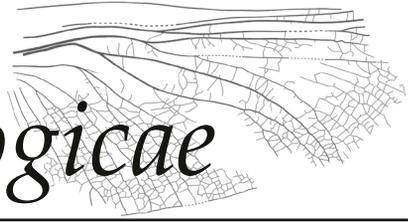


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A new family of primitive serphitoid wasps in Lebanese amber (Hymenoptera: Serphitoidea)

Michael S. Engel^{1,2}

Abstract. A new family of serphitoid wasps (Bipetiolarida: Serphitoidea) is described and figured as *Archaeoserphitidae* Engel, new family. The family is based on *Archaeoserphites melqarti* Engel, new genus and species, preserved in Early Cretaceous amber from Lebanon, and shares with Serphitidae a two-segmented, tubular petiole. *Archaeoserphites* have several primitive features relative to Serphitidae (*e.g.*, reduced pterostigma, similar to many chalcidoids; a greater number of flagellomeres; a distinct malar sulcus), while simultaneously exhibiting its own derived features (*e.g.*, angulate lower face, with clypeus downward; smaller mandibles; large pronotum; fused propleura). Diagnoses of and keys to the higher taxa of Bipetiolarida are provided, and the subfamily *Microserphitinae* Engel, new subfamily, is established.

INTRODUCTION

The various fossiliferous resins spanning the Cretaceous period contain a wide variety of parasitoid/predatory Hymenoptera, and representing many of the major superfamilial lineages (Grimaldi & Engel, 2005). While the numerous species are often primitive for their respective clades, they nonetheless are frequently rather easily placed in modern families as circumscribed or as clear stem groups to those families (*e.g.*, Townes, 1973; Krombein, 1986; Engel & Grimaldi, 2004, 2006a, 2007a, 2013; Engel, 2003, 2005a, 2006, 2008; Engel *et al.*, 2013a, 2013b; Liu *et al.*, 2007; Perrichot & Nel, 2008; Perrichot *et al.*, 2009; Ortega-Blanco *et al.*, 2009, 2011a, 2011b, 2014; Peñalver *et al.*, 2010;

¹ Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045-4415, USA (msengel@ku.edu).

² Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA.

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McKellar & Engel, 2012; McKellar *et al.*, 2013; Olmi *et al.*, 2014). Nonetheless, there are a series of distinctive extinct families that are almost hallmarks of the Cretaceous, representing apparently monophyletic groups that did not persist into the Cenozoic and were perhaps dwindling long before the Mesozoic came to its climactic closure. Each can be assigned to a superfamily and associated with their modern cousins, and inform us of the early branching events within these groups and of putatively ground-plan features aiding phylogenetic studies through the breaking up of otherwise long branches separating our surviving wasp clades. These period-distinctive families include the minute ceraphronoids of the Stigmaphronidae (Kozlov in Rasnitsyn, 1975; Engel & Grimaldi, 2009; Ortega-Blanco *et al.*, 2011c; McKellar & Engel, 2011a), mymarommatoids of the Alavarommatidae and Gallorommatidae (Gibson *et al.*, 2007; Engel & Grimaldi, 2007b; Ortega-Blanco *et al.*, 2011d), diapiroids of the Spathiopterygidae (Engel *et al.*, 2013c, 2015; Krogmann *et al.*, in prep.), trigonaloids of the Maimetshidae (Perrichot *et al.*, 2011; Perrichot, 2013; Engel, in press), and most interestingly the Serphitoidea, relatives of the Mymarommatoidea (Kozlov & Rasnitsyn, 1979; Gibson *et al.*, 2007; Ortega-Blanco *et al.*, 2011e; McKellar & Engel, 2011b). Serphitoidea have been represented by four genera and at least 14 species (two of which are undescribed at this time) of distinctive parasitoid wasps in Cretaceous amber ranging in age from the Albian through to the Campanian and from deposits in Spain (Ortega-Blanco *et al.*, 2011e), Myanmar (Engel, in prep.), New Jersey (Engel *et al.*, 2011), Vendée (Engel & Perrichot, 2014), Taimyria (Kozlov & Rasnitsyn, 1979), and Canada (Brues, 1937; McKellar & Engel, 2011b). Naturally, there are other extinct parasitoid families, some of dubious monophyly, from the Mesozoic and scattered across the diversity of Hymenoptera (*e.g.*, Rasnitsyn, 1988; Grimaldi & Engel, 2005). Unlike the above lineages, many of these are either little known regarding their temporal and geographic distribution, such as the Stolamissidae, Protimaspidae, and varied evanioids (*e.g.*, Liu *et al.*, 2007; Engel *et al.*, in press); are not restricted to the Cretaceous, such as Praeaulacidae (*e.g.*, Zhang & Rasnitsyn, 2008); or are clearly paraphyletic.

Here is reported a new family of parasitoid wasps closely allied to the Serphitidae and preserved in Early Cretaceous amber from Lebanon (Fig. 1). This extends the age of the superfamily deeper into the Early Cretaceous, the prior earliest records being those individuals in Albian Spanish amber (Ortega-Blanco *et al.*, 2011e) and in basalmost Cenomanian amber from Myanmar (Engel, in prep.). The new family possesses numerous plesiomorphic features relative to Serphitidae as well as its own putatively unique apomorphies relative to Mymarommatoidea and Serphitoidea (clade Bipetiolarida). The group is documented here in the hopes that further material and species may be discovered, and more fully inform us of the unique characters embodied by these tiny wasps and evolutionary patterns across the Proctotrupomorpha. In addition to describing the new family, brief diagnoses and keys are given to the higher groups of bipetiolate proctotrupomorphs.

MATERIAL AND METHODS

The two female individuals are preserved near each other in a single piece of relatively light yellow and clear Lebanese amber. Several fracture planes around and through the specimens makes particular views difficult, but most features can be observed on one or both individuals. The piece was trimmed and polished to a rectangle of 15 mm × 10.5 mm × 4 mm, and embedded in epoxy following the method of Nascimbene & Silverstein (2000). The wasps have a superficial habitus reminiscent



Figure 1. Photograph of piece from narrow, lateral edge, with holotype (left) and paratype (right) (AMNH L-AE-8) males of *Archaeoserphites melqarti*, new genus and species, in Early Cretaceous amber from Lebanon.

of Platygastroidea, but the details of their venation and bipetiolate metasoma betray their affinities to Serphitoidea. None of the wings are outstretched perfectly flat, and instead are bent or even folded at various points, giving in some views the deceptive appearance of additional veins (owing to looking edgewise at a fold in the membrane), but the actual venation can be determined easily between the two specimens and by tilting the piece at various points, and from one direction one wing from each specimen is comparatively unhindered (Fig. 1). Both specimens are well preserved and the individual with fewer surrounding fractures and with the genitalia observable was selected to serve as the holotype.

A Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens was used to prepare photographs, while an ocular micrometer on an Olympus SZX-12 stereomicroscope was used to make measurements. Measurements are provided for the holotype, with those of the paratype in parentheses, while a dash indicates a given measurement not possible for one of the individuals (owing to preservation). Descriptive accounts were prepared with the underlying belief that such work forms the foundation of broader explanatory theories (*vide* Grimaldi & Engel, 2007). Morphological terminology and the format for the descriptions generally follow those of Engel *et al.* (2011), McKellar & Engel (2011b), and Ortega-Blanco *et al.* (2011e), although wing venational terms are provided in both the standard Comstock-Needham system (*e.g.*, Gibson, 1997) as well as that used widely for Chalcidoidea and Mymarommatoida (*e.g.*, Huber & Sharkey, 1993). The term metasoma is used for all abdominal segments beyond the propodeum, while the term gaster is employed to refer to those metasomal segments beyond the petiole (as typically used in various groups such as ants: *e.g.*, Bolton, 1994). General information on the paleobiota, age, and origin

of amber deposits in Lebanon has been overviewed by Azar *et al.* (2010) and Maksoud *et al.* (2014). The Hymenoptera fauna is comparatively underexplored, with only eight families hitherto documented in sufficient detail from varied deposits across the country (*e.g.*, Olmi, 1998; Basibuyuk *et al.*, 2002; Deans *et al.*, 2004; Nel & Azar, 2005; Engel & Grimaldi, 2006b, 2007a; Johnson *et al.*, 2008; Perrichot *et al.*, 2011; Azevedo & Azar, 2012; Engel, in press; Krogmann *et al.*, in prep.), although others are known from undescribed material (Engel, pers. obs.).

SYSTEMATIC PALEONTOLOGY

Clade Bipetiolarida Engel

Bipetiolarida Engel, 2005b: 331 [for Mymarommatoidea + Serphitoidea].

DIAGNOSIS: Minute proctotrupomorph wasps, less than 4 mm in total length. Antenna geniculate; flagellum with 6–12 flagellomeres, never with basal anelliform flagellomere; flagellomeres lacking multiporous plate sensilla; face without prominent antennal shelf; occipital carina lacking; labial and maxillary palpi reduced or absent. Pronotum triangular in profile, usually with posterodorsal angle extending to forewing base; propleura abutting along length; prepectus not visible externally. Forewing with venation variously reduced, almost always lacking C as tubular vein; hind wing reduced, sometimes dramatically so, with venation largely restricted to C+Sc+R. Metasoma inserted low on mesosoma, between and slightly above level of metacoxae; always bipetiolate, petiole narrowed posteriorly, individual petiolar segments cylindrical.

REMARKS: The group comprises two superfamilies and five families, four of which are extinct. Table 1 summarizes the current hierarchical classification of Bipetiolarida to the level of genus. Superfamilies and families of Proctotrupomorpha are summarized in an appendix.

Key to Superfamilies of Bipetiolarida

1. Body size 0.75–3.5 mm in length; head with vertex convex and rounded into medially concave occiput; antennal toruli situated low on face, near base of clypeus; 6–12 flagellomeres; mandibles usually prominent, always endodont; notauli present, sometimes weakly so; tibial spur formula 1-2-2; forewing not pedunculate, with broad disc, with at most marginal fringe of fine setae, membrane never wrinkled or with lineations; venation extending well into disc of wing, with at least tubular Sc+R (submarginal vein) and R1 (marginal and postmarginal veins), as well as either tubular or nebulous r-rs (stigmatal vein), pterostigma, some indication of apical abscissa of Rs, and frequently with M+Cu, M, Cu, and 1m-cu; hind wing with stub of Rs, membrane distinct and extending well beyond position of apical hamuli [Barremian–Campanian] Serphitoidea Brues
- Body size less than 1 mm in length; posterior of head usually with pleated membrane forming bellows-like structure separating occipital plate from remainder of head (Mymarommatoidea), or without such a structure (Gallorommatoidea and Alavarommatoidea) antennal toruli situated often at or above upper tangent of compound eyes, rarely closer to midlevel of face; 7–11 flag-

Table 1. Hierarchical, supraspecific classification of Bipetiolarida (Proctotrupomorpha), with temporal ranges indicated.

Clade BIPETIOLARIDA Engel	
Superfamily †SERPHITOIDEA Brues	
Family †Archaeoserphitidae, n. fam.	
Genus † <i>Archaeoserphites</i> , n. gen.	Barremian
Family †Serphitidae Brues	
Subfamily †Microserphitinae, n. subfam.	
Genus † <i>Microserphites</i> Kozlov & Rasnitsyn	Albian–Santonian
Subfamily †Serphitinae Brues	
Genus † <i>Aposerphites</i> Kozlov & Rasnitsyn	Albian–Santonian
Genus † <i>Serphites</i> Brues	Albian–Campanian
Genus † <i>Jubaserphites</i> McKellar & Engel	Campanian
Superfamily MYMAROMMATOIDEA Debauche	
Family †Alavarommatidae Ortega-Blanco <i>et al.</i>	
Genus † <i>Alavaromma</i> Ortega-Blanco <i>et al.</i>	Albian
Family †Gallorommatidae Gibson <i>et al.</i>	
Genus † <i>Galloromma</i> Schlüter	Cenomanian–Santonian
Family Mymarommatidae Debauche	
Genus † <i>Archaeoromma</i> Yoshimoto	Albian–Campanian
Genus † <i>Palaeomymar</i> Meunier	Eocene (Ypresian–Lutetian)
Genus <i>Mymaromella</i> Girault	Miocene–Holocene
Genus <i>Mymaromma</i> Girault	Holocene
Genus <i>Zealaromma</i> Gibson <i>et al.</i>	Holocene

ellomeres, often clavate (not clavate in Alavarommatidae); mandibles short, usually exodont, rarely endodont; notauli lacking; tibial spur formula 1-0-0; forewing pedunculate, with stalk and either spatulate or nearly lanceolate disc, often with marginal fringe of stiff, elongate, setae well set into margin of disc, and membrane wrinkled or with lineations (both lacking in Alavarommatidae); venation greatly reduced, disc without venation, veins confined to stalk, at most represented by submarginal vein, marginal vein, and vestigial pterostigma; hind wing without stub of Rs, membrane narrow or scarcely present, not exceeding apical hamuli, which are often modified into pincer-like structure [Albian–present] Mymarommatoidea Debauche

Superfamily Mymarommatoidea Debauche

Mymarommatidae Debauche, 1948: 42, *nomen imperfectum* (*recte* Mymarommatidae; *vide* Brues *et al.*, 1954). Type genus: *Mymaromma* Girault, 1920.

DIAGNOSIS (modified from Gibson *et al.*, 2007): Minute species, less than 1 mm in length. Head hypognathous, often with a flat, semicircular occipital plate separated from frontal portion of head by hyperoccipital band of pleated membrane dorsally and laterally, occipital plate articulating with postgenal region of head above occipital foramen (in Mymarommatidae), or without such plates and vertex convex and rounded into medially concave occiput (Alavarommatidae and Gallorommatidae); ocelli present or absent; toruli subcontiguous and slightly protrudent, at or above level of dorsal margin of compound eyes (Mymarommatidae), or at about middle of face (Alavarommatidae and Gallorommatidae), well separated from base of clypeus; antenna geniculate; flagellum without multiporous plate sensilla, first flagellomere often shorter than

second flagellomere, female flagellum composed of 7–9 flagellomeres (Mymarommatidae) or 11 flagellomeres (Gallorommatidae), and usually distinctly clavate [funicle with 6–7, clava with 1–2 flagellomeres (Mymarommatidae); funicle with 7, clava with 4 flagellomeres (Gallorommatidae)] or not clavate (Alavarommatidae), male flagellum usually composed of 11 flagellomeres, rarely 10 (Alavarommatidae); compound eyes variable but usually large and encompassing majority of head in profile; malar space variable, rarely with malar sulcus; mandible bidentate or tridentate, exodont (Mymarommatidae) or endodont (Gallorommatidae and Alavarommatidae); labial palpi lacking, maxillary palpi vestigial (unknown for Alavarommatidae).

Pronotum not visible dorsally, with posterodorsal angle extending to base of forewing; pronotum not contiguous ventrally (sides not meeting posterior to propleura); propleura divided mediolongitudinally (Alavarommatidae, Gallorommatidae, and some Mymarommatidae), or variously fused; prepectus not visible; tegula lacking; mesoscutum without notauli or parapsidal lines, transscutal sulcus straight; mesoscutellum without differentiated axillae, with transverse anterior mesoscutellum and posterior concave frenum; mesopleuron without differentiated mesepisternum and mesepimeron; metanotum largely concealed by posterior border of mesoscutellum; meso- and metapleuron partially fused to separated by oblique suture (completely separated in Gallorommatidae, unknown in Alavarommatidae); metapleuron fused with propodeum; propodeal spiracle below level of propodeal surface (Mymarommatidae) or near posterior margin of mesoscutellum (Gallorommatidae) (unknown in Alavarommatidae).

Forewing pedunculate, remigium with slender stalk and broadly spatulate to somewhat lanceolate disc; remigium sometimes almost flat but usually more or less distinctly convoluted by folds; venation often indiscernible (Gallorommatidae and Mymarommatidae, but with greatly reduced vein along anterior border of stalk corresponding to vestigial submarginal and marginal vein), or with more distinct short submarginal vein, marginal vein, and vestigial 'stigma' all of which scarcely exceed wing stalk (Alavarommatidae), disc with lineations on upper and lower surfaces of membrane forming mesh-like pattern (Gallorommatidae and Mymarommatidae); wing margin with elongate marginal setae arising from within disc (Gallorommatidae and Mymarommatidae) or fine fringe of short setae (Alavarommatidae); hind wing with bulbous base and slender veinal stalk terminated by pincer-like structure formed by hamulus and opposing projection, stalk sometimes with slender band of posterior membrane (Gallorommatidae and Mymarommatidae), or with C+Sc+R, two apical hamuli, and slender membrane not exceeding position of hamuli (Alavarommatidae).

Legs slender; all femora with differentiated trochantellus; tibial spur formula 1-0-0; protibial calcar curved and apically simple (Alavarommatidae) or bifurcate, or straight and simple; tarsi pentamerous; pretarsal claws simple, arolium present.

Metasoma 8-segmented, bipetiolate, basal two segments narrow, cylindrical; gaster usually dorsoventrally compressed, tergum IV largest of terga; terga broadly overlapping sterna laterally and without defined laterotergites; without spiracles except on tergum VII; terga VIII and IX united as syntergum; ovipositor concealed; male with parameres often externally protruding and large medial aedeagus, in dorsal view divided apically.

INCLUDED FAMILIES: Three families presently included, the extinct Alavarommatidae and Gallorommatidae, known only from Cretaceous amber, and the Mymarommatidae, occurring at least as far back as the Albian and surviving today with three genera (Gibson *et al.*, 2007).

REMARKS: A treatment of the families of Mymarommatoidea is beyond the scope of the present work and is not provided here. Gibson *et al.* (2007) have provided an exhaustive treatment of the superfamily, families Gallorommatidae and Mymaromatidae, as well as the included living and fossil genera, while Ortega-Blanco *et al.* (2011d) provided a description for Alavarommatidae and tabulated similarities and differences among the families.

Superfamily Serphitoidea Brues

DIAGNOSIS: Minute species, less than 4 mm in length. Head hypognathous, ovoid or rounded, with vertex convex and rounded into medially concave occiput; ocelli present; toruli subcontiguous and slightly protrudent, near or below lower tangent of compound eyes, near base of clypeus; antenna geniculate; flagellum without multiporous plate sensilla, first flagellomere often as long as or slightly longer than second flagellomere, flagellum composed of 6–8 (Serphitidae) or 12 flagellomeres (Archaeoserphitidae), weakly clavate or not clavate; compound eyes large and encompassing majority of head in profile; malar space variable, sometimes with malar sulcus (Archaeoserphitidae); mandibles asymmetrical, bidentate or tridentate, endodont; labial and maxillary palpi present but reduced, apparently with fewer than 4 palpomeres (labial palpi unknown for Archaeoserphitidae).

Pronotum visible dorsally, sometimes scarcely so (Serphitidae), with posterodorsal angle extending to base of forewing, rarely not reaching base (*Microserphites* Kozlov & Rasnitsyn), triangular in lateral view; pronotum not contiguous ventrally (sides not meeting posterior to propleura); propleura abutting along length, divided mediolongitudinally (Serphitidae) or fused (Archaeoserphitidae); prepectus not visible; tegula reduced (Serphitidae) or absent (Archaeoserphitidae); mesoscutum with notauli (sometimes weakly impressed), transscutal sulcus straight; mesoscutellum with (Archaeoserphitidae) or without (Serphitidae) differentiated axillae; mesopleuron without differentiated mesepisternum and mesepimeron; metanotum short, consisting of a thin transverse band, not concealed by posterior border of mesoscutellum; meso- and metapleuron separated by oblique suture; metapleuron fused with propodeum; propodeal spiracle near posterior margin of metanotum.

Forewing with slender base but not pedunculate, remigium broad apically but not spatulate; remigium flat, without lineations or mesh-like patterning; venation with tubular submarginal (Sc+R), marginal (R1 proximal to r-rs), and postmarginal veins (R1 apical to r-rs), and at least nebulous, if not tubular, M+Cu, M, Cu, and partial Rs veins (M+Cu, basal vein, and basal portion of Cu tubular in Serphitidae, nebulous in Archaeoserphitidae), C either absent or nebulous (sometimes thinly tubular in Serphitinae), Rs+M lacking, r-rs always with slightly thickened apex (corresponding to 'stigma' of chalcidoid veinal terminology, but apparently formed of thickened juncture of r-rs and Rs); sometimes with large, triangular pterostigma composed of diffuse or sclerotized area between r-rs and postmarginal vein (Serphitidae); wing margin with fringe of fine, short setae; hind wing distinct, slender, sometimes almost lanceolate, with well-delimited, narrow membrane; venation reduced, with C+Sc+R and short stub of Rs; two distal hamuli positioned at terminus of R1 just beyond wing midlength; margin with fringe of fine, short setae.

Legs slender; all femora with differentiated trochantellus; tibial spur formula 1-2-2; protibial calcar curved, apically simple or bifurcate; tarsi pentamerous; pretasal claws simple, arolium present.

Metasoma 8-segmented, bipetiolate, basal two segments narrow, cylindrical; gaster somewhat dorsoventrally compressed, anterior terga of approximately equal lengths, sometimes tergum IV slightly larger; terga broadly overlapping sterna laterally, without distinct laterotergites or at most with slight crease on more anterior terga (some Serphitidae); without spiracles except perhaps on tergum VII; possible syntergum present through fusion of terga VIII and IX; ovipositor concealed; male with parameres externally protruding, with narrow medial aedeagus protruding, in dorsal view emarginate.

INCLUDED FAMILIES: The superfamily consists of two families, the nominate Serphitidae and the new family described herein (*vide infra*).

Key to Families of Serphitoidea

- 1. Malar sulcus present; 12 flagellomeres; face with angulate ridge immediately below antennal toruli; pronotum with prominent dorsal surface in dorsal view; propleurae mediolongitudinally fused; forewing with narrow pterostigma composed of thick vein along wing margin; M+Cu, M, Cu, and Rs nebulous; C absent; apical abscissa Rs not reaching wing margin; body length less than 2 mm [Barremian] Archaeoserphitidae, n. fam.
- Malar sulcus absent; 6–8 flagellomeres; face without angulate ridge immediately below antennal toruli; pronotum largely obscured in dorsal view; propleurae mediolongitudinally separated; forewing with large, triangular to weakly trapezoidal, nebulous or sclerotized pterostigma; M+Cu, M, and at least part of Cu and Rs tubular; C variable; apical abscissa Rs reaching wing margin; body length less than 4 mm [Albian–Campanian] Serphitidae Brues

Family Serphitidae Brues

DIAGNOSIS: Minute wasps, less than 4 mm in length. Head rounded, often large in female, with vertex rounded; antennal toruli subcontiguous, low on face, near base of clypeus; antenna geniculate; scape cylindrical; flagellum composed of 6–8 flagellomeres, weakly clavate; face without angulate ridge immediately below antennal toruli; compound eyes large and encompassing majority of head in profile; malar space comparatively long, without malar sulcus; labial and maxillary palpi present, short.

Mesosoma narrow, slightly higher than wide or about as high as wide. Pronotum scarcely visible in dorsal view, with strongly sloping anterior surface, with posterodorsal angle extending to base of forewing (except in *Microserphites*); propleura abutting along length, mediolongitudinally divided; prepectus not visible; tegula present, generally reduced; mesoscutum with notauli present, sometimes faintly so, parapsidal lines absent, transscutal sulcus straight; mesoscutellum without differentiated axillae; propodeum weakly areolate.

Forewing with slender base and broad disc; venation with tubular submarginal (Sc+R), marginal (R1 proximal to r-rs), and postmarginal veins (R1 apical to r-rs), and tubular to nebulous M+Cu, basal vein, and basal portion of Cu, C typically nebulous (*e.g.*, McKellar & Engel, 2011b) but sometimes absent (*Microserphitinae*) or thinly tubular (some *Serphitinae*), Rs+M absent, r-rs with thickened apex at juncture with nebulous abscissa of Rs, apical abscissa of Rs reaching wing margin (*i.e.*, marginal cell closed), A nebulous to absent; large, triangular or weakly trapezoidal pterostigma, ei-

ther nebulous (*Microserphitinae*) or sclerotized (*Serphitinae*); wing margin with fringe of minute setae. Hind wing short, narrow, with distinct membrane; C+Sc+R tubular, Rs present as stub extending posteriorly, R present apically as short stub beyond position of distal hamuli; two distal hamuli present; margin with fringe of minute setae.

Legs slender; protibial calcar generally curved, apically simple or bifurcate; pre-tarsal claws simple, arolium present.

Metasoma bipetiolate, petiolar segments narrow, cylindrical; gaster generally dorsoventrally compressed, with convex terga and flattened sterna; tergum IV sometimes slightly larger than remaining terga; terga overlapping sterna laterally, usually with weak crease laterally, at least on anterior terga, thus with weakly defined laterotergites; without spiracles except perhaps on tergum VII; male with parameres and narrow medial aedeagus externally protruding.

Microserphitinae Engel, new subfamily

ZooBank: urn:lsid:zoobank.org:act:707C6790-B50F-405E-995A-099DAC7D6F14

TYPE GENUS: *Microserphites* Kozlov & Rasnitsyn, 1979.

DIAGNOSIS: Antennal flagellum with 7 flagellomeres; posterodorsal angle of pronotum not reaching forewing base; forewing with C lacking, pterostigma nebulous.

INCLUDED GENERA: At present the subfamily includes only the type genus, known from Spanish Early Cretaceous amber (Ortega-Blanco *et al.*, 2011e) and Taimyrian Late Cretaceous amber (Kozlov & Rasnitsyn, 1979).

Subfamily Serphitinae Brues

Serphitidae Brues, 1937: 33. Type genus: *Serphites* Brues, 1937.

DIAGNOSIS: Antennal flagellum with 6–8 flagellomeres; posterodorsal angle of pronotum reaching forewing base; forewing with C nebulous or thinly tubular apically, pterostigma sclerotized.

INCLUDED GENERA: Three genera included — *Serphites* Brues in diverse amber deposits spanning the Early and Late Cretaceous (summarized in Engel & Perrichot, 2014); *Aposerphites* Kozlov & Rasnitsyn in Spanish Early Cretaceous amber (Ortega-Blanco *et al.*, 2011e) and Taimyrian Late Cretaceous amber (Kozlov & Rasnitsyn, 1979); and *Jubaserphites* McKellar & Engel from Canadian Late Cretaceous amber (McKellar & Engel, 2011b).

Archaeoserphitidae Engel, new family

ZooBank: urn:lsid:zoobank.org:act:844FC27E-4F44-4A73-AF68-F049D5804420

TYPE GENUS: *Archaeoserphites* Engel, new genus.

DIAGNOSIS: Minute wasps, less than 2 mm in length. Head ovoid, with vertex rounded; antennal toruli subcontiguous, low on face, near base of clypeus; antenna geniculate; scape stout, cylindrical; flagellum composed of 12 flagellomeres, not clavate; angulate ridge immediately below antennal toruli, such that clypeus more ventrally directed; compound eyes large and encompassing majority of head in profile; malar space comparatively long, with malar sulcus; maxillary palpus present, short (labial palpus not visible, or perhaps absent; if lacking, then this could be a groundplan trait of Bipetolarida and Chalcidoidea).

Mesosoma narrow, slightly higher than wide. Pronotum with distinct, broad dorsal surface, medially about as long as one-quarter mesoscutal length, with strongly sloping anterior surface, with posterodorsal angle extending to base of forewing; propleura abutting along length, fused along mediolongitudinal borders; prepectus not visible; tegula lacking; mesoscutum with distinctly impressed notauli, parapsidal lines absent, transscutal sulcus straight; mesoscutellum with differentiated axillae; propodeum weakly areolate.

Forewing with slender base, disc broad; venation with tubular submarginal (Sc+R), marginal (R1 proximal to r-rs), and postmarginal veins (R1 apical to r-rs), and nebulous M+Cu, M, Cu, and partial Rs veins, C and Rs+M absent, r-rs with thickened apex at juncture with nebulous abscissae of Rs, apical abscissa of Rs not reaching wing margin (*i.e.*, marginal cell open); without large, triangular pterostigma; wing margin with fringe of fine, short setae. Hind wing short, narrow, lanceolate, with distinct membrane, but greatly narrowed base, maximum width near at position of distal hamuli; C+Sc+R tubular, Rs present as nebulous stub extending posteriorly, R present apically as short stub beyond position of distal hamuli; two distal hamuli present; margin with fringe of short setae.

Legs slender; protibial calcar long, curved, apically simple; pretasal claws simple, arolium present.

Metasoma bipetiolate, petiolar segments narrow, cylindrical; gaster somewhat dorsoventrally compressed, with convex terga and comparatively flat sterna; terga broadly overlapping sterna laterally, without distinct laterotergites; without spiracles except perhaps on tergum VII; male with parameres and narrow medial aedeagus externally protruding.

INCLUDED GENERA: At present the family includes only the type genus from Lebanese Early Cretaceous amber. Given the superficial similarity of these wasps to primitive Scelionidae and the abundance of the latter family in Cretaceous amber, it is possible that further material has gone unnoticed among fossil scelionids.

Archaeoserphites Engel, new genus

ZooBank: urn:lsid:zoobank.org:act:1D5433BC-E0CB-4FD9-8021-FBEC1AD02592

TYPE SPECIES: *Archaeoserphites melqarti* Engel, new species.

DIAGNOSIS: As for the family (*vide supra*).

ETYMOLOGY: The generic name is a combination of the Greek *archaios*, meaning, "from the beginning", and *Serphites* Brues, type genus of the related Serphitidae. The gender of the name is masculine.

Archaeoserphites melqarti Engel, new species

ZooBank: urn:lsid:zoobank.org:act:56A56FE3-23B0-4E8B-B7D5-91A4A1011605

(Figs. 1–7)

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

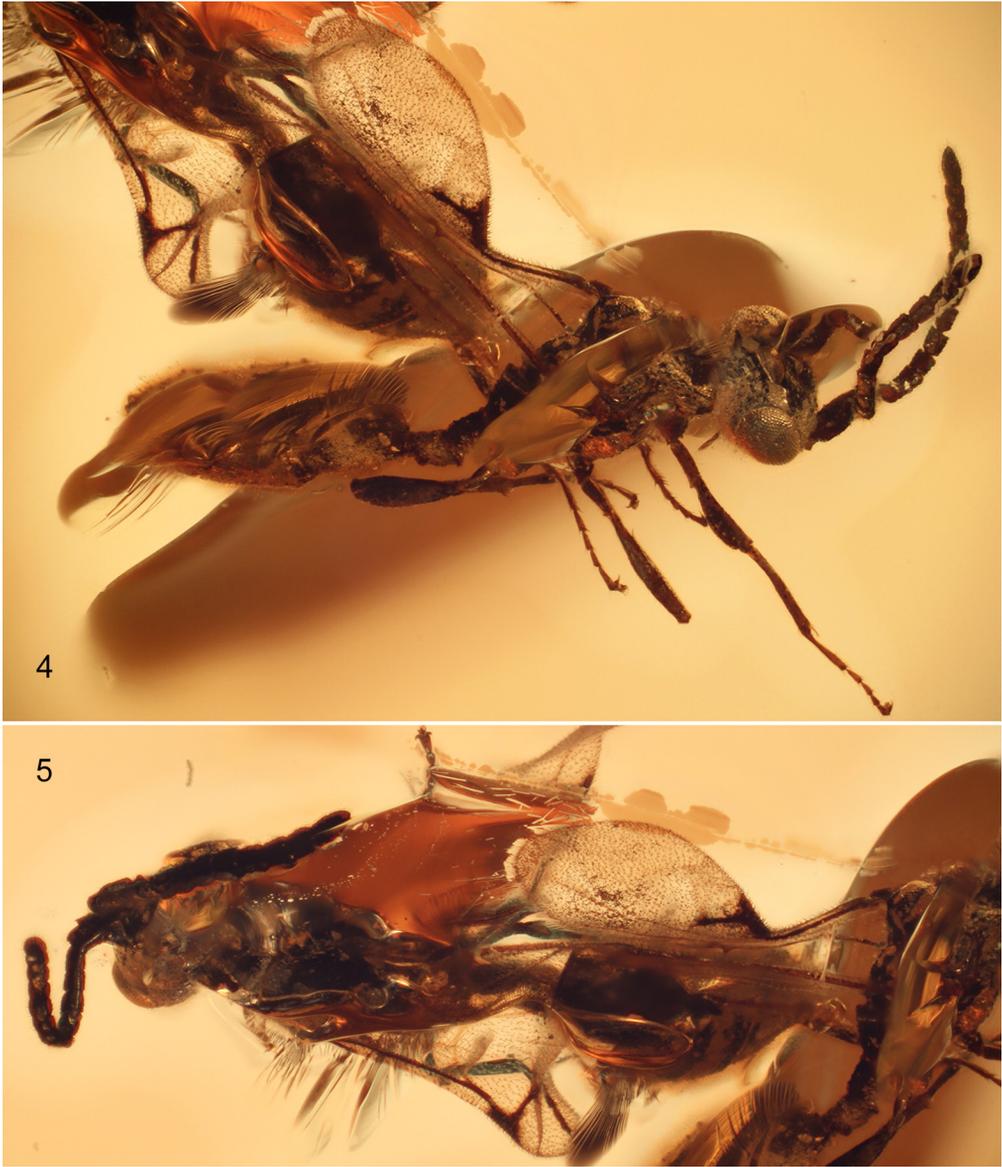
DESCRIPTION: ♂: Total body length as preserved approximately 1.59 mm (1.80 mm); forewing length 1.22 mm (1.27 mm), maximum width 0.49 mm (0.51 mm); hind wing length 0.66 mm (— mm). Integument dark brown to black (Figs. 1–5), granulose to coarsely imbricate; setae sparse throughout.

Head broader than long, medial length 0.31 mm (0.36 mm), width across compound eyes 0.43 mm (— mm), vertex weakly arched in frontal view, with rounded



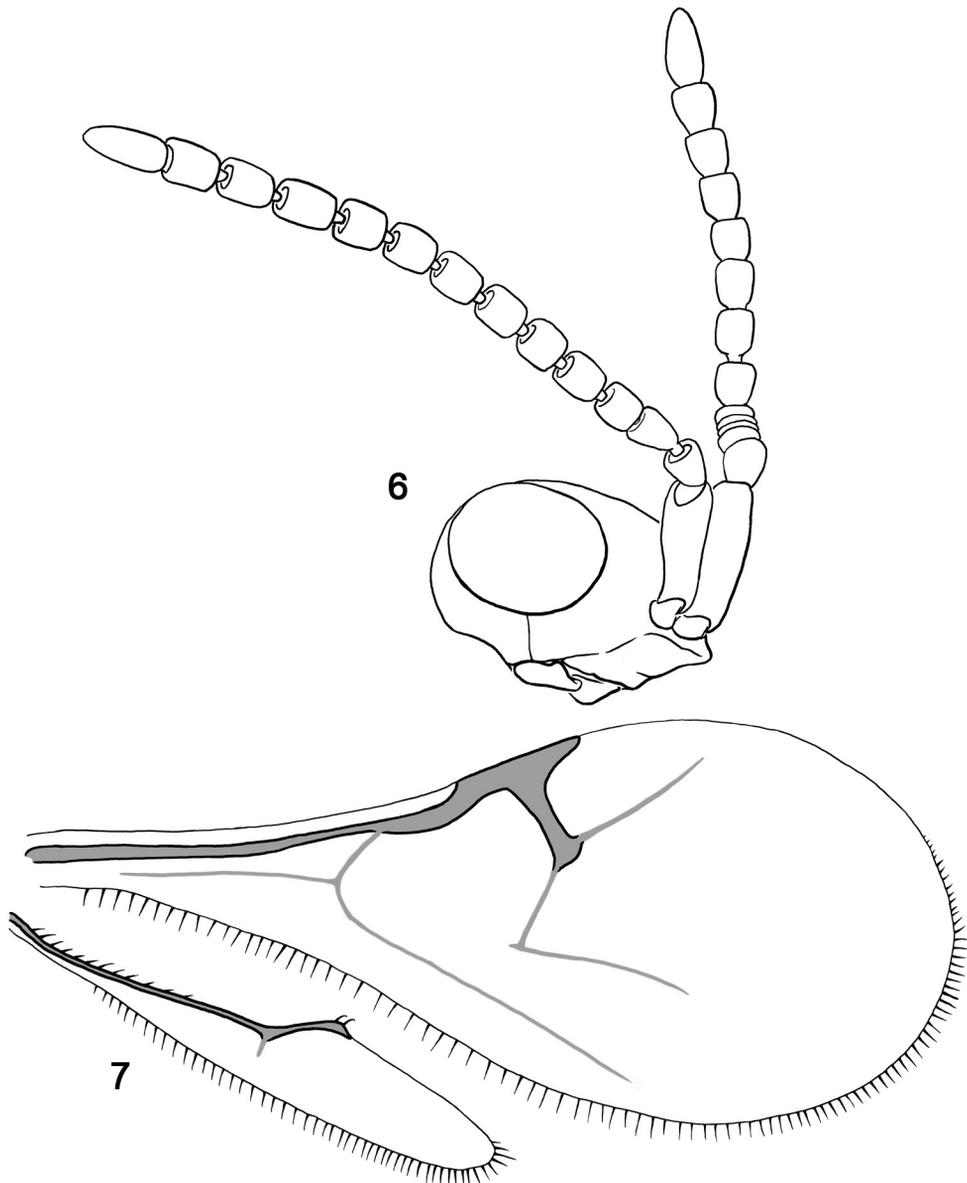
Figures 2–3. Photographs of holotype and paratype (AMNH L-AE-8) males of *Archaeoserphites melqarti*, new genus and species. **2.** Right view through amber piece, with holotype (at right) in dorsal oblique view and paratype (at left) in dorsal view. **3.** Left view through piece, with holotype (at left) in ventral oblique view but largely obscured by fracture plane, and paratype (at right) in ventral view.

occipital ridge. Lateral ocelli at or slightly below upper tangent of compound eyes; separated from compound eye margin by distance nearly twice ocellar diameter; median ocellus separated from lateral ocelli by about ocellar diameter; lateral ocelli separated by ocellar diameter or slightly more. Compound eye semi-circular, comparatively large, length 0.18 mm (0.19 mm), occupying majority of head in profile, inner margin comparatively straight, separated by distance slightly greater than compound eye length; inner borders roughly parallel. Gena evenly rounded posteriorly, narrow



Figures 4–5. Photographs of holotype and paratype (AMNH L-AE-8) males of *Archaeoserphites melqarti*, new genus and species. 4. Dorsal oblique view of holotype; metasoma is twisted so that it is in partial lateral view relative to the mesosoma and head. 5. Dorsal detail of paratype.

in profile, only slightly widening ventroapically toward malar space. Postgena broad. Frons broad, slightly convex, without medial line, depression, carinae, or distinctive sculpturing. Antennal toruli low on face, situated below lower tangent of compound eyes, toruli close together, nearly contiguous, widely separated from compound eye margin, situated posterior to angled ridge demarcating clypeal base (Fig. 6); scape thick, much longer than wide, slightly shorter than compound eye length, length 0.17 mm (0.17 mm), width 0.06 mm (0.06 mm); pedicel about as long as apical width; flagellum with 12 flagellomeres, not clavate, individual flagellomeres comparatively thick, about as long as wide except first flagellomere slightly longer than apical width; first



Figures 6–7. Details of *Archaeoserphites melqarti*, new genus and species. 6. Detail of head and antennae in lateral view (note that individual's left antenna is twisted at base and foreshortened). 7. Forewing and hind wing venation.

flagellomere slightly longer than second flagellomere; apicalmost flagellomere slightly narrower and longer, terminating in broadly-rounded point, all flagellomeres with scattered, minute, fine, inclined, silvery setae, without multiporous plate sensilla. Malar space comparatively long, longer than basal mandibular width and scape diameter, with weak malar sulcus present and extending to anterior border of posterior mandibular articulation. Clypeus broad, apparently slightly trapezoidal, situated ventroapically on face and below ridge anterior to toruli. Mandible short, scarcely overlapping apex of opposing mandible in repose, tapering in width along length to apparently

narrow apex, with at least two blunt teeth (dentition of opposing mandible obscured, so whether dentition is asymmetrical is unknown). Palpi apparently short; labial palpus not visible; maxillary palpus with at least three short, slender palpomeres.

Mesosoma narrow, length 0.56 mm (0.63 mm), maximum lateral height 0.28 mm (– mm). Pronotum prominent, with broad, comparatively flat (or faintly convex) dorsal surface, dorsal surface sloping to pronotum collar, without demarcated anterior border or carina such that dorsal surface is ill defined, but approximately one-quarter length of mesoscutum, with posterodorsal border comparatively straight; posterodorsal angle extending to base of forewing, without anterior carina and without lateral carina; lateral surface triangular, separated from dorsal sloping surface and collar by rounded angle; pronotum not contiguous ventrally; propleura narrow, fused medially. Prepectus lacking (or, at least not visible externally). Mesoscutum about as long as wide, weakly convex; notauli prominent, arching from point near posterodorsal angle of pronotum to transverse mesoscutal sulcus, narrow but apparently finely areolate, widely separated along transverse sulcus, mesoscutellar lateral lobes broad and convex; median line absent. Tegula lacking. Mesoscutellum about as long as wide, only slightly shorter than mesoscutum, weakly convex, with well-defined, small axillae. Mesepisternum without defined carinae or ridges, surface slightly depressed, with strongly demarcated mesepisternal-metepisternal suture. Metanotum exceedingly short. Metepisternum fused to propodeum. Propodeum gently sloping to petiolar articulation, without pronounced posterior ridge, weakly areolate, propodeal spiracle prominent, rimmed, situated at rounded ridge between dorsal and lateral propodeal surfaces and separated from metanotal posterior margin by about diameter of spiracle; articulation with metasoma low, slightly above and between metacoxae.

Forewing with membrane hyaline and clear, tubular veins dark brown, remaining veins nebulous, with pigmentation fairly faint; C absent, thus costal cell open along anterior wing margin; Sc+R tubular (Fig. 7), slightly widening apically, extending to base of narrow pterostigma along wing margin [using the vein terminology typical for Myrmarommatoidea and Chalcidoidea, this corresponds to an elongate submarginal vein, distinct marginal vein, and postmarginal vein], M+Cu nebulous, with nebulous basal vein; Rs nebulous and arising from Sc+R basad of pterostigmal base, distance from pterostigmal base about as long as length of basal vein (Fig. 7); Cu nebulous, arching away from M+Cu and then extending straight toward posterior wing margin, terminating before wing margin at point slightly apical to transverse tangent with pterostigmal apex; Rs+M absent; pterostigma linear, much longer than wide, with broad r-rs (stigmal vein) extending to apical thickening from which nebulous abscissae of Rs extend (Fig. 7); apical abscissa straight, extends apically toward anterior wing margin, terminating well before margin and leaving marginal cell open; basal abscissa extends posteriorly and slightly proximally, length about that of r-rs, then meeting nebulous apical abscissa of M, which extends longitudinally, disappearing at about transverse tangent with terminating of apical abscissa Rs (Fig. 7); A absent; margin with fine fringe of short setae. Hind wing short, narrow, lanceolate, with distinct membrane, but greatly narrowed base, maximum width near at position of distal hamuli, membrane hyaline and clear; C+Sc+R tubular (Fig. 7), running along anterior wing margin, Rs present as nebulous stub extending posteriorly, R1 present apically as short stub beyond position of distal hamuli; two apical hamuli present (Fig. 7); margin with fine fringe of short setae.

Legs with moderately numerous fine, minute setae on tibiae and tarsi, otherwise with sparsely scattered, minute setae; trochantellus short, well defined on all legs; fem-

ora slightly swollen; tibiae slender, cylindrical, only slightly longer than corresponding femora; metatibial length 0.31 mm (0.33 mm); tibial spur formula 1-2-2, protibial calcar long, strongly curved, with apex simple, mesotibial spurs exceedingly short, metatibial spurs short but longer than those of mesotibia; tarsi pentamerous, basitarsus longest tarsomere, shorter than combined lengths of tarsomeres II–IV, tarsomere II about as long as tarsomere V; pretarsal claws simple, arolium large.

Metasoma longer than mesosoma, bipetiolate, sparsely setose; petiole approximately one-third gaster length, composed of two cylindrical segments, first petiolar segment slightly longer than second petiolar segment, first petiolar segment length 0.13 mm (0.14 mm), width 0.07 mm (0.07 mm), second petiolar segment length 0.10 mm (0.11 mm), width 0.07 mm (0.07 mm); first petiolar segment weakly rugose, second petiolar segment apparently granular; gaster elongate ovoid in dorsal view and slightly dorsoventrally compressed, length approximately 0.64 mm (0.61 mm), maximum width 0.36 mm (0.36 mm), terga slightly convex and coarsely imbricate, with sparsely scattered, fine, minute setae, apparently with six visible terga, first gastral tergum slightly longer than other segments, otherwise terga of comparatively equal lengths except apical two segments shorter and tapered in width; terga without evident spiracles (this cannot be confirmed for the apicalmost tergum); sterna comparatively flat, with sparsely scattered, minute, fine setae, with apparently six visible sterna. Male genitalia at least partially exposed, short, thumb-like parameres protruding, widely separated, with scattered minute setae; thick medial aedeagus protruding, apically emarginate.

♀: *Latet.*

HOLOTYPE: ♂ (Fig. 4), AMNH L-AE-8; amber, Early Cretaceous (Barremian), northern Lebanon, Bchare [Bcharré] Mountain, 2300 m; deposited in the amber fossil collection of the Division of Invertebrate Zoology, American Museum of Natural History, New York.

PARATYPE: ♂ (Fig. 5), in same piece of amber as holotype, AMNH L-AE-8; amber, Early Cretaceous (Barremian), northern Lebanon, Bchare [Bcharré] Mountain, 2300 m; deposited in the amber fossil collection of the Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet is a patronym for the Phoenician god Melqart, the famous tutelary deity of Tyre. When the citizens of Tyre did not grant him permission to visit the temple of Melqart and make sacrifice, Alexander III of Macedon, a.k.a. 'the Great' (356–323 B.C.), was denied permission to worship there in 332 B.C.

DISCUSSION

The discovery of *Archaeoserphites melqarti* extends the geological record of Bipetolarida back to the Barremian, and provides the first evidence of their occurrence in the region of ancient Lebanon. Many of the features of Archaeoserphitidae are understandably plesiomorphic relative to Serphitidae when compared across closely allied superfamilies such as Mymarommatoidea, Chalcidoidea, Diaprioidea, Platygastroidea, and Cynipoidea. In particular, the wing venation which, like most of the aforementioned superfamilies, lacks a traditional pterostigma (which in Serphitidae is quite different than those of Monomachidae or various proctotrupoids), is more reminiscent of Chalcidoidea or some derived members among the Scelionidae (the primitive condition for Platygastroidea, however, is subtly different; *vide infra*). Rather than the more enriched venation of Serphitidae being primitive, their pattern is likely derived

with the reacquisition of numerous veins and, among some, an enlarged pterostigma. The serphitid pattern of wing venation can easily be seen as a modification of that of the Archaeoserphitidae. By the development of Rs to the wing margin and a thickening of the space between the postmarginal vein (R1) and stigmal vein (r-rs), a blocky pterostigma is formed. The posterior corner of the pterostigma of Serphitidae has a sclerotized (*Serphites* and *Aposerphites*) or nebulous (*Microserphites*) nodus that corresponds to the expanded structure at the apex of r-rs in Archaeoserphitidae. This same structure is likewise a probable homolog of the traditional 'stigma' of Chalcidoidea and the stub posteroapically on the marginal vein of Alavarommatidae, suggesting it to be present in the groundplan of Mymarommatoidea. This broadened area represents the juncture of r-rs with Rs, with its apical stub ('uncus' of chalcidoid terminology), the base of the apical abscissa of Rs. By comparing this with the venation observed in Serphitidae, whereby the apical abscissa of Rs that closes the narrow marginal cell arises from the apical corner of this node, one would conclude that the posterior border of the serphitid pterostigma is composed of r-rs, and therein quite different from other pterostigmata in which r-rs is distinct and extends beyond the bounds of the pterostigma. This can be seen rather clearly in various taxa in which the body of the pterostigma is much less sclerotized than the bordering veins (e.g., *Serphites bruesi* McKellar & Engel: *vide* McKellar & Engel, 2011b, their figure 1d). The large serphitid pterostigma is composed of a thickening and sclerotization of space between r-rs and R1 along the costal margin. It may very well be that the narrow proximal base of the pterostigma corresponds to the anterior contact of Sc+R with the wing margin and an exceedingly shortened 'marginal vein', as this entire base of the pterostigma is broader than the usual vein width. The pterostigmal base is also separated from C, when this vein is present, tending to support the notion that the marginal vein is composed of R rather than C+R (alternatively, this separation is merely the position of the more usual fenestra present among most Hymenoptera). Indeed, C is either absent (*Microserphites*) or nebulous to slightly more tubular, albeit almost always thinner and weaker than Sc+R [all other serphitids: e.g., nebulous in *Jubaserphites* (McKellar & Engel, 2011b) and various species of *Serphites* such as *S. lamiak* Ortega-Blanco *et al.* (Ortega-Blanco *et al.*, 2011e, their figure 5b)]. The complete absence of C in Archaeoserphitidae tends to imply that the various developments of C among Serphitinae are secondary reversals rather than indicative of a groundplan presence of the vein, and which would also support a basal placement of *Microserphites* within Serphitidae (Fig. 8). This scenario, coupled with the presence of the distinctive nodus posteriorly at the apical corner of the pterostigma in Serphitidae, tends to indicate that the pterostigma of serphitids is secondarily derived, with the diffuse condition observed in *Microserphites* being plesiomorphic.

Based on the above interpretation, one would conclude that a true 'marginal vein', composed of a section of R along the wing margin prior to r-rs is a groundplan feature of Mymarommatoidea, Serphitoidea, and Chalcidoidea, while in Cynipoidea and the putative groundplan of Platygastroidea, where C is also lacking, the condition is for r-rs to diverge from the apex of Sc+R prior to R contacting the wing margin (e.g., Masner *et al.*, 2007) (in which case the crossvein might be better denoted as sc+r-rs). Here, Archaeoserphitidae would seem to intermingle traits between Serphitidae and putative plesiomorphies of Mymarommatoidea and Chalcidoidea.

The toruli are high in Chalcidoidea and Mymarommatoidea, articulating at or above the middle of the face, while in Serphitoidea they are universally positioned low on the face, either near or even below the lower tangent of the compound eyes. The putatively apomorphic situation of the antennal toruli near the clypeal base is

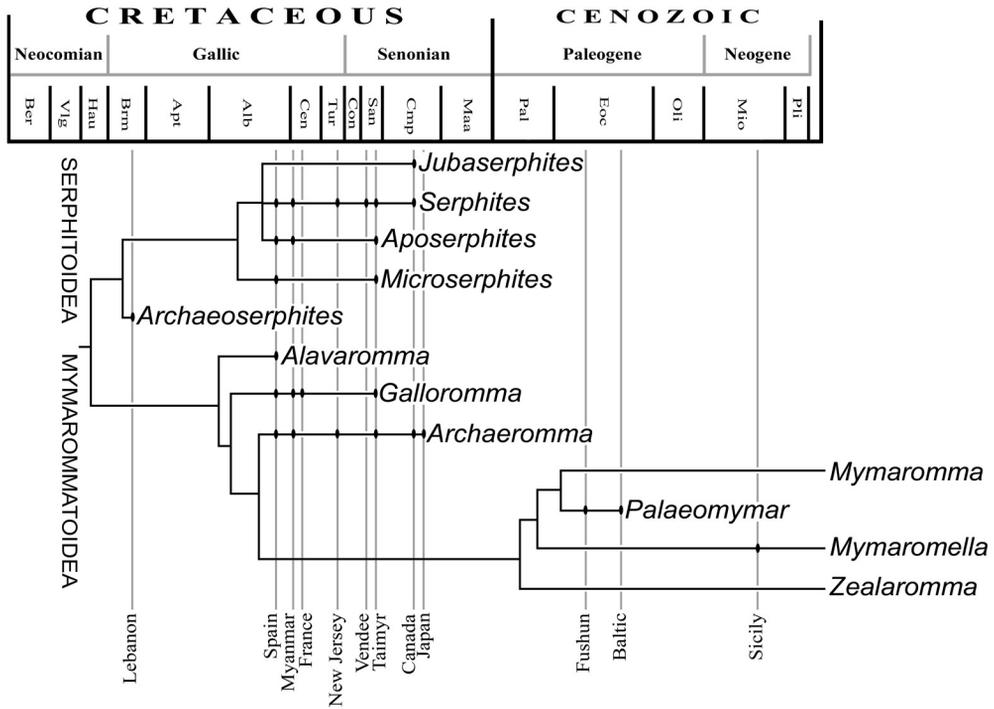


Figure 8. Putative relationships among genera of Bipetiolarida; relationships among mymarommatoid genera after Gibson *et al.* (2007). Fossil occurrences based on those outlined in Gibson *et al.* (2007), Ortega-Blanco *et al.* (2011d, 2011e), and Engel & Perrichot (2014), as well as records of taxa from Fushun and Burmese amber (Grimaldi *et al.*, 2002; Wang *et al.*, 2014; Engel, pers. obs.).

analogous to that of Platygastroidea, but apparently convergent. The greater number of flagellomeres is seemingly consistent with the plesiomorphic condition of Proctotrupomorpha, whereby many males have 12 flagellomeres. It is interesting to note that in this context the 10 flagellomeres of Alavarommatidae would likely be apomorphic for that family and despite its more basal position among Mymarommatoidae (Ortega-Blanco *et al.*, 2011d). Like the Mymarommatoidae, serphitoids lack the multiporous plate sensilla characteristic of chalcidoid antennae.

Mymarommatoidae, Chalcidoidea, and Archaeoserphitidae also lack an acetabular carina low on the mesepisternum (*e.g.*, Gibson *et al.*, 2007), and among serphitids examined by the author a true acetabular carina as found in other Hymenoptera is lacking (*contra* Gibson *et al.*, 2007), but admittedly for several serphitids this cannot be observed as preserved. Mymarommatoidae and Serphitoidea both have the prepectus not exposed, in contrast with the distinctive externally visible prepectus of Chalcidoidea, and Serphitoidea have the plesiomorphic tibial spur formula of 1-2-2, with Mymarommatoidae possessing 1-0-0 and Chalcidoidea 1-1-2.

The absence of laterotergites in Archaeoserphitidae, whereby the terga arch laterally continuously and without a sharp angle, is similar to the condition found in Mymarommatoidae and Chalcidoidea, suggesting that the weak angle or crease observed in Serphitidae is independent from the true laterotergites of Platygastroidea. Serphitoidea, Mymarommatoidae, and Chalcidoidea also all lack spiracles on most gastral terga. The free parameres of Mymarommatoidae and Serphitoidea are likely symplesiomorphic, versus those that are fused to the aedeagus in Chalcidoidea.

Given the distribution of observable characters, Mymarommatoidea and Serphitoidea are united by the shared condition of a bipetiolate metasoma and whereby the petiolar segments are cylindrical, with the first longer than the second and the former typically with some degree of distinctive sculpturing. This condition is unique among Hymenoptera and perhaps the best evidence for the monophyly of the combined group. In addition, the propleura of both abutt along their lengths, with partial fusion occurring among some Mymaromatidae and apparently complete fusion in Archaeoserphitidae. In Chalcidoidea the propleura diverge slightly, exposing a portion of the prosternum. Chalcidoidea and Bipetiolarida share in their groundplans the loss of C in the forewing, loss of the occipital carina, and the loss of the acetabular carina, as well as the putative formation of a 'true' marginal vein, albeit at times greatly reduced in length.

For the time being, the family Archaeoserphitidae is monotypic, but it is greatly hoped that additional material, particularly females, and taxa will be discovered and in order to provide a more comprehensive accounting of the unique character of the group. In addition, through the continued documentation of fossil parasitoid Hymenoptera, the potential for incorporating this past diversity into extensive phylogenetic studies will grow. Naturally, the cladistic interpretation of any fossil species is of value, but for a truly robust estimation of relationships a dense sampling of the diversity is necessary and emphasizes the importance of efforts to describe the faunas of past epochs. This is particularly true for those stages of the Mesozoic, as this is when the Hymenoptera underwent its considerable diversification into the varied familial lineages we are familiar with today.

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APPENDIX

An outline of the higher classification of Proctotrupomorpha [modified from Liu *et al.* (2007), Engel & Krombein (2012), and Aguiar *et al.* (2013)].

Infraorder PROCTOTRUPOMORPHA Rasnitsyn

Superfamily Proctotrupoidea Latreille

- Family Proctotrupidae Latreille
- Family Vanhorniidae Crawford
- Family Roproniidae Bradley
- Family Austroniidae Kozlov
- Family Peradeniidae Naumann & Masner
- Family Heloridae Förster
- Family Peleciniidae Haliday
- Family Proctorenyxidae Lelej & Kozlov
- Family †Jurapriidae Rasnitsyn
- Family †Mesoserphidae Kozlov

Parvorder Cynipiformia Engel

Superfamily Platygastridae Haliday

- Family Nixonidae Masner
- Family Sparasionidae Dahlbom
- Family Platygastridae Haliday
- Family Scelionidae Haliday

Superfamily Cynipoidea Latreille

- Family Austrocynipidae Riek
- Family Ibaliidae Thomson
- Family †Protimaspidae Liu & Engel
- Family †Stolamissidae Liu & Engel
- Family Liopteridae Ashmead
- Family †Gerocynipidae Liu & Engel
- Family Figitidae Hartig
- Family Cynipidae Latreille

Parvorder Chalcidiformia Engel

Nanorder Diaprioidae Engel

Superfamily Diaprioidea Haliday

- Family Monomachidae Ashmead
- Family Diapriidae Haliday (including Ismaridae Thomson)
- Family Maamingidae Early *et al.*
- Family †Spathiopterygidae Engel & Ortega-Blanco

Nanorder Chalcidoidae Engel

Superfamily Chalcidoidea Latreille

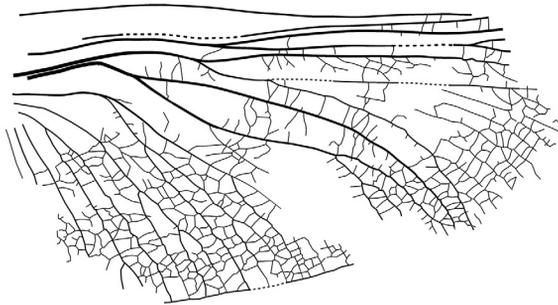
Clade Bipetolarida Engel

Superfamily †Serphitoidea Brues

- Family †Archaeoserphitidae Engel
- Family †Serphitidae Brues

Superfamily Mymarommatoidae Debauche

- Family †Alavarommatidae Ortega-Blanco *et al.*
- Family †Gallorommatidae Gibson *et al.*
- Family Mymarommatidae Debauche



Pharciphyzelus lacefieldi Beckemeyer & Engel, 2011

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