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Paleontological Contributions

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THE EXTINCT WASP FAMILY SERPHITIDAE IN LATE CRETACEOUS VENDEAN AMBER (HYMENOPTERA)

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ABSTRACT

A new species of the extinct genus *Serphites* Brues (Proctotrupomorpha: Bipetiolarida: Serphitidae) is described from two individuals preserved in Late Cretaceous (Cenomanian to Santonian) amber from Vendée, northwestern France. *Serphites fannyae* n. sp., is distinguished from its congeners and brief comments are made on the significance of finding a serphitid wasp in Vendean amber as well as potential character polarities in the family Serphitidae.

Keywords: Insecta, Apocrita, Proctotrupomorpha, Bipetiolarida, Cretaceous, France

RÉSUMÉ

Une nouvelle espèce du genre fossile *Serphites* Brues (Proctotrupomorpha: Bipetiolarida: Serphitidae) est décrite d'après deux spécimens préservés dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, dans le nord-ouest de la France. *Serphites fannyae* n. sp., est comparée à ses congénères et la présence d'un Serphitide dans l'ambre de Vendée est brièvement commentée ainsi que la possible polarité de caractères pour la famille Serphitidae.

Mots-clés: Insecta, Apocrita, Proctotrupomorpha, Bipetiolarida, Crétacé, France

INTRODUCTION

There are several families of Hymenoptera which are diagnostic for the Cretaceous. Each of these families is known almost exclusively from amber and typically ranges from the Early Cretaceous through the latter stages of the Mesozoic, and obviously none have been hitherto discovered in the Paleogene. These families include the Maimetshidae of the Trigonalyoidea (Perrichot & others, 2011), Serphitidae of the Serphitoidea (Brues, 1937; Kozlov & Rasnitsyn, 1979; McKellar & Engel, 2011a; Engel, Grimaldi, & Ortega-Blanco, 2011; Ortega-Blanco & others, 2011a), Alavarommatidae and Gallorommatidae of the Mymarommatoidea (Engel & Grimaldi, 2007; Gibson, Read, & Huber, 2007; Ortega-Blanco & others, 2011b), Stigmaphronidae and Radiophronidae of the Ceraphronoidea (Kozlov, 1975; Engel & Grimaldi, 2009; Ortega-Blanco, Rasnitsyn, & Delclòs, 2010; McKellar & Engel, 2011b; Ortega-Blanco, Delclòs, & Engel, 2011), Spathiopterygidae of the Diaprioidea (Engel & others, 2013), and Falsiformicidae of the Chrysidoidea (Rasnistyn, 1975; Perrichot & others, 2014). In all cases but Falsiformicidae, individuals are relatively small and their virtual exclusivity to amber is assuredly a representation of the suitability of this medium for preserving minute organisms with sufficient fidelity. Not surprisingly for clades of Mesozoic parasitoids, hosts of these lineages remain unknown and entirely speculative thereby hindering any conclusions as to whether the occurrence of their victims greatly influences their presence and abundance in specific deposits, although some kind of association must assuredly exist. Syninclusions have provided to date no insight into possible host taxa and all that can be surmised has come from their phylogenetic association with related lineages (e.g., Engel & Grimaldi, 2009).

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The family Serphitidae was first recognized by Brues (1937) based on a couple of male inclusions in Campanian amber from Alberta, Canada. As can be deduced from the name, Brues considered the family to be related to the Serphidae (a synonym of Proctotrupidae), although he did note several possible associations and placed particular emphasis on the two-segmented petiole, an otherwise rare feature among the Hymenoptera. Subsequent to Brues's (1937) account there remained almost no work on the family for nearly half a century. In 1979, Kozlov and Rasnitsyn described several new serphitids, including two new genera, from the Cenomanian and Santonian amber of Siberia and noted a number of traits shared between serphitids and the Mymarommatidae, particularly the form of the two-segmented petiole (later the combined clade was named Bipetiolarida). Indeed, Kozlov and Rasnitsyn (1979) suggested merging the two as subfamilies within a single family. Again, the group remained dormant until recently several additional taxa were added based on a revision of the original Canadian fauna (McKellar & Engel, 2011a) as well as material from the Albian of Spain (Ortega-Blanco & others, 2011a) and Turonian of New Jersey (Engel, Grimaldi, & Ortega-Blanco, 2011). A review of the fauna from Burmese amber is presently underway by one of us. Recently, two serphitids have been recovered in the Cenomanian–Santonian amber of Vendée in northwestern France. Herein is provided a brief account of this material.

MATERIAL AND METHODS

The material comprises two specimens. The first individual (Figs. J1.1, J2.2) is preserved in a small piece of clear yellow amber with one true fly (Diptera: Dolichopodidae: Microphorinae: *Microphorites magaliae* Perrichot & Engel – see issue 10G in this volume) as a syninclusion. The specimen is mostly complete, although the gaster is missing beyond the first gastral segment and portions of some legs are missing at the amber surface. Some areas are difficult to observe owing to deformities in the amber surface (particularly near the metasoma), a large blackened bit of debris to the specimen's right, and the position of *M. magaliae* masking the specimen's face. The second serphitid (Figs. J1.2, J2.1) is similarly preserved but rests alongside a darkened fracture plane rendering it impossible to see the specimen in dorsal-oblique view from the left. This orientation also resulted in the wings being less than ideally preserved (hind wings present, right forewing largely destroyed except for extreme base; left forewing present but mixed into fracture plane making interpretation challenging) and portions of the dorsum of the prothorax and head are obscured, including a direct facial view. Nonetheless, this is the most complete individual and because the head is twisted, gives the best view of the opened mouthparts along with antennal structure. This is also the only specimen with a complete metasoma (the sting is exposed along with the short associated styli), and it was duly selected as the holotype.

The amber pieces were slightly polished and subsequently embedded in blocks of epoxy resin which were again polished on all sides. This facilitated optimal viewing of the specimens, although the ideal vantage for particular structures was still not possible given the placement of syninclusions or other impurities with the amber. The amber was collected in 2002 by Magali Weigandt and Fanny Dupé from a deposit exposed briefly during work along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. In a preliminary account of this amber deposit, Perrichot and others (2013) suggested a Santonian age but contradictory data have been found since then, so an uncertainty remains on the exact age and until new elements are found we cannot discriminate between Middle Cenomanian, Turonian, or Early Santonian (≈ 97–85 Ma), as discussed by Perrichot and Néraudeau (2014: 10A in this volume). Morphological terminology and the format for the description generally follows that of Engel, Grimaldi, and Ortega-Blanco (2011) and McKellar and Engel (2011a). Photographs were taken with a Canon 5D Mark II digital camera attached to a Leica MZ APO stereomicroscope, and stacks of images taken at different depths of field were merged using Helicon Focus 5.3 (HeliconSoft Ltd) to obtain sharpness throughout the entire images. Metrics were taken with an ocular micrometer set on an Olympus SZX-12 stereomicroscope.

SYSTEMATIC PALEONTOLOGY

Family SERPHITIDAE Brues, 1937
Genus SERPHITES Brues, 1937

Type species.—*Serphites paradoxus* Brues, 1937, p. 33, fig. 5A.

Included species.— Presently 12 species included in the genus (see the key below).

Comment.—The emended generic diagnosis by McKellar and Engel (2011a) is followed here and requires no modification to incorporate the present species.

Key to species of *Serphites*

1. Pterostigma isosceles 2
   Pterostigma equilateral 3
2. Body small, 1.3 mm long in male; 1st petiolar segment twice as long as 2nd petiolar segment, the latter flattened dorsally; gaster with lateral carina between tergites and sternites [Campanian, Canada] .... *S. paradoxus* Brues
   Body large, 3.0 mm long in female; 1st petiolar segment 3× as long as 2nd petiolar segment, the latter not flattened dorsally; gaster longer than mesosoma, without lateral carina [Santonian, Taimyr] .... *S. gigas* Kozlov & Rasnitsyn
3. 1st petiolar segment longitudinally striate 4
   1st petiolar segment not longitudinally striate [Cenomanian–Santonian, France] .... *S. fannyae* n. sp.
4. 1st petiolar segment not rimmed anteriorly 5
   1st petiolar segment rimmed anteriorly [Early Albian, Spain] .... *S. lamiak* Ortega-Blanco, Delclòs, Peñalver, & Engel
5. Gaster shorter than mesosoma 6
   Gaster as long as or slightly longer than mesosoma 9
6. Metatarsus shorter than metafemur; metabasitarsus shorter than combined length of remaining tarsomeres 7
   Metatarsus as long as or longer than metafemur; metabasitarsus as long as combined length of remaining tarsomeres 8
7. Body small, female 1.10 mm long, male 1.45 mm long; forewing vein Rs not tubular, straight; 1st petiolar segment 2.7× as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Turonian, New Jersey] .... *S. raritanensis* Engel & Grimaldi

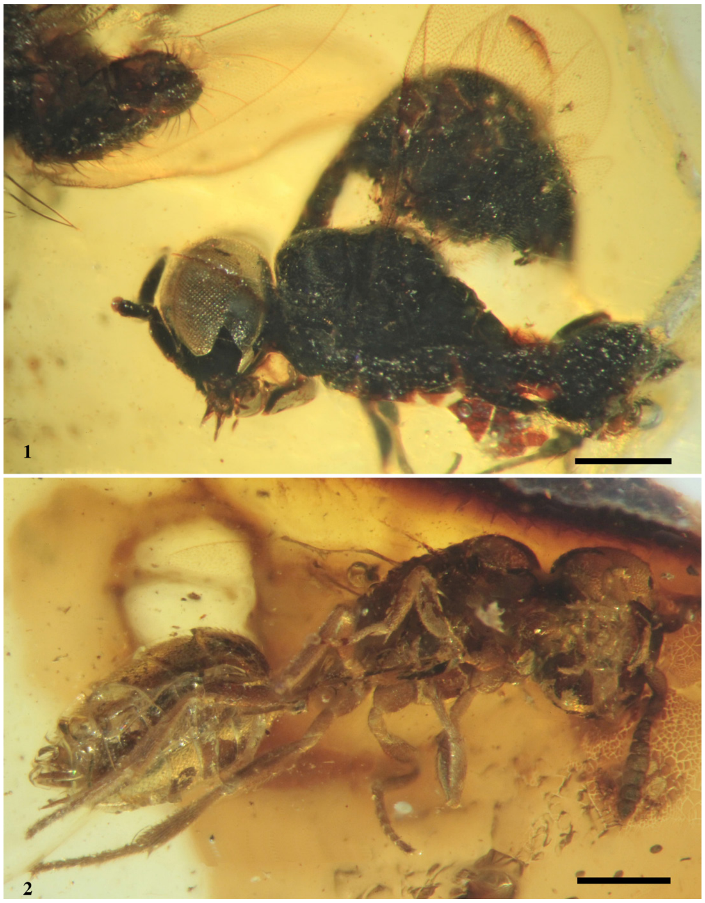

Figure J1. Photographs of *Serphites fannyae* n. sp., in Late Cretaceous (Cenomanian–Santonian) amber of Vendée, NW France; *1*, paratype male IGR.GAR-106b; *2*, holotype female IGR.GAR-26. Scale bars = 0.25 mm.

Body larger, female 2.6 mm long; forewing vein Rs tubular, curved apically; 1st petiolar segment 3× as long as 2nd petiolar segment; 1st and 2nd gastral segments longer than combined length of remaining segments [Campanian, Canada] .... *S. kuzminae* McKellar & Engel

8. Body length 2.6 mm, female with nine antennomeres; left mandible with lower tooth slightly longer than upper tooth; metatarsus longer than metafemur; 1st petiolar segment 2.5× as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Turonian, New Jersey] .... *S. navesinkae* Engel & Grimaldi

Body length 2.95 mm; left mandible with lower and upper teeth equal in size; metatarsus as long as metafemur; 1st petiolar segment twice as long as 2nd petiolar segment; 1st and 2nd gastral segments longer than combined length of remaining segments [Early Albian, Spain] .... *S. silban* Ortega-Blanco, Delclòs, Peñalver, & Engel

9. Body very small, 0.9 mm long; basal flagellomere about 1/3 as long as apical one; right mandible with middle tooth longest of three teeth, left mandible with two equal teeth [Campanian, Canada .... *S. pygmaeus* McKellar & Engel

Body length at least 1.5 mm; right and left mandibles with lower tooth longest 8

10. Body length 1.5 mm; forewing vein Rs nebulous; 1st petiolar segment twice as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Campanian, Canada] .... *S. hynemani* McKellar & Engel

Body length 2.0 mm; forewing vein Rs tubular; 1st petiolar segment 2.4× as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Santonian, Taimyr] .... *S. dux* Kozlov & Rasnitsyn

Body length 2.1 mm; forewing vein Rs tubular; 1st petiolar segment 3× as long as 2nd petiolar segment; 1st and 2nd gastral segments longer than combined length of remaining segments [Campanian, Canada] .... *S. bruesi* McKellar & Engel

SERPHITES FANNYAE new species

Figures J1–J2

Type material.—Holotype female IGR.GAR-26 (Figs. J1.2, J2.1), ex coll. Dupé, and paratype male IGR.GAR-106b (Figs. J1.1, J2.2), ex coll. Weigandt; in Late Cretaceous (Middle Cenomanian to Early Santonian, ≈ 97–85 Ma) Vendean amber. Both specimens are deposited in the Geological Department and Museum of the University Rennes 1, France.

Type locality.—La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, Vendée, France.

Etymology.—The specific epithet is a matronym honoring Fanny Dupé, who collected one of the amber pieces containing the type series.

Diagnosis.—Total body length under 2 mm (differs from *S. navesinkae* at ca. 2.6 mm and *S. silban* and *S. gigas* at ca. 3 mm); trochantelli short (long in *S. lamiak*, extremely short and superficially absent in *S. gigas* and *S. dux*); metatarsus very slightly longer than metafemur (about as long as in *S. silban* and *S. gigas*); metabasitarsus distinctly shorter than combined length of remaining tarsomeres, about two-thirds length of remainder of metatarsus (as long as or nearly so in *S. lamiak* and *S. raritanensis*, about twice in *S. dux*); first petiolar segment not rimmed anteriorly (rimmed in *S. lamiak*); second petiolar segment not flattened dorsally (flattened dorsally in *S. paradoxus*); first petiolar segment not longitudinally striate (striate in most species); first petiolar segment about twice the length of second petiolar segment (more than twice, 2.7–3× as long in *S. raritanensis* and *S. kuzminae*, respectively); and gaster longer than mesosoma (shorter in *S. raritanensis*, as long as in *S. dux*).

Description.—Female. Total body length 1.63 mm; forewing length 0.82 mm. Integument apparently dark brown (although many areas with artificial metallic silver sheen owing to microscopic separation from amber causing reflections), with scattered, minute, fine setae throughout body, such setae particularly numerous on tibiae and tarsi. Head not greatly enlarged but with relatively sizeable gena, gena only slightly narrower than compound eye; antenna 10-segmented; scape barely extending half-way to vertex, with length approximately three times the greatest width (0.14 mm long); flagellum with relative lengths of articles 1.0, 0.8, 0.9, 1.2, 1.4, 1.4, 1.5, 2.0; first flagellar article chalice-like in outline, second article nearly square in outline, following articles almost rectangular in outline, broader than long, fifth article broadest flagellomere; apical flagellar article terminating in rounded acute point; right mandible tridentate, lower two teeth longest and most prominent, uppermost tooth distinctly shorter,

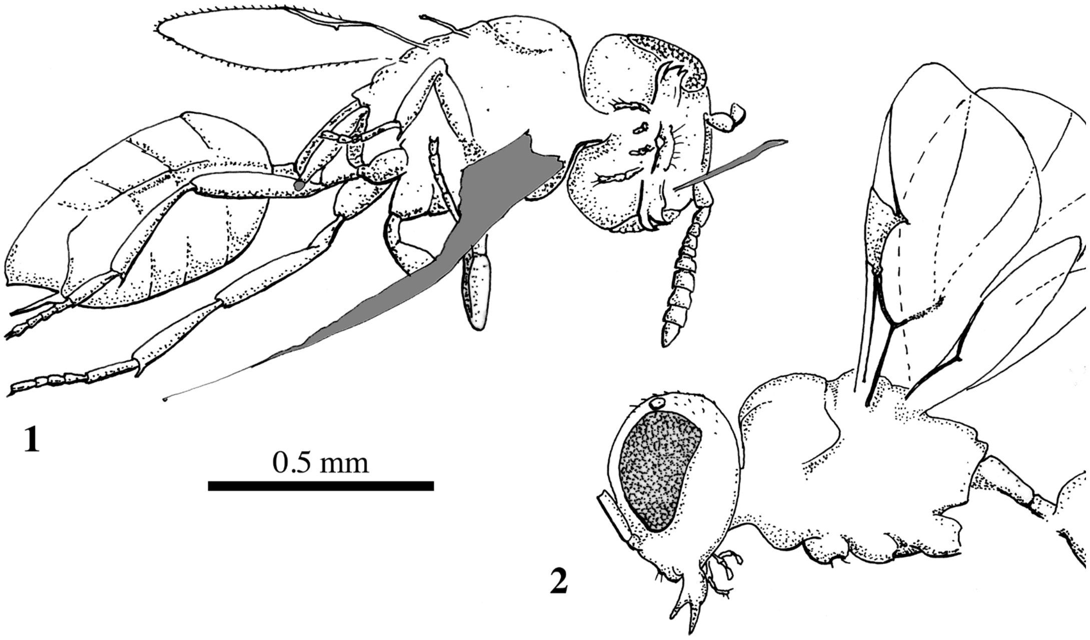

Figure J2. Line drawings of *Serphites fannyae* n. sp., Late Cretaceous (Cenomanian–Santonian) amber of Vendée, NW France. *1*, habitus of holotype female IGR.GAR-26; *2*, lateral left habitus of paratype male IGR.GAR-106b.

apparently one-half length of midtooth, lowermost tooth longest, only slightly longer than midtooth, all teeth with sharply pointed apices; left mandible bidentate, both teeth long with sharp apices, lower tooth distinctly longer than upper tooth. Mesosoma 0.53 mm in length, mostly obscured by preservation and with dorsal surface not visible. Forewing with numerous microtrichia, slightly longer setae forming continuous fringe along wing margins; venation typical for species of the genus (see McKellar & Engel, 2011a; Engel, Grimaldi, & Ortega-Blanco, 2011); C not fused to Sc+R, forming a distinct costal cell, C not pigmented (perhaps due to preservation); pterostigma massive, triangular, approximately equilateral, uniformly pigmented and sclerotized; r-rs arising from pterostigmal midlength, about as long as wide; Rs strongly pigmented, not tubular, straight, reaching wing margin; Rs+M absent; M+Cu, basal vein, and 1Cu tubular, other abscissae of Cu and M nebulose, apicalmost abscissa of M reaching wing margin, that of Cu disappearing shortly before margin; 1A tubular proximally, becoming nebulous well before 1Cu. Hind wing with numerous microtrichia, with short setae forming marginal fringe, with only C+Sc+R along anterior margin and with three hamuli apically. Legs thin, although not especially long, with scattered, minute, fine setae; trochantelli short; femora not especially swollen; meso- and metatibiae with two short, thin apical spurs (often difficult to discern from surrounding setae), single protibial spur; tarsi pentamerous; metabasitarsus two-thirds length of remaining tarsomeres combined; pretarsal claws simple and short, arolium large. Metasoma bipetiolate; first petiolar segment not rimmed anteriorly (as in *S. raritanensis*), about twice the length of second petiolar segment, petiolar segments apparently smooth and without distinct sculpturing; gaster slightly longer than mesosoma, 0.63 mm long, terga and sterna apparently smooth with minute punctures at setal bases, discs of terga and sterna with several scattered, suberect setae, sterna not concave, instead slightly convex on discs, segments generally of same size except apically larger; sting exposed, relatively short, scarcely longer than associated sheaths and only somewhat longer than an individual gastral segment (although the sting may not be fully exserted), sting simple, apparently without preapical dorsal notch.

Male. Very similar but specimen incomplete, with most of gaster missing so total length in life is unknown. Body length as preserved 1.28 mm. Forewing length 0.84 mm. Mesosomal length 0.52 mm. Antenna 9-segmented, which suggests it is a male rather than a female according to the sexual dimorphism in the number of antennomeres of *Serphites*.

DISCUSSION

The discovery of a serphitid wasp in Vendean amber, as well as a species of the microphorine genus *Microphorites* Hennig, 1971 (Perrichot & Engel, 2014: 10G in this volume), is in accordance with the Cretaceous age of this amber even though the precise layer is unknown within the Cenomanian–Santonian interval. Both *Microphorites* and, as noted above, the Serphitidae are classical Cretaceous amber taxa, and both became extinct sometime by the end of the Mesozoic. The new species can be easily assigned to *Serphites* based on the eight-segmented female flagellum (six-segmented in *Jubaserphites* McKellar & Engel, 2011), absence of distinctively elongate and numerous setae on the vertex (present in *Jubaserphites*), pronotum large and extending back to the tegula (not reaching tegula in *Microserphites* Kozlov & Rasnitsyn, 1979), pterostigma large, well defined, and sclerotized (indistinct in *Microserphites*), first petiolar segment twice length of second petiolar segment (less than twice length in *Aposerphites* Kozlov & Rasnitsyn, 1979), and lateral ocellus nearly touching compound eye (distinctly separated from compound eye margin in *Aposerphites*). *Serphites* is the most diverse and widespread of the four genera in Serphitidae and may ultimately prove to be paraphyletic with respect to one of the other genera, thereby requiring its segregation into multiple groups. For the time being serphitids remain too poorly known to speculate on relationships or to build a sufficiently rich character matrix for cladistic analysis among the various species. Some statements can possibly be made, however, about the polarity of particular characters within the family. Serphitidae are the presumed sister group to the Mymarommatoidea (Kozlov & Rasnitsyn, 1979; Grimaldi & Engel, 2005), and the putatively most plesiomorphic group within the latter is the extinct family Alavarommatidae (Ortega-Blanco & others, 2011b). If alavarommatids are employed as a possible outgroup for polarizing features within Serphitidae, then the sexually dimorphic number of antennomeres (at least in *Serphites*, with ten antennomeres in females and nine in males, with the exception of *S. navesinkae* which has nine antennomeres in female) is a striking synapomorphy of Serphitidae. The more reduced flagellum in Serphitidae (seven or eight flagellomeres in most species *versus* the ten flagellomeres in Alavarommatidae and 11 in Gallorommatidae) would be apomorphic, particularly so for the autapomorphically reduced number of flagellomeres (six) in *Jubaserphites*. Similarly, the more elongate first petiolar segment typical across all of the serphitid genera except *Aposerphites* would be considered plesiomorphic. The uniquely massive form of the pterostigma in *Jubaserphites*, *Serphites*, and *Aposerphites* may be an apomorphy relative to Mymarommatoidea and other related lineages (e.g., Ortega-Blanco & others, 2011b). The more diffuse and unsclerotized condition observed for *Microserphites* is either a primitive condition among serphitids, prior to sclerotization of the pterostigmal region, or is an autapomorphic reduction. The latter scenario seems most likely given that both of the known species of *Microserphites* are the smallest of the family (Kozlov & Rasnitsyn, 1979; Ortega-Blanco & others, 2011b). An alternative scenario would interpret the diffuse condition of *Microserphites* as a plesiomorphy as the pterostigma is absent in Mymarommatoidea and other related lineages, and could conceivably form a transformation series between the state of complete absence and the large, well-defined condition observed in other serphitid genera. Certainly a cladistic treatment of living and fossil bipetiolarid clades (Mymarommatoidea and Serphitoidea) is needed to more fully understand the complex evolutionary history of these tiny wasps.

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