are photomicrographic composites of several individual focal planes, which were digitally stacked using Helicon Focus 8. The figures were made with Adobe Photoshop CS6. The description of the characters follows the nomenclature of Santer et al. (2022). The holotype is housed in the collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China, under collection number NIGP205634.

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Notes on the forewing venation nomenclature in Spathiopterygidae

Spathiopterygid wasps are characterized by a forewing venation consisting of nebulous or spectral veins, along with rows of microtrichiae, which may be interpreted as spectral veins. Additionally, the forewings in this family usually present wrinkles that can be regarded as spectral veins (e.g., *Diameneura marveni* and *Spathopria sayrevillensis*). Overall, the forewing morphology of Spathiopterygidae is quite unique in Hymenoptera, rendering the nomenclature of veins difficult to establish. We suggest that the venation nomenclature should follow that of the family Diapriidae (Fig. 1A), due to the similar appearance and putative close phylogenetic relationship between the two families. Originally, the forewing venation was interpreted as a series of diverging Y-shape veins (Fig. 1B), with vein A separating first, followed by the bifurcation of R and Cu, and more apically Rs and M (Engel et al., 2013, 2015). However, the basal cell complex was not described in these earlier works. Later, Krogmann et al. (2016) interpreted the forewing venation differently (Fig. 1C). They identified a basal cell (named as radial cell) delimited by Sc+R anteriorly, M+Cu posteriorly and M+Rs distally. The vein Cu was noted to emerge from the posteroapical part of this cell, while a more apical vein stem (not connected to the basal cell) was labelled Rs+M, branching into Rs and M. Two possible spectral veins were also mentioned in the space between Rs and M.

Santer et al. (2022) reinterpreted the forewing venation of Spathiopterygidae (Fig. 1D). In their interpretation, the basal cell is delimited by Sc+R anteriorly, M+Cu posteriorly, and B (=1M) distally. Similar to the interpretation of Krogmann et al. (2016), the vein Cu emerges from the posteroapical part of the basal cell, as is usual in Hymenoptera (Goulet & Huber, 1993: fig. 18). A parastigma, which Krogmann et al. (2016) identified as pterostigma, is present on the anteroapical part of the basal cell, while the vein R extends toward wing apex. The vein stem, not connected to the basal cell, is identified as Rs+M, which bifurcates into Rs and M. Santer et al. (2022) also observed the presence of a few possible spectral veins, in form of wrinkles in the spaces between Rs and M, and between M and Cu.

Finally, Szabó et al. (2022) and Brazidec (2023) largely followed the venation nomenclature established by Engel et al. (2013). However, these authors referred to the vein originating from the posteroapical part of the basal cell as A instead of Cu (Fig. 1E), which deviates from the typical interpretation for Hymenoptera (Goulet & Huber, 1993: fig. 18). This interpretation also conflicts with the nomenclature used for other Diaprioidea (e.g., Brazidec & Vilhelmsen, 2022: fig. 1E) and another fossil micro-proctotrupomorphans (e.g., Ulmer et al., 2023: fig. 2). Therefore, the vein they identified as Cu should be M, while the vein they named M may actually be one of the possible spectral veins mentioned by Krogmann et al. (2016) and Santer et al. (2022).

Here, based on the discussion above, and in line with the standard venation nomenclature for Hymenoptera (Goulet & Huber, 1993: fig. 18) and Diaprioidea (Brazidec & Vilhelmsen, 2022: fig. 1E), we choose to follow the forewing venation nomenclature proposed by Santer et al. (2022: fig. 2D). Additionally, due to the unique forewing venation of Spathiopterygidae, we suggest naming the potential spectral veins (in form of rows of

microtrichiae or membrane wrinkles) in the spaces between Rs and M and between M and Cu, “pseudoveins”, as their true nature and origin remain unclear.

The distinction between the pseudoveins and the vein M can be challenging, but usually both veins Rs and M are at least weakly sclerotized at the base, in contrast to the pseudoveins (e.g., Engel et al., 2013: fig. 6b; Brazidec, 2023: fig. 4b). The number and location of the pseudoveins along the forewing membrane may be of taxonomical importance, and accordingly it is essential to consider them in the descriptions and forewing drawings. However, a deep study is required yet to assess the significance of the pseudoveins in the evolution of spathiopterygids.

Forewing venation abbreviations— C: Costal vein; Sc: Subcostal vein; pst: Parastigma; Rs: Radial sector; M: Medial vein; B: Basal vein (=1M); Cu: Cubital vein; A: Anal vein.

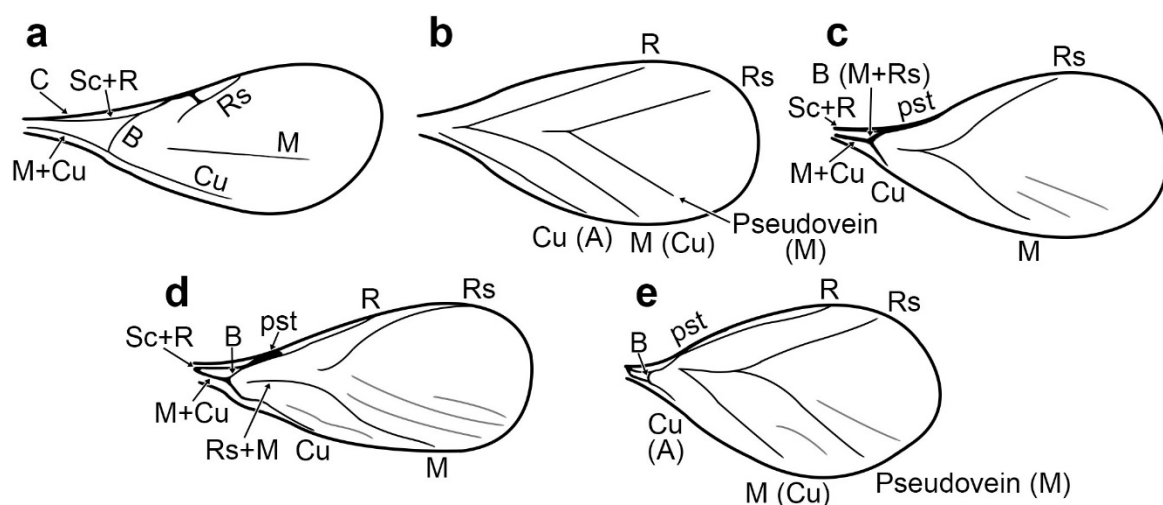


Fig. 1. Forewing schemas for venation nomenclature in Diapriidae and Spathiopterygidae (Diaprioidea). **a** *Pantolyta augustinusii* Brazidec & Vilhelmsen, 2022 (Diapriidae: Belytinae) (Brazidec & Vilhelmsen, 2022). **b** *Diaspathion ortegai* Engel & Huang, 2015 (Spathiopterygidae) (Engel et al., 2015). **c** *Mymaropsis baabdaensis* Krogmann, Azar, Rajaei & Nel, 2016 (Spathiopterygidae) (Krogmann et al., 2016). **d** *Diameneura marveni* Santer & Álvarez-Parra, 2022 (Spathiopterygidae) (Santer et al., 2022). **e** *Spathiopteryx soosi* Szabó, Brazidec & Perrichot, 2022 (Spathiopterygidae) (Szabó et al., 2022). Forewings are re-drawn based on the original articles and are not at the same scale. Previous venation labeling is indicated in parentheses. Marginal setae and microtrichia on membrane are not included for easier visualization.

Results

Systematic paleontology

Order **Hymenoptera** Linnaeus, 1758

Suborder **Apocrita** Gerstaecker, 1867

Superfamily **Diaprioidea** Haliday, 1833

Family **Spathiopterygidae** Engel & Ortega-Blanco, 2013

Type genus. *Spathiopteryx* Engel & Ortega-Blanco, 2013

Other genera. *Argemiones* Brazidec, 2023; *Diameneura* Santer & Álvarez-Parra, 2022; *Diaspathion* Engel & Huang, 2015; *Karaweik* gen. nov.; *Mymaropsis* Engel & Ortega-Blanco, 2013; *Spathopria* Engel, Ortega-Blanco & Grimaldi, 2013.

Karaweik Álvarez-Parra & Jouault gen. nov.

LSID:

Type species. *Karaweik splendida* sp. nov., by present designation and monotypy.

Etymology. A fantastic bird from Burmese mythology and related to Buddhism. From the Pali language *karavika*. The gender of the name is feminine.

Diagnosis. Head surface alveolate; malar space $1.3\times$ longer than eye height; antenna with pedicel quill-shape, about $4\times$ longer than wide; flagellomeres 1–4 distinctly elongate, distinctly longer than remaining flagellomeres; mesoscutum with longitudinal striations, not punctured between striae; notauli indistinct; forewing paddle-like, smooth without wrinkles; pattern of microtrichiae on membrane uniform; marginal setae present along apex; parastigma sclerotized and slightly thickened; small basal cell delimited by desclerotized veins; Rs and M not contacting other veins; hind wing present as venal stub and small membranous section; protibial spur strongly curved and bifid; metasoma about as long as mesosoma.

Karaweik splendida Álvarez-Parra & Jouault sp. nov.

LSID:

Figures 2–5

Type material. Holotype NIGP205634, a complete female specimen; metasoma somewhat deformed. Eusyninclusion with one Diptera, one Hemiptera, and plant trichomes. Deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Locality and horizon. Noiye Bum, Hukawng Valley, Kachin State, northern Myanmar; late Albian–early Cenomanian, ca. 99 Ma, mid-Cretaceous.

Etymology. From the Latin word *splendida*, meaning splendid or magnificent, and referring to the good preservation of the holotype.

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

Description. Female; body length about 0.86 mm (ovipositor excluded); integument castaneous (Figs. 2, 3); macropterous (Fig. 4).

Head: Hypognathous, globular, 0.20 mm long in full-face view, maximal width 0.23 mm, surface alveolate (Fig. 3); compound eye slightly bulging, occupying less than half of head lateral surface, with 40–50 ommatidia; ocelli indiscernible (Fig. 3A, B); malar space 1.3× longer than eye height; antenna filiform (Figs. 2, 5A), longer than body, about 1 mm long, arising upward from prominent torulus and inserted on distinctly developed frontal shelf (Fig. 5B); toruli located above eyes mid-length, widely separated from clypeus; scape elongate, about 0.11 mm, longer than first flagellomere; pedicel quill-shaped, widening medially, 4× longer than wide; 12 flagellomeres cylindrical to slightly trapezoidal, elongate, covered by fine setae, trichoid sensillae apparently present on apex of flagellomeres (Fig. 5A); flagellomeres 1–11 progressively shortening, and widening, lengths of flagellomeres (in mm, from base to apex): f1: 0.09, f2: 0.10, f3–f4: 0.08, f5–f6: 0.07, f7–f11: 0.06, and f12: 0.08; flagellomere 12 acuminate, about as long as f5; flagellomeres without carinae; flagellomeres with setation denser toward apex of antenna; occipital carina absent, with an arista separating dorsal and occipital surfaces (Fig. 3); clypeus short, wider than long; labrum short with rounded apex; mandible endodont and bidentate (Fig. 5B); maxillary palp two-segmented, with two setae on apex; labial palp not visible; gena ventrally with tooth-like structures lateral to mandible (Fig. 5B).

Mesosoma: Stout, about 0.34 mm long (Fig. 3); pronotum without sculpture, nearly reaching tegula; mesoscutum large, convex, about half length of mesosoma, with longitudinal striations, not punctured between striae; notauli indistinct; mesoscutellum somewhat trapezoidal, wider than long, anterior and posterior margins convex; metanotum short, with longitudinal strips, about half mesoscutellum length, shorter than basal area of propodeum; propodeum apparently smooth.

Forewing: Paddle-like (Fig. 4A, B), longer than body, about 1.15 mm long and 0.50 mm wide; membrane apparently smooth without wrinkles, uniformly covered by microtrichiae; fringe of long setae visible along margin, longest at apex; venation mostly spectral or nebulous; vein C sclerotized, visible a long anterobasal margin; parastigma sclerotized and slightly thickened, not reaching mid length of wing; small basal cell present (Fig. 4C, D), 0.06 mm long, delimited by desclerotized veins Sc+R (anteriorly), M+Cu (posteriorly), and very short B (distally); vein R not contacting with parastigma, basally weakly sclerotized, extending along membrane nearly parallel to margin in form of row of microtrichiae; vein Rs basally weakly sclerotized, not contacting other veins, extending along membrane in form of row of microtrichiae; vein shortly sclerotized basally, not contacting other veins, extending along membrane in form of row of microtrichiae; vein Cu emerging from posterodistal part of basal cell, weakly sclerotized, very short, not reaching margin; two pseudoveins between Rs and M; one pseudovein between M and Cu.

Hind wing: Right hind wing visible as venal stub adjoining small membranous section (Fig. 4C, E).

Legs: Slender, long with respect to body (Fig. 2), covered by setae; procoxa widely separated from mesocoxa; mesocoxa nearly touching metacoxa; trochantellus present; tibial spur formula 1-1-1 (Fig. 5C–F); basitarsus longest tarsomere, shorter than combined lengths of rest of tarsomeres; tarsi 5-segmented; foreleg with femur 0.21 mm long, widening medially, tibia 0.25 mm long, with long and strongly curved bifid spur (Fig. 5C, D), comb of setae present on basal part of probasitarsus, tarsus 0.25 mm long; mid leg with femur 0.23 mm long, widening medially, tibia 0.30 mm, tarsus 0.31 mm long; hind leg with femur 0.25 mm long, widening medially, tibia 0.35 mm long, tarsus 0.40 mm long; tarsal claws simple, angled apically; arolium well developed.

Metasoma: About 0.32 mm long; petiole visible between metacoxa, cylindrical, slightly longer than wide, 0.06 mm long and 0.05 mm wide, smooth (likely obscured by gaster in normal condition, but gaster is deformed in studied specimen). Gaster globular (Fig. 5G), length 0.28 mm long; second metasomal tergite and sternite longest, other tergites and sternites hidden; ovipositor 0.08 mm long.

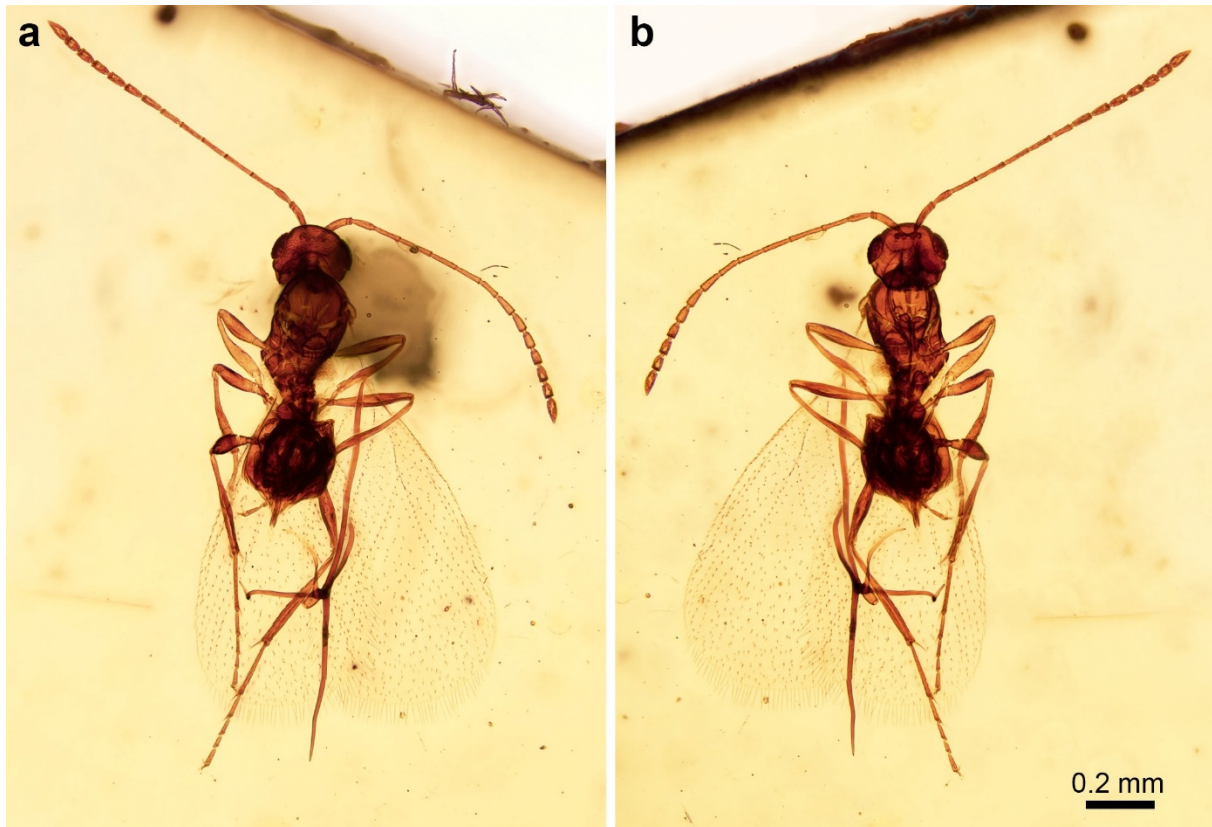


Fig. 2. *Karaweik splendida* gen. et sp. nov. (Hymenoptera: Spathiopterygidae) from mid-Cretaceous Kachin amber, Myanmar; holotype NIGP205634, female. **a** Habitus, from dorsal view. **b** Habitus, from ventral view. Both to the same scale.



Fig. 3. Head and mesosoma, from dorsal view, of *Karaweik splendida* gen. et sp. nov. (Hymenoptera: Spathiopterygidae) from mid-Cretaceous Kachin amber, Myanmar; holotype NIGP205634, female. **a** Under optical microscope with incident and transmitted light. **b** Under confocal laser scanning microscope. Both to the same scale.

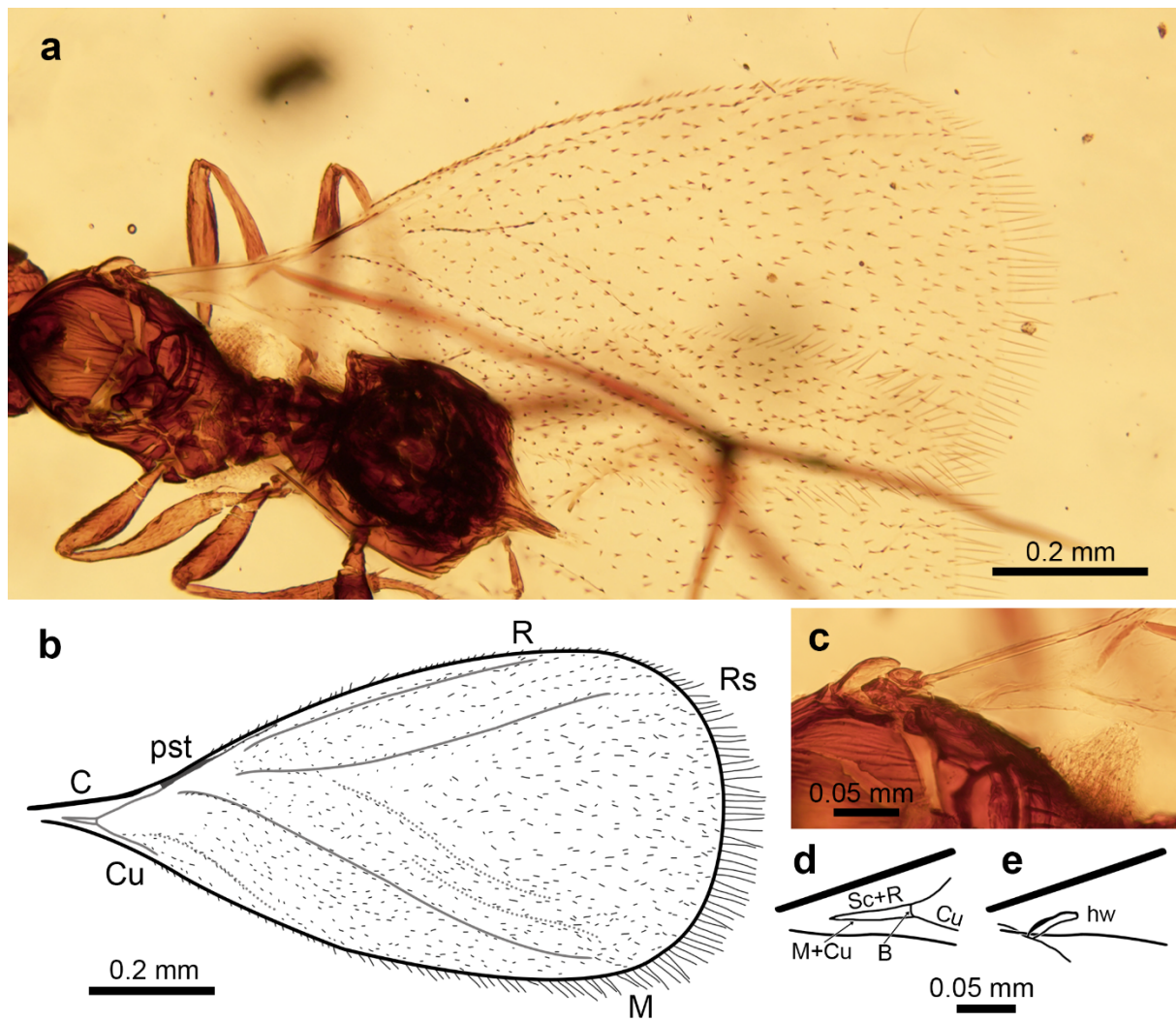


Fig. 4. Wings of *Karaweik splendida* gen. et sp. nov. (Hymenoptera: Spathiopterygidae) from mid-Cretaceous Kachin amber, Myanmar; holotype NIGP205634, female. **a** Forewing, from dorsal view. **b** Schematic drawing of forewing. **c** Base of right forewing and hind wing, from dorsal view. **d** Schematic drawing of the base of forewing and basal cell. **e** Schematic drawing of hind wing (hw). Subfigures **d** and **e** to the same scale.

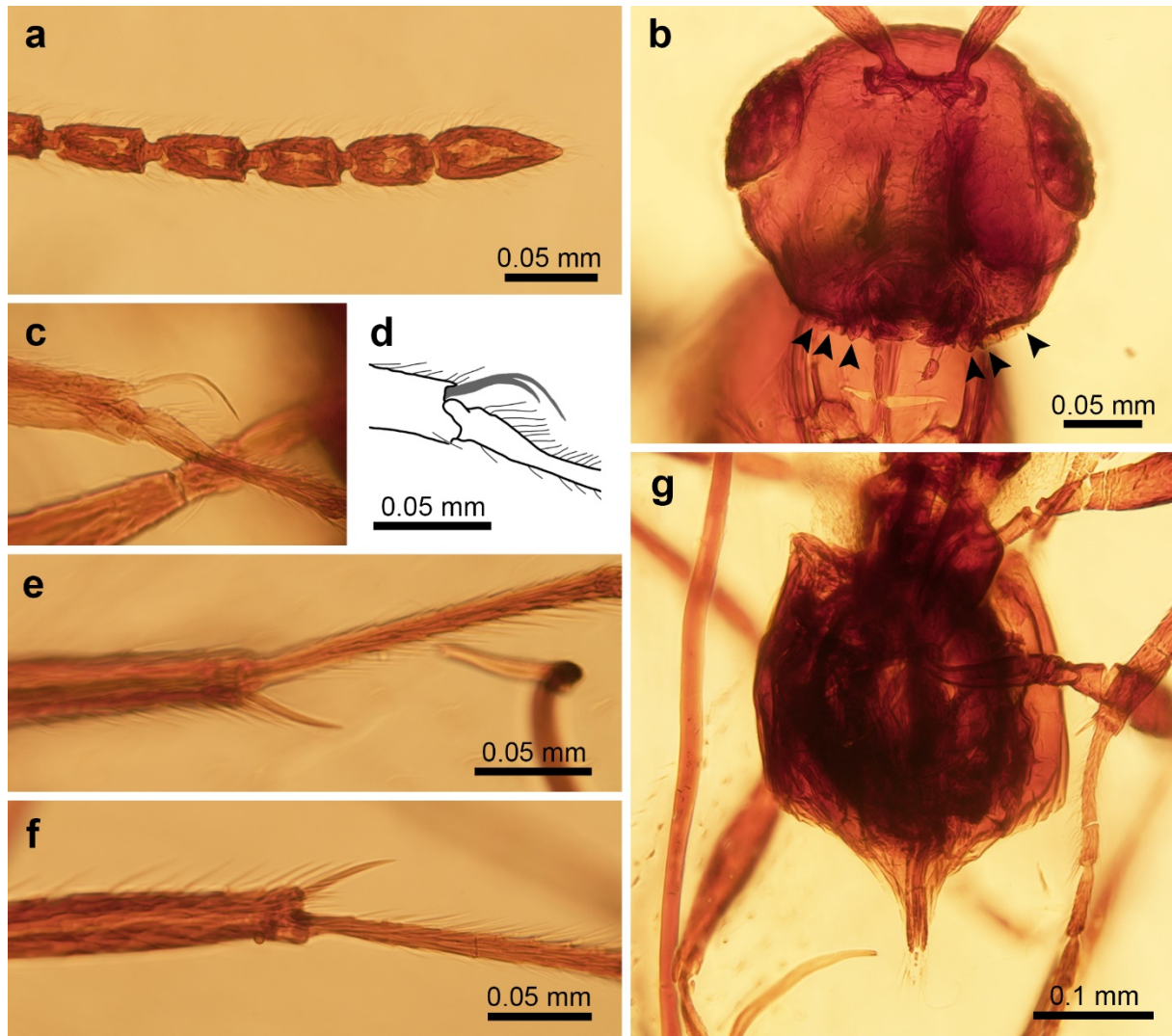


Fig. 5. *Karaweik splendida* gen. et sp. nov. (Hymenoptera: Spathiopterygidae) from mid-Cretaceous Kachin amber, Myanmar; holotype NIGP205634, female. **a** Apical flagellomeres of left antenna. **b** Head and mouthparts from frontal view, tooth-like structures indicated with arrowheads. **c**, **d** Photograph and drawing of right protibial spur. **e**, **f** Left and right, respectively, metatibial spurs. **g** Gaster and ovipositor, from ventral view. Subfigures **c** and **d** to the same scale.

Key to the genera and species of Spathiopterygidae

The key is modified from that of Brazidec (2023) to include the new taxa herein described.

1. Forewing with a well-defined marginal fringe of setae.....2
- Forewing without a marginal fringe of setae.....8
2. Compound eye bulging with few ommatidia ('berry-like'), parastigma thin (thinner than other visible veins).....3
- Compound eye with more than 40 ommatidia, parastigma thick (at least as thick as other visible veins).....4

3. Compound eye with about 40 ommatidia, pronotum with transverse striations, vertex punctured.....*Spathiopteryx alavarammopsis* Engel & Ortega-Blanco, 2013
 —. Compound eye with about 20 ommatidia, pronotum smooth, vertex punctate to areolate.....*Spathiopteryx soosi* Szabó, Brazidec & Perrichot, 2022
4. Forewing membrane entirely wrinkled, with a positive gradient of microtrichiae density toward apex.....*Diameneura marveni* Santer & Álvarez-Parra, 2022
 —. Forewing membrane partly smooth, microtrichiae distributed evenly on membrane.....5
5. Antennae inserted on distinctly developed frontal shelf, forewing with M+Cu desclerotized, hind wing reduced.....6
 —. Antennae inserted on reduced frontal shelf, forewing with M+Cu sclerotized, hind wing with membrane and hamuli.....7
6. Back of head coarsely punctured, antenna with pedicel globular, mesoscutum apparently smooth with distinct notauli, hind wing present as a venal stub.....*Argemiones stupeflip* Brazidec, 2023
 —. Head surface alveolate, antenna with pedicel quill-shaped, mesoscutum with longitudinal striations and indistinct notauli, hind wing present as a venal stub and a small membranous section.....*Karaweik splendida* gen. et sp. nov.
7. Scape slightly expanded ventrally, pedicel globular, flagellomeres 5–12 twice as wide as flagellomeres 1–4.....*Mymaropsis baabdaensis* Krogmann, Azar, Rajaei & Nel, 2016
 —. Scape not ventrally expanded, pedicel almost globular, flagellomeres evenly wide.....*Mymaropsis turolensis* Engel & Ortega-Blanco, 2013
8. Head coarsely punctured, antennae short, not longer than body length, gaster globose, nearly as long as mesosoma.....*Spathopria sayrevillensis* Engel, Ortega-Blanco & Grimaldi, 2013
 —. Head imbricate, antennae elongate, longer than body length, gaster ovoid, longer than mesosoma.....*Diaspathion ortegai* Engel & Huang, 2015

Discussion and conclusions

Karaweik splendida gen. et sp. nov. is readily attributed to the Diaprioidea based on several diagnostic traits, including the long scape, oligomeric antennae (14 antennomeres), and a specialized petiolate first metasomal segment, all considered putative apomorphies of Diaprioidea *sensu* Rasnitsyn & Öhm-Kühnle (2020). Additionally, the insertion of the antennae on a frontal shelf above the clypeus is a distinguishing characteristic of the superfamily (Rasnitsyn & Öhm-Kühnle, 2020). The specimen is further attributed to the family Spathiopterygidae due to its minute size, globular head, flagellomeres without carinae, paddle-like forewings, short and stout mesosoma, and reduced forewing venation pattern with veins weakly sclerotized (Engel et al., 2013). However, the specimen presents a bifid protibial spur, which differs from the diagnosis of the family and other spathiopterygids (Engel et al.,

2013), with the exception of *Mymaropsis baabdaensis* from Lebanese amber (Krogmann et al., 2016). This suggests that this trait may be unstable within the family and subject to interspecific variability.

Following the key by Brazidec (2023), the new specimen would fall close to *Argemiones* and *Mymaropsis* based on: 1) compound eye with more than 50 ommatidia (the studied specimen has 40–50 ommatidia, like the genus *Mymaropsis*, as in Engel et al. (2013) and Santer et al. (2022), thus the key has been corrected to “more than 40 ommatidia”), 2) forewing with a well-defined marginal fringe of setae, 3) partly smooth forewing membrane, 4) microtrichiae distributed evenly on membrane, and 5) parastigma thick, at least as thick as other visible veins. *Karaweik splendida* gen. et sp. nov. can be differentiated from the genera *Spathopria* and *Diaspathion* due to the presence of marginal setae on the forewing, which is absent in both genera (Engel et al., 2013, 2015). As mentioned in the updated key above, the new specimen differs from the genus *Spathiopteryx* in the number of ommatidia and the thick parastigma (Engel et al., 2013; Szabó et al., 2022), and from the genus *Diameneura* in the aspect of the forewing membrane and the pattern of microtrichiae (Santer et al., 2022). The studied specimen is excluded from *Mymaropsis* based on the antennae inserted on a developed frontal shelf (vs. on reduced frontal shelf), desclerotized M+Cu in forewing (vs. sclerotized), and hind wing present as a venal stub and a small membranous section (vs. present with membrane and hamuli) (Engel et al., 2013; Krogmann et al., 2016; Santer et al., 2022).

The new specimen shares several characters with other spathiopterygid genera. For instance, the shape of the antennae and the size of the flagellomeres are similar to those observed in the genus *Argemiones*. However, the specimen differs from the genus *Argemiones* due to (Brazidec, 2023): its head surface alveolate (vs. back of the head coarsely punctured), quill-shaped pedicel (vs. globular), slightly trapezoidal flagellomeres 7 to 11 (vs. elongate), mesoscutum with longitudinal striations (vs. apparently smooth), notauli absent (vs. present), very short forewing vein Cu (vs. very long, labelled as A), and hind wing represented by a venal stub and a small membranous section (vs. present as a venal stub). Additionally, distinct longitudinal striations in the mesoscutum, present in the genus *Spathopria*, are also present in the studied specimen, although there are not punctures between the striae (Engel et al., 2013). Based on these distinctions, we consider the description of a new genus for this specimen to be well justified.

Cretapria tsukadai is an enigmatic species of diapiroid wasps described from Aptian Choshi amber (Japan) and originally assigned to the Ismaridae (Fujiyama, 1994), although this group was considered a subfamily within Diapriidae at that time. Rasnitsyn & Öhm-Kühnle (2020) later suggested that this species might belong to Spathiopterygidae. Chemyreva et al. (2024) further discussed its taxonomic affinities, excluding it from Ismaridae and leaving its classification as *incertae sedis*. They also indicated that the holotype is lost, thus the name should be considered *nomen dubium* until a neotype is assigned.

Unfortunately, these authors did not evaluate the possibility of assigning *C. tsukadai* to Spathiopterygidae.

We agree with Chemyreva et al. (2024) that the morphology of *C. tsukadai* does not align with either Diapriidae or Ismaridae. Several characters of this species suggest affinities with Spathiopterygidae, such as its apparently large compound eyes, antennae with an elongate scape and 12 flagellomeres, the first four flagellomeres thin and tubular and the rest slightly wider, paddle-like forewings with sparse microtrichiae on membrane (and possible marginal setae, not clearly described), the absence of pterostigma, a thin costal cell and apparent parastigma, Y-shaped veins, the hind wing apparently absent, thin and long legs, and a tibial spur formula of 1-1-1. These features seem particularly similar to the genus *Mymaropsis*, especially in terms of antennal segments' shape and forewing characters, such as the microtrichiae pattern and venation (Engel et al., 2013; Krogmann et al., 2016; Santer et al., 2022). However, the original description and photographs by Fujiyama (1994) are insufficient to confirm this interpretation. While the frontal shelf characteristic of Diaprioidea is supposedly absent in *C. tsukadai*, this structure is often weakly developed in Spathiopterygidae, making it easy to overlook. Assigning a neotype and providing a detailed redescription are necessary to determine whether *C. tsukadai* belongs to Spathiopterygidae.

As commented above, the paleobiology of spathiopterygids remains largely unknown. Given their minute size, the length of the ovipositor, and phylogenetic inference with extant Diaprioidea, it is plausible that they were endoparasitoids of Diptera egg or larvae. However, assigning specific life modes to fossil hymenopteran families is speculative. *Karaweik splendida* gen. et sp. nov. features tooth-like structures on the posteroventral part of the head, which might have served functions related to emergence from pupation sites, grasping during copulation, host detection, attachment to host, or wood-dwelling habit (Jervis, 1998).

Interestingly, the hind wing is completely absent in *Spathopria* and *Diaspathion*, while it is highly reduced in the other spathiopterygids (Engel et al., 2013, 2015; Krogmann et al., 2016; Santer et al., 2022; Szabó et al., 2022; Brazidec, 2023). This variability in the presence or absence of hind wings within a single family is unique in Hymenoptera, and is reminiscent of the situation in Mymarommatoidea, where hind wings are either highly reduced (Gibson et al., 2007) or absent (Rasnitsyn et al., 2019). Considering the characteristics of the forewings (microtrichiae on membrane and reduced venation) and the absence/reduction of hind wings, it is evident that the flight mode of spathiopterygids was unusual and potentially similar to that of extant Mymaridae and Mymaromatidae (Gibson et al., 2007; Shen et al., 2022), though differing in the lack or short length marginal setae compared to the longer setae found in these extant families.

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Data availability. All the data used is already included in the article.

Declarations

Conflict of interest. The authors declare that they have no conflicts of interest and no competing interests.

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