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The oldest false fairy wasp (Hymenoptera: Mymarommatidae) from Lower Cretaceous Lebanese amber

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Abstract

Mymarommatidae (Hymenoptera), also known as false fairy wasps, are mainly characterised by their minute size, the peculiar wings, and the bi-segmented petiole. They form part of the superfamily Mymarommatoidea together with the Cretaceous families †Alavarommatidae, †Dipterommatidae, and †Gallorommatidae. The clade Bipetiolarida embraces Mymarommatoidea and †Serphitoidea, the two proctotrupomorphan superfamilies whose members have bi-segmented petiole. The biology of the mymarommatids is poorly known and only one extant species is known to be an egg endoparasitoid of barklice (Psocodea). Here, we describe a new species of mymarommatid wasp, *Archaeromma phoenicium* **sp. nov.**, from Lower Cretaceous (Barremian) amber of Lebanon. We compare it with the other species of the genus and discuss the validity of some characters for generic identification. This new species is the oldest representative of the genus *Archaeromma* Yoshimoto, 1975 and of the family Mymarommatidae. A checklist and a key to the species of *Archaeromma* is included. Furthermore, we discuss the palaeobiogeography of the Cretaceous mymarommatoids. The description of the new species increases the list of insect co-occurrences between Lebanese and Spanish ambers to 21 genera.

Key words: Bipetiolarida, Mymarommatoidea, *Archaeromma*, Lebanon, Barremian, palaeobiogeography

Introduction

Mymarommatidae are a family of tiny wasps commonly called false fairy wasps due to their resemblance to the members of the chalcidoid family Mymaridae, commonly known as fairy wasps. Mymarommatids form part of the apocritan group Microprocta within the infraorder Proctotrupomorpha (Rasnitsyn & Öhm-Kühnle 2020). They are characterised by their minute size range of 0.3–0.8 mm and for possessing special characters among hymenopterans, which has led to consider them as the most enigmatic group of wasps (Vilhelmsen & Krogmann 2006; Gibson *et al.* 2007). The main characteristics of the mymarommatids are (Gibson *et al.* 2007): 1) head with a pleated membrane separating the frontal and occipital plates allowing articulation in a bellows-like manner; 2) forewing pedunculate with a marginal fringe of long, erect setae, a mesh-like pattern membrane and highly reduced venation; 3) hind wing reduced to a stalk with a bifurcate apex; and 4) petiole bi-segmented. Given the minute size of the mymarommatids, it is probable that they are egg parasitoids (Gibson *et al.* 2007), but their biology is mostly obscure and there is evidence of only one species from the Hawaiian Islands being solitary egg endoparasitoid of barklice (Psocodea) belonging to the family Lepidopsocidae (Honsberger *et al.* 2022).

The family Mymarommatidae is included in the superfamily Mymarommatoidea together with the Cretaceous families †Alavarommatidae, †Dipterommatidae, and †Gallorommatidae (Ortega-Blanco *et al.* 2011; Rasnitsyn *et al.* 2019). Considering living groups, Mymarommatoidea is recognised as the sister group of Chalcidoidea (Gibson

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et al. 1999, 2007; Blaimer *et al.* 2023). The clade Bipetiolarida was erected for the superfamilies †Serphitoidea and Mymarommatoidea (Engel 2015). †Serphitoidea is a diverse group of wasps restricted to Cretaceous ambers composed of the families †Archaeoserphitidae and †Serphitidae, both characterised by having the petiole bi-segmented (Engel 2015). However, the relationship between serphitoids and mymarommatoids is not yet clearly resolved, as phylogenetic analyses regarding these groups have not been performed so far.

The Cretaceous record of Mymarommatoidea is represented by one monospecific genus in both †Alavarommatidae and †Dipterommatidae (Ortega-Blanco *et al.* 2011; Rasnitsyn *et al.* 2019), two genera including seven species in †Gallorommatidae (Rasnitsyn *et al.* 2022), and the genus *Archaeromma* Yoshimoto, 1975 including 12 species in Mymarommatidae (Table 1). Today, the only representatives of the superfamily are 19 species in three genera within Mymarommatidae (Villemant *et al.* 2023): *Mymaromma* Girault, 1920, *Mymaromella* Girault, 1931, and *Zealaromma* Gibson, Read & Huber, 2007.

Here, we describe a new species of the genus *Archaeromma* from Lower Cretaceous Lebanese amber, the oldest representative of the family Mymarommatidae recorded so far. Furthermore, the palaeodistribution of the Cretaceous species of Mymarommatoidea is discussed.

TABLE 1. Checklist of species belonging to the genus *Archaeromma* Yoshimoto, 1975 (Hymenoptera: Mymarommatidae).

Species	Notes	Known sexes	Age	Locality	References
Archaeromma trigonokephalion Cockx, McKellar, Tappert, Vavrek & Muehlenbachs, 2020	Probably belonging to a different genus *sensu* Cockx *et al.* (2020)	♂	late Campanian	Pipestone Creek, Canada. Amber.	Cockx *et al.* (2020)
A. masneri (Yoshimoto, 1975)	Transferred from *Protooctonus* Yoshimoto, 1975 by Gibson *et al.* (2007)	♀	Campanian	Cedar Lake, Canada. Amber.	Yoshimoto (1975); Gibson *et al.* (2007)
A. minutissimum (Brues, 1937)	Transferred from *Ooctonus* Haliday, 1833 by Yoshimoto (1975)	♀, ♂	Campanian	Cedar Lake and Grassy Lake, Canada. Amber.	Brues (1937); Yoshimoto (1975); Gibson *et al.* (2007)
A. nearcticum Yoshimoto, 1975		♀, ♂	Campanian	Cedar Lake and Grassy Lake, Canada. Amber.	Yoshimoto (1975); Gibson *et al.* (2007)
A. japonicum (Fursov, Shirota, Nomiya & Yamagishi, 2002)	Transferred from *Palaeomymar* Meunier, 1901 by Gibson *et al.* (2007)	♂	Santonian	Kuji, Japan. Amber.	Fursov *et al.* (2002); Gibson *et al.* (2007)
A. mandibulatum (Kozlov & Rasnitsyn, 1979)	Transferred from *Palaeomymar* by Gibson *et al.* (2007)	♀	Santonian	Yantardakh, Russia. Amber.	Kozlov & Rasnitsyn (1979); Gibson *et al.* (2007)
A. senonicum (Kozlov & Rasnitsyn, 1979)	Transferred from *Palaeomymar* by Gibson *et al.* (2007)	♀	Santonian	Yantardakh, Russia. Amber.	Kozlov & Rasnitsyn (1979); Gibson *et al.* (2007)
A. chisatoi Aiba & Inosa, 2024		♀, ♂	Coniacian	Iwaki, Japan. Amber	Aiba & Inosa (2024)
A. carnifex Engel & Grimaldi, 2007		♂	Turonian	Sayreville, USA. Amber	Engel & Grimaldi (2007)
A. gibsoni Engel & Grimaldi, 2007		♂	early Cenomanian	Hukawng Valley, Myanmar. Amber.	Engel & Grimaldi (2007)
A. hispanicum Ortega-Blanco, Peñalver, Delclòs & Engel, 2011		♀, ♂	middle Albian and late Albian	El Soplao and Peñacerrada I, Spain. Amber.	Ortega-Blanco *et al.* (2011)
A. phoenicium **sp. nov.**		♀	early Barremian	Hammana-Mdeyrij, Lebanon. Amber.	This paper

Material and methods

The holotype was collected from Hammana-Mdeyrij amber-bearing outcrop, Caza (= District) Baabda, Central Lebanon. Most of the Lower Cretaceous amber outcrops in Lebanon are assigned to the Sandstone of Lebanon Unit, also known as "Grès du Liban" Alloformation (Maksoud *et al*. 2020, 2022). Amber is found in three intervals at the upper part of this unit in thin levels of dark shales together with lignite and plant remains. These intervals have been deposited during early–late Barremian based on charophytes, foraminifers, and echinoids (Maksoud *et al*. 2017). It is considered that the resin pieces underwent short transport before burial (Maksoud *et al*. 2020). The palaeoenvironmental interpretation corresponds to dense resiniferous forests within a fluvial system affected by marine influence under a humid, warm, tropical climate (Maksoud *et al*. 2017, 2020). The Hammana-Mdeyrij amber-bearing outcrop is stratigraphically located in the upper interval, and the amber pieces are reworked in late Barremian estuarian or margin-littoral shelves, while the original resin is early Barremian in age (Maksoud *et al*. 2017). The Lower Cretaceous Lebanese amber is highly rich in bioinclusions of diverse arthropod groups (Maksoud *et al*. 2022). In particular, the order Hymenoptera is represented by 32 species in 22 genera within 15 families of 'Parasitica' and Aculeata (Álvarez-Parra & Azar 2024).

The amber piece containing the specimen was manually cut with a razor blade, separating the different syninclusions for an appropriate visualisation. Polishing was made with increasing grade emery papers and diatomite. The specimen was embedded in Canada balsam between two cover-slips. The holotype was photographed and drawn with an Olympus BX53 compound microscope equipped with a digital camera Olympus DP74 and a camera lucida tube. Figures were processed with Helicon Focus 8 and Adobe Photoshop CS6 softwares. We follow the nomenclature and systematics of Gibson *et al*. (2007). The holotype is deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

Systematic palaeontology

Superfamily Mymarommatoidea Debauche, 1948

Family Mymarommatidae Debauche, 1948

Genus *Archaeromma* Yoshimoto, 1975

Type species. *Archaeromma minutissimum* (Brues, 1937)

Other species. *Archaeromma carnifex* Engel & Grimaldi, 2007; *A. chisatoi* Aiba & Inosa, 2024; *A. gibsoni* Engel & Grimaldi, 2007; *A. hispanicum* Ortega-Blanco, Peñalver, Delclòs & Engel, 2011; *A. japonicum* (Fursov, Shirota, Nomiya & Yamagishi, 2002); *A. mandibulatum* (Kozlov & Rasnitsyn, 1979); *A. masneri* (Yoshimoto, 1975); *A. nearcticum* Yoshimoto, 1975; *A. phoenicium* **sp. nov.**; *A. senonicum* (Kozlov & Rasnitsyn, 1979); *A. trigonokephalion* Cockx, McKellar, Tappert, Vavrek & Muehlenbachs, 2020.

Archaeromma phoenicium sp. nov.

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(Figs 1–3)

Type material. Holotype 1701-A; a complete female specimen; left antenna and left forewing are affected by fractures in the amber. Syninclusion with two spiders (Araneae) and two springtails (Collembola). The holotype is deposited at the Natural History Museum of the Lebanese University, Faculty of Science II, Fanar, Lebanon.

Etymology. After Phoenicia, ancient name of the region of modern-day Lebanon.

Diagnosis. Female. Compound eyes composed by about 30–40 ommatidia; no ocelli; mandibles exodont, bidentate; toruli not contiguous, inserted above compound eyes; antenna with funicle 7-segmented and clava 4-segmented; scape 2.8× longer than wide; pedicel longer than cumulative lengths of f1 and f2; clava slightly longer than cumulative lengths of scape and pedicel; forewing: submarginal and marginal veins separated by a bulla, stigmal vein present as a bulbous area, marginal fringe composed by: six short anterior setae, eight mid-sized anterior setae, 38 long erect setae deeply inserted in membrane, and four mid-sized posterior setae, no long posterobasal marginal seta; hind wing: stalk-like, with posterior membrane slender, distal pincer-like structure present; protibial calcar curved and simple; mesotibiae with two pseudospurs; metatibiae with four pseudospurs; basitarsi as long as cumulative lengths of second and third tarsomeres; petiole bi-segmented with first segment 1.2× longer than second; gaster flattened; dorsal part of gaster setose.

Locality and horizon. Hammana-Mdeyrij amber-bearing outcrop, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian (Lower Cretaceous), upper interval at the upper part of "Grès du Liban" (Maksoud *et al*. 2017).

Description. Female. Body length 0.43 mm (Fig. 1A–C); macropterous (Fig. 2); colour dark brown (preservational), without metallic shine; setae on antennae, head, wings, legs, and dorsal part of gaster.

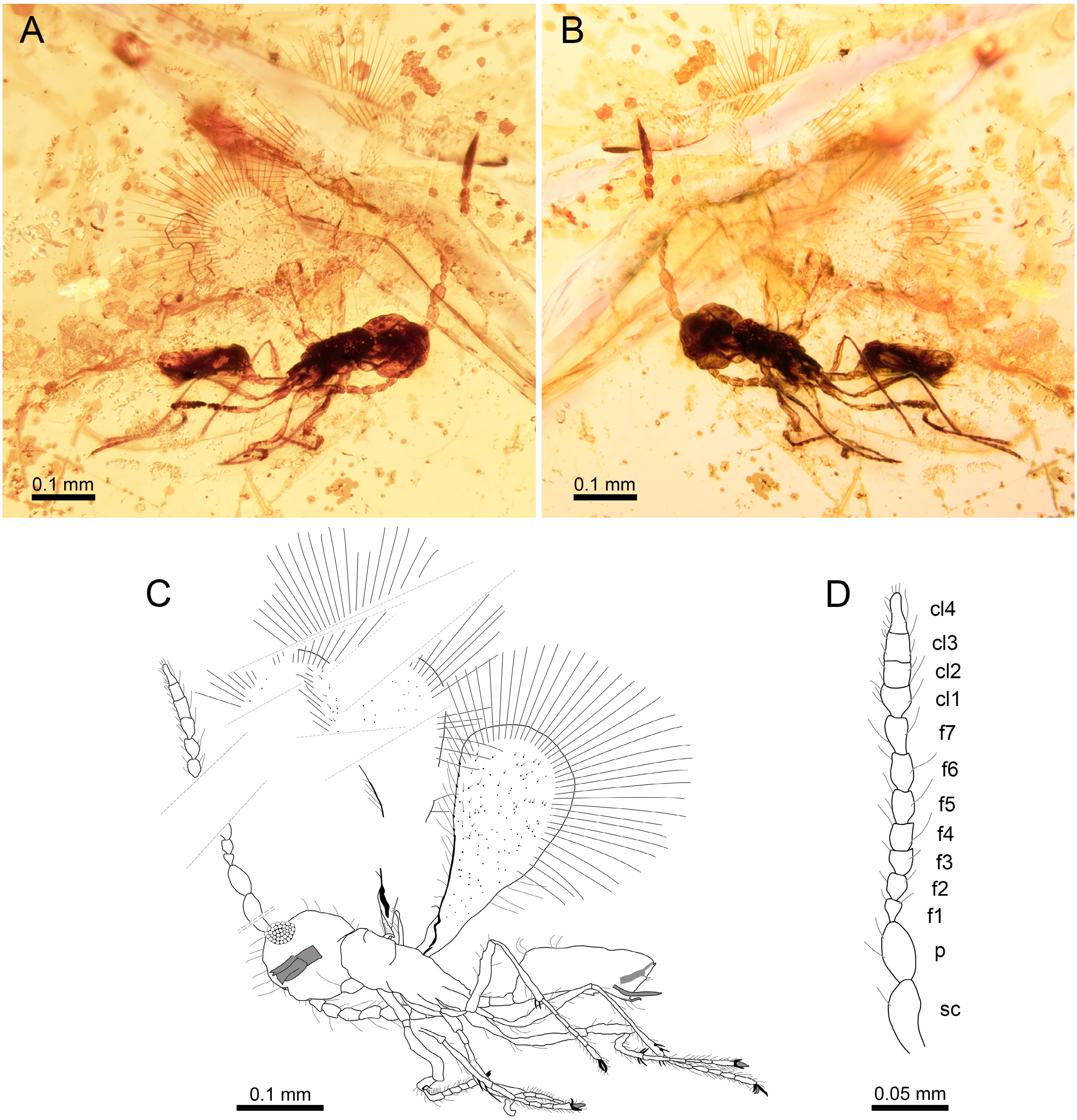

FIGURE 1. *Archaeromma phoenicium* **sp. nov.**, holotype, female. **A**, Habitus, right lateral view. **B**, Habitus, left lateral view. **C**, Drawing of the specimen from left lateral view, head from ventral view. **D**, Interpretative drawing of antenna. Abbreviations: sc—scape, p—pedicel, f1–f7—funicular segments, cl1–cl4—claval segments.

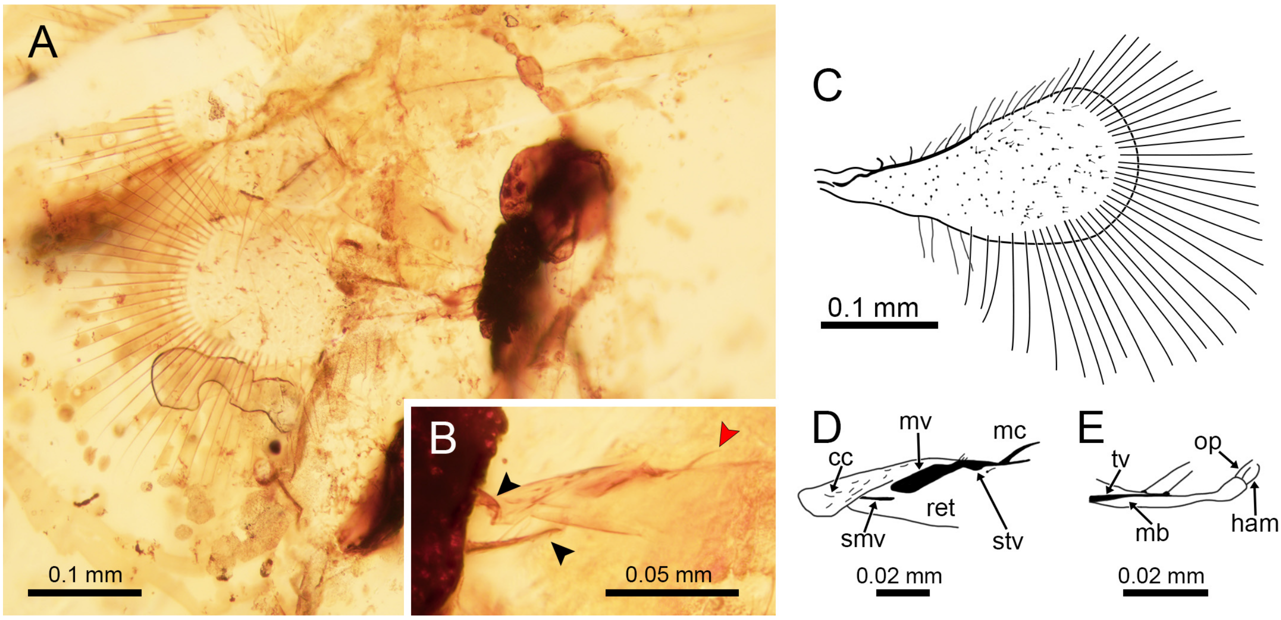

FIGURE 2. *Archaeromma phoenicium* **sp. nov.**, holotype, female. **A**, Forewings in right lateral view. **B**, Detail of stigmal complex of left forewing indicating macrochaeta (red arrowhead) and hindwings (black arrowheads). **C**, Drawing of right forewing. **D**, Interpretative drawing of stigmal complex of left forewing. **E**, Interpretative drawing of hind wing. Abbreviations: cc—costal cell, ham—hamulus, mb—hind wing membrane, mv—marginal vein, op—opposite projection, ret—retinaculum, smv—submarginal vein, stv—stigmal vein, tv—hind wing tubular vein.

Head: 0.10 mm long (Fig. 3A, B); frontal plate convex; occipital plate seemingly flat; pleated membrane in the articulation between frontal and occipital plates not visible; compound eyes small, 0.04 mm in diameter, composed of about 30–40 ommatidia; no ocelli; mandibles exodont, bidentate; labrum flap-like, with straight apex; toruli not contiguous, inserted above compound eyes; antenna clavate, 13-segmented (Fig. 1D); scape elongate, 2.8× longer than wide; pedicel wider and slightly shorter than scape, about 2× longer than wide; funicle 7-segmented; f1–f3 short and ovoid, f4–f7 mostly rectangular; pedicel longer than cumulative lengths of f1 and f2; each funicular segment with at least two trichoid sensillae; clava 4-segmented, segments closely compacted; clava slightly longer than cumulative lengths of scape and pedicel; distal claval segment elongate, with apex thin and rounded; lengths of antennal segments in µm: sc: 44, p: 36, f1: 17, f2: 15, f3: 18, f4: 17, f5: 19, f6: 24, f7: 23, cl1: 18, cl2: 18, cl3: 17, cl4: 23.

Mesosoma: 0.15 mm long, narrower than head; mesoscutum convex, apparently granulose, lacking evident notauli (Fig. 3A, B); other mesosomal structures obscure.

Forewing: pedunculate with a broadly spatulate disc (Fig. 2A, C); 0.27 mm long and 0.13 mm maximum wide, 2× longer than wide; forewing stalk with venation extending 0.08 mm from wing base; proximal part of stalk (Fig. 2D) with margin folded, corresponding to costal cell, with scattered spicules and lacking apparent campaniform sensillum; submarginal vein thin and short; marginal vein wide, extending to wing margin; submarginal and marginal veins separated by a bulla; macrochaeta present on distalmost part of marginal vein; stigmal vein present as a bulbous area at distal part of marginal vein; disc flat, without venation; discal setae combined as short and spine-like; a few hair-like discal setae close to anterior margin; marginal fringe composed by: six short anterior setae, eight mid-sized anterior setae, 38 long erect setae deeply inserted in membrane, and four mid-sized posterior setae; no long posterobasal marginal seta.

Hind wing: short and slender, stalk-like (Fig. 2B, E); 0.04 mm long; base formed by a tubular vein short reaching anterior margin and a posterior membranous section slender; two sub-basal setae on anterior margin; distal part with a pincer-like structure composed of hamulus and opposite projection.

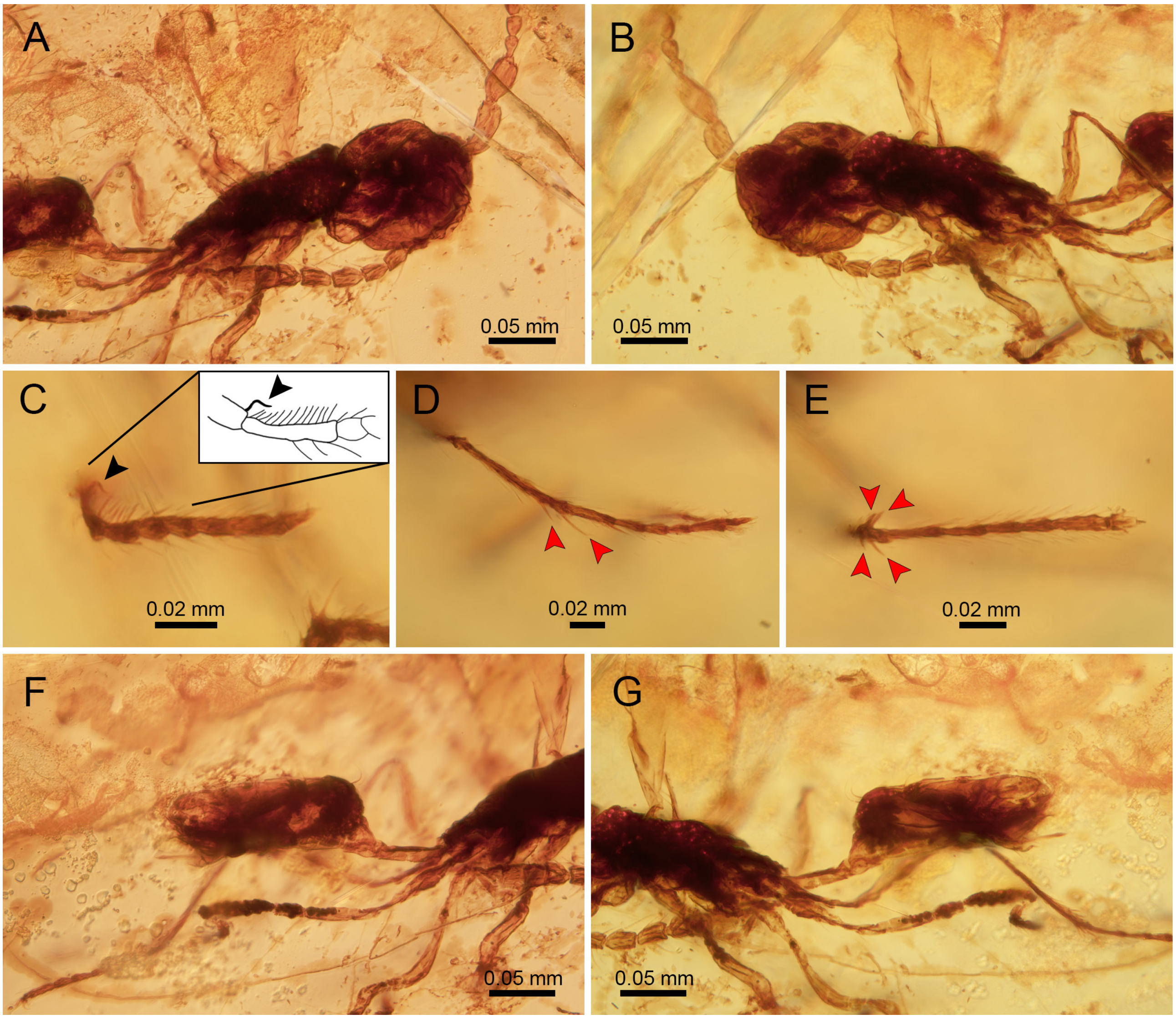

FIGURE 3. *Archaeromma phoenicium* **sp. nov.**, holotype, female. **A**, Head in dorsal view and mesosoma in right lateral view. **B**, Head in ventral view and mesosoma in left lateral view. **C**, Protarsus and interpretative drawing of protibial calcar and basitarsus. **D**, Mesotarsus with two pseudospurs (red arrowheads). **E**, Metatarsus with four pseudospurs (red arrowheads). **F**, Metasoma in right lateral view. **G**, Metasoma in left lateral view.

Legs: elongate and slender; tibiae and tarsi setose; mesofemorae with a few setae emerging from small protuberances; tibial spur formula 1:0:0; protibial calcar curved and simple (Fig. 3C); mesotibiae with two pseudospurs (Fig. 3D); metatibiae with four pseudospurs (Fig. 3E); tarsi 5-segmented; basitarsi as long as cumulative lengths of second and third tarsomeres; two small pretarsal claws; arolium wide with a thin, short projection at distal part.

Metasoma: composed of petiole bi-segmented and gaster globular (Fig. 3F, G); first petiolar segment 0.03 mm long, second petiolar segment 0.02 mm long, first segment 1.2× longer than second, both segments narrow and same height, no sculpture; petiole inserted on the anterobasal part of gaster; gaster flattened, 0.16 mm long and 0.05 mm heigh; tergites indiscernible; cerci and ovipositor sheath not visible; ovipositor thin, 0.05 mm long; hypopygium setose.

Key to the species of the genus *Archaeromma* (Mymarommatidae)

1. Clava 3-segmented 2
- Clava 4-segmented 5
2. Forewing posterobasal marginal seta present 3
- Forewing posterobasal marginal seta absent 4
3. Pronotum reaching tegula; forewing marginal fringe with 42 long, erect setae .... *A. mandibulatum* (Kozlov & Rasnitsyn, 1979) (♀), Taimyr amber, Santonian
- Pronotum not reaching tegula; forewing marginal fringe with 55 long, erect setae .... *A. carnifex* Engel & Grimaldi, 2007 (♂), New Jersey amber, Turonian
4. Pedicel shorter than scape; mesosoma narrower than head .... *A. masneri* (Yoshimoto, 1975) (♀), Canadian amber, Campanian
- Pedicel as long as scape; mesosoma broader than head .... *A. gibsoni* Engel & Grimaldi, 2007 (♂), New Jersey amber, Turonian
5. Notauli present; petiole with second segment longer than first segment .... *A. trigonokephalion* Cockx, McKellar, Tappert, Vavrek & Muehlenbachs, 2020 (♂), Canadian amber, Campanian
- Notauli absent; petiole with first segment longer or as long as second segment 6
6. Forewing posterobasal marginal seta present 7
- Forewing posterobasal marginal seta absent 11
7. Claval segments strongly compacted (sutures almost undistinguishable) 8
- Claval segments not strongly compacted (sutures distinguishable) 9
8. Lengths of funicular segments increase towards apex; mesosoma longer than gaster .... *A. minutissimum* (Brues, 1937) (♀, ♂), Canadian amber, Campanian
- Lengths of funicular segments similar; mesosoma shorter than gaster in females .... *A. nearcticum* Yoshimoto, 1975 (♀, ♂), Canadian amber, Campanian
9. Mesoscutum without apparent sculpture; forewing marginal fringe with 31 long, erect setae .... *A. chisatoi* Aiba & Inosa, 2024 (♀, ♂), Japanese amber, Coniacian
- Mesoscutum with evident sculpture; forewing marginal fringe with 36–38 long, erect setae 10
10. Mesoscutum with transverse, striate sculpture; forewing posterobasal marginal seta offset by a series of nine short, posterior setae .... *A. japonicum* (Fursov, Shirota, Nomiya & Yamagishi, 2002) (♂), Japanese amber, Santonian
- Mesoscutum with reticulate sculpture; forewing posterobasal marginal seta offset by a series of four–five short, posterior setae .... *A. senonicum* (Kozlov & Rasnitsyn, 1979) (♀), Taimyr amber, Santonian
11. Forewing marginal fringe with 42–43 long, erect setae; forewing without mid-sized posterior setae; mesotibiae and metatibiae without pseudospurs; metatibiae with four distinct setae forming a comb on posterior distal margin .... *A. hispanicum* Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 (♀, ♂), Spanish amber, Albian
- Forewing marginal fringe with 38 long, erect setae; forewing with four mid-sized posterior setae; mesotibiae with two pseudospurs and metatibiae with four pseudospurs; metatibiae without setae forming a comb on posterior distal margin .... *A. phoenicium* **sp. nov.** (♀), Lebanese amber, Barremian

Discussion

Archaeromma phoenicium **sp. nov.** clearly belongs to the family Mymarommatidae based on (Gibson *et al.* 2007, Engel 2015): 1) toruli above dorsal margin of compound eyes, 2) forewing pedunculate with long, erect marginal setae and mesh-like pattern membrane, and venation extremely reduced, 3) hind wing stalk-like with a pincer-like apical structure, 4) tibial spur formula 1:0:0, and 5) petiole bi-segmented. Unfortunately, the pleated membrane between frontal and occipital plates, characteristic of mymarommatids, is not visible in the head of the studied specimen. The exodont mandibles and having the claval segments closely compacted of the studied specimen allow us to exclude affinity with †Gallorommatidae, characterised by endodont mandibles and claval segments distinctly separated (Gibson *et al.* 2007; Engel 2015). †Alavarommatidae have the hind wing well developed (Ortega-Blanco *et al.* 2011), and in †Dipterommatidae the hind wing is absent (Rasnitsyn *et al.* 2019). Within Mymarommatidae, the only Cretaceous genus is *Archaeromma*, characterised by the females having the antenna 13-segmented with 7 funicular segments and compacted clava 3- or 4-segmented (Gibson *et al.* 2007), matching with the studied specimen. Furthermore, it shows protibial calcar curved and simple, typical for the genus *Archaeromma*, while *Palaeomymar* and *Mymaromma* have a short protibial calcar straight and simple, and that of *Mymaromella* and *Zealaromma* is curved and bifurcate (Gibson *et al.* 2007).

Among the species of *Archaeromma*, *A. phoenicium* **sp. nov.** shares with *A. hispanicum* a 4-segmented clava and absence of posterobasal marginal seta on forewing (Ortega-Blanco *et al.* 2011). Both species differ on the arrangement of the forewing marginal setae and the apical structures of meso- and metatibiae. Interestingly, *A.*

phoenicium **sp. nov.** shares with *A. japonicum* and *A. senonicum* the number (38) of long, erect setae on forewing margin, but these two species have long posterobasal marginal seta (Kozlov & Rasnitsyn 1979; Fursov *et al*. 2002). Thus, the description of a new species for the studied specimen is justified. *Archaeromma phoenicium* **sp. nov.** corresponds to the oldest representative of the genus *Archaeromma* and of the family Mymarommatidae.

As mentioned by Gibson *et al*. (2007), there are no autapomorphies supporting the monophyly of the genus *Archaeromma*. The species *A. trigonokephalion* apparently has notauli on mesoscutum and the second petiolar segment is 2× longer than the first segment (Cockx *et al*. 2020). The petiolar segments relative proportions are different to the rest of Mymarommatidae and the presence of notauli would be even unique within Mymarommatoidea (Gibson *et al*. 2007; Engel 2015). However, the photographs and drawing of Cockx *et al*. (2020, fig. 3) seem to show the first petiolar segment being longer than the second segment. Considering this information, it is evident that the species of *Archaeromma* require a detailed revision and probably also the limits of the taxon itself, together with a phylogenetic analysis that helps to evaluate anatomical similarities and differences between the included species.

Four *Archaeromma* species have the clava 3-segmented, whereas eight species have the clava 4-segmented. Aiba & Inosa (2024, table 1) indicated that the clava of *A. masneri* is 4-segmented, although it is actually 3-segmented according to Gibson *et al*. (2007). Likewise, Aiba & Inosa (2024, table 1) mentioned clava 3-segmented for *A. trigonokephalion*, but it is 4-segmented following the description by Cockx *et al*. (2020). Among the 12 species belonging to the genus *Archaeromma*, both female and male specimens are known only for four of them: *A. chisatoi*, *A. hispanicum*, *A. minutissimum*, and *A. nearcticum*. The males originally assigned to *A. masneri* by Yoshimoto (1975) correspond in fact to an unidentified species of Mymaridae (Gibson *et al*. 2007). Therefore, the knowledge on sexual dimorphism in the genus *Archaeromma* is limited to proportions of the antennal segments, head, mesosoma, legs, and metasoma. The females of *A. minutissimum* and *A. nearcticum* are bigger than the males (Yoshimoto 1975), while in *A. chisatoi* the females are smaller than males (Aiba & Inosa 2024). Differential measurements between females and males of *A. hispanicum* are not known (Ortega-Blanco *et al*. 2011). It is important to note that differentiation of species of *Archaeromma* is challenging based on the high anatomical resemblance, for example between *A. chisatoi*, *A. minutissimum* and *A. nearcticum*. Aiba & Inosa (2024) compared these three species considering the arrangement of the posterobasal marginal seta and the series of short posterior setae distal to it. However, Gibson *et al*. (2007) noticed that the arrangement of these setae is variable within *A. minutissimum* and *A. nearcticum*. A re-evaluation of the diagnostic characters and states for the species of the genus is required to better assess the intraspecific variability.

The Mymarommatoidea were widely distributed during the Cretaceous (Fig. 4). However, there is a bias towards a record in amber probably due to their minute size, which hindered their preservation in lacustrine settings but facilitated their inclusion in resin (Martínez-Delclòs *et al*. 2004). In relation to this fact, the Cretaceous record of mymarommatoids is restricted to the Northern Hemisphere, due to the lack of Cretaceous fossiliferous amber outcrops from the Southern Hemisphere (Delclòs *et al*. 2023). The families †Alavarommatidae and †Dipterommatidae are represented by only two specimens from Spanish ambers and one specimen from Burmese amber respectively (Ortega-Blanco *et al*. 2011; Rasnitsyn *et al*. 2019). The family †Gallorommatidae consists of the genus *Cretaceomma*, only present in Lebanese and Spanish ambers, and the genus *Galloromma*, identified in Spanish, French, Burmese, and Taimyr ambers (Ortega-Blanco *et al*. 2011; Rasnitsyn *et al*. 2022). The mymarommatoid genus with the widest Cretaceous distribution is *Archaeromma*, the only representative of Mymarommatidae in this period. Species belonging to this genus are present in Lebanese, Spanish, Burmese, Taimyr, New Jersey, Japanese, and Canadian ambers (Table 1, Fig. 4). Interestingly, several co-occurrences of insect genera have been identified between the Barremian Lebanese ambers and the Albian Spanish ambers (Peris *et al*. 2016; Álvarez-Parra *et al*. 2023; Davranoglou *et al*. 2024). The description of *A. phoenicium* **sp. nov.** increases the list of insect genera co-occurrences between these two ambers to 21. The wide palaeodistribution of *Archaeromma* may point to an adaptation to resiniferous forests under different palaeoenvironmental conditions and indicates that they were good dispersers, probably passively ballooning ('air plankton') like extant mymarommatids. The high resemblance between species might be related to a similar ecological niche in the resiniferous forests. Considering the small body size of *Archaeromma* species, they were probably egg endoparasitoids similarly to the living mymarommatid species *Mymaromma menehune* Honsberger & Huber, 2022 (Honsberger *et al*. 2022). However, the previously commented absence of autapomorphies might lead to a re-evaluation of the genus *Archaeromma*. The description of new species both from amber or compression specimens and their inclusion in phylogenetic analyses will provide new keys to better understand the validity of the genus and its role in the evolutionary history of Mymarommatoidea.

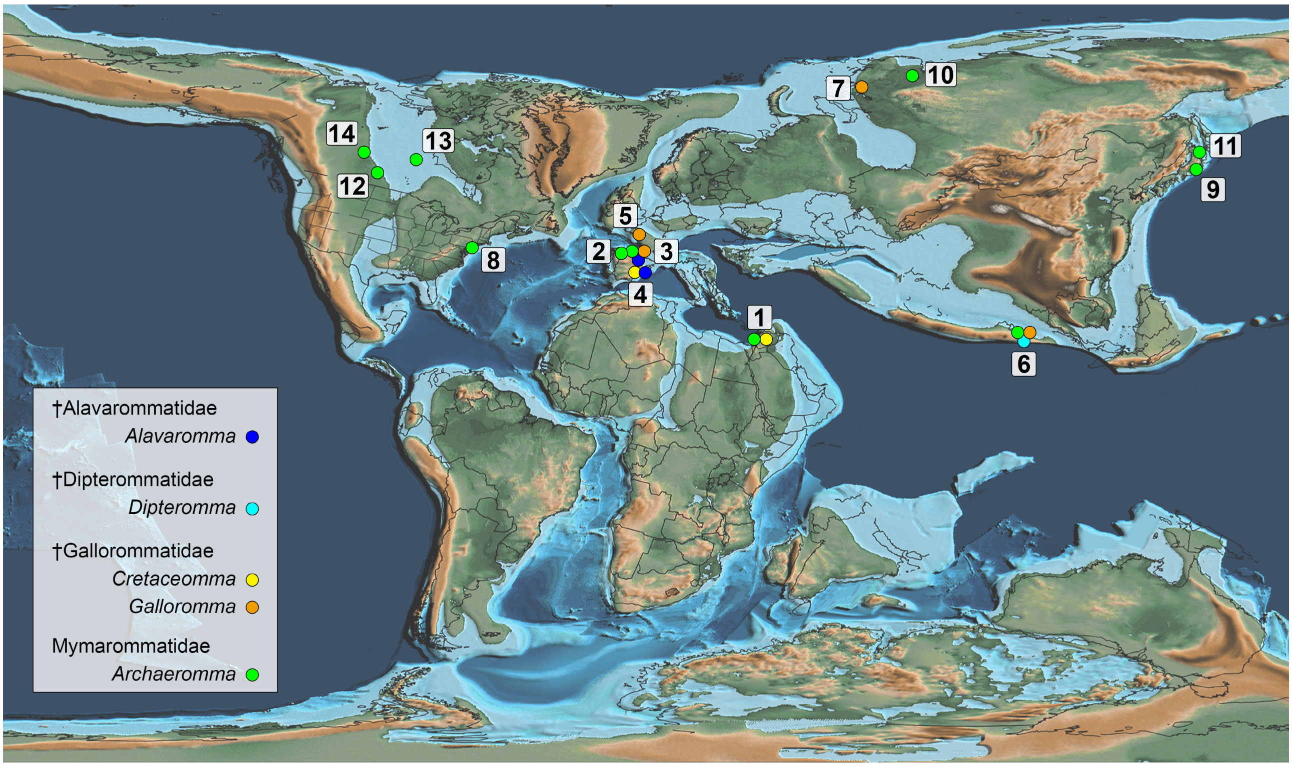

FIGURE 4. Palaeodistribution of the Cretaceous genera belonging to the superfamily Mymarommatoidea. 1: Lebanese amber, early Barremian; 2: El Soplao amber, middle Albian; 3: Peñacerrada I amber, late Albian; 4: San Just amber, late Albian; 5: Bezonnais amber, Cenomanian; 6: Kachin amber, early Cenomanian; 7: Nizhnyaya Agapa amber, late Cenomanian; 8: Sayreville amber, Turonian; 9: Iwaki amber, Coniacian; 10: Yantardakh amber, Santonian; 11: Kuji amber, Santonian; 12: Cedar Lake amber, Campanian; 13: Grassy Lake amber, Campanian; 14: Pipestone Creek amber, late Campanian. Palaeogeographic map of the world *ca*. 100 Ma from Scotese (2001).

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