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A new family of ceraphronoid wasps from Early Cretaceous Álava Amber, Spain

JAIME ORTEGA-BLANCO, ALEXANDER P. RASNITSYN, and XAVIER DELCLÒS



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Radiophronidae, a new ceraphronoid fossil family including two new genera and species, is described here from the Early Cretaceous (Albian) amber from the Basque Cantabrian Basin (Spain). *Radiophron ibericus* gen. et sp. nov. and *Microcostaphron parvus* gen. et sp. nov. are described from eight and one specimens respectively. The new fossils show some similarities with the extinct family Stigmaphronidae but are distinguished from it and the extant ceraphronoids mainly by the presence of not fused radial and costal veins, among other characteristics. A first cladistic analysis retrieves Radiophronidae as the basal sister-group to all other ceraphronoids (Ceraphronidae, Megaspilidae, and Stigmaphronidae).

Key words: Hymenoptera, Radiophronidae, Ceraphronoidea, amber, Albian, Basque Country, Spain.

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Introduction

Ceraphronoidea is a group of parasitic wasps composed of two extant families, Ceraphronidae and Megaspilidae, and the extinct Stigmaphronidae. Its fossil record is largely unknown, with fossil Ceraphronidae still not recorded, Megaspilidae only recorded from Taymir amber (Santonian), Baltic amber (Priabonian) and two compressions in Spanish oil shales (Burdigalian) and Stigmaphronidae from various localities as New Jersey, Lebanon, Siberia, Spain, Alaska, Myanmar, Canada, and Mongolia (all Cretaceous) (Alekseev and Rasnitsyn 1981; Peñalver and Engel 2006; Engel and Grimaldi 2009).

The few proved hosts for modern ceraphronoids are very diverse, viz., for Megaspilidae: Homoptera: Coccoidea, Aphidiidae (as hyperparasites through Braconidae: Aphidiinae); Neuroptera; Mecoptera; pupae of various Diptera; for Ceraphronidae: Cecidomyiidae (Diptera), Thysanoptera, Lepidoptera, Neuroptera, pupae of higher Diptera (as endoparasitoids), and Braconidae (as hyperparasites) (Masner 1993). Several fossil representatives of these groups were found in Álava amber (Delclòs et al. 2007; Ortega-Blanco et al. 2009), that may have been potential hosts for the radiophronids.

Here, we present two new genera and species showing very primitive state of characters for Ceraphronoidea, from Peñacerrada (Spain) Albian amber. Morphological data provided by these new ceraphronoids are of high interest for cladistic analyses, as they have several characters not shared with other Ceraphronoidea.

The phylogenetic position of Ceraphronoidea remains unclear due to the lack of consensus of modern works on the phylogeny of the Hymenoptera (Rasnitsyn 1988; Dowton and Austin 1994, 2001; Vilhelmsen 1997, 2001; Ronquist et al. 1999; Rasnitsyn 2002; Schulmeister et al. 2002; Sharkey and Roy 2002; Sharkey 2007). For this reason, the main points discussed in recent phylogenetic works are summarized below.

Institutional abbreviation.—MCNA, Museo de las Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava Province, Spain.

Other abbreviations.—C, costal vein; CI, consistency index; L, tree length; r, radial crossvein; R, radial vein; RI, retention index; Rs, radial sector; Sc, subcostal vein.

Remarks on parasitic Hymenoptera

Parasitic Hymenoptera, the so-called "Parasitica", is comprised predominantly of wasps with parasitoid lifestyles. Nevertheless, Parasitica is neither a monophyletic grouping nor is it exclusively composed of parasites, as some lineages evolved from being parasites into predators or phytophages (Quicke 1997). Eggleton and Belshaw (1993) propose that parasitism evolved only once, probably in Orussidae or another close relative (e.g., see proposals in Dowton and Austin 1994; Quicke 1997; Dowton et al. 1997; Vilhelmsen 2003;

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Rasnitsyn et al. 2006). The earliest known parasitic wasps, the Jurassic–Cretaceous families Karatavitidae, Paroryssidae, and Ephialtitidae, had their metasoma less specialized than their descendants for laying eggs precisely in respect to the target insect host (Rasnitsyn 1980; Rasnitsyn et al. 2006). The Jurassic family Karatavitidae has been considered recently as ancestor of all higher (parasitic and predatory) wasps, including the orussid wasps long considered as "parasitic Symphyta" (Rasnitsyn et al. 2006).

Ceraphronoidea sensu stricto are minute parasitoid wasps, mainly endoparasitoid, of several others groups of insects. Megaspilidae and Ceraphronidae contain endo- and ectoparasitoid species (Cooper and Dessart 1975). It is phylogenetically accepted that the ectoparasitoidism is the ground-plan state of the Apocrita, but the endoparasitoidism evolved a number of times within the group (Dowton and Austin 1994; Sharkey 2007). Ceraphronids vary extensively in their insect host choices, but they commonly prefer hosts that are weakly concealed, and megaspilids parasite scale insects, mecopterans, fly puparia, neuropteran cocoons, and they are hyperparasites of aphids parasitized by braconids (Masner 1993; Höller et al. 1994; Chow and Mackauer 1996). Haviland (1920) described a tertiary parasitic system where a megaspilid hyperparasitoid attacks a chalcidoid hyperparasitoid of a braconid primary parasite of an aphid.

The morphology of the new species found in Spanish amber and their placement within Ceraphronoidea strongly suggest they had a parasitic lifestyle (see Masner and Dessart 1967; Alekseev and Rasnitsyn 1981; Alekseev 1995; Peñalver and Engel 2006; Engel and Grimaldi 2009).

Phylogenetic position of Ceraphronoidea

Phylogenetic analyses of Hymenoptera were initiated by Rasnitsyn (1988) who shows "Symphyta" as a paraphyletic grade relative to Apocrita and Orussoidea (solely "symphytan" with parasitoid lifestyle). Though Rasnitsyn's (1988) study is not considered as a standard cladistic work, many of his lineages have been accepted as clades by more recent cladistic proposals (Dowton et al. 1997; Ronquist et al. 1999). On the basis of morphological evidence from recent and fossil groups, Rasnitsyn (1988) divided the Apocrita in four lineages: Ichneumonoidea (Ichneumonomorpha), Aculeata (Vespomorpha), Proctotrupomorpha, and Evaniomorpha. He grouped Megaspilidae and Ceraphronidae into the superfamily Stephanoidea, along with Stephanidae, Megalyridae, Trigonalidae, and the extinct Stigmaphronidae and Maimetshidae, and established the lineage Evaniomorpha to join all of them with the superfamily Evanioidea. Ceraphronoidea is now considered a monophyletic group that includes the Megaspilidae and Ceraphronidae (Sharkey 2007) with fossil and extant species, the exclusively Cretaceous Stigmaphronidae (Engel and Grimaldi 2009), and maybe the Cretaceous Maimetshidae (see Perrichot 2009), represented only in the fossil record, although a third fossil ceraphronoid family was proposed in Perrichot et al. (2004) in order to place the genus *Guyotemaimetsha*, which did not fit well in any other ceraphronoid family. Alternatively, Rasnitsyn and Brothers (2009) consider *Guyotemaimetsha* as a member of Maimetshidae, the Cretaceous family from Siberian and French ambers and southern African rocks that is hypothesized an intermediate form between typical Megalyridae and the Ceraphronoidea, inclusive of the Cretaceous family Stigmaphronidae (Rasnitsyn 1988, 2002; Rasnitsyn and Brothers 2009). As well, Perrichot found new specimens of *Guyotemaimetsha* fossils recently which confirmed the genus as a Maimetshidae, and suggest the family to be more related to Trigonalidae (Vincent Perrichot, personal communication 2009). Unlike this, Shaw (1988, 1990) considers it belonging to megalyrids, related to the tribe Dinapsini. Rasnitsyn (2002) has published a revised version of his 1988's proposal introducing much fossil evidences. He proposed a new relationship between the Evaniomorpha, Ceraphronoidea being the descendant group of what is now called [Trigonaloidea + (Stephanoidea + Megalyroidea)] (in fact, Stephanidae Leach, 1815 has priority over Trigonalidae Cresson, 1867).

Rasnitsyn's (2000, 2002) concept of Ceraphronoidea comprises seven families: Trigonalidae (Early Cretaceous–Recent), Stephanidae (Late Cretaceous–Recent), Megalyridae (Early Jurassic–Recent), Maimetshidae (latest Early to Upper Cretaceous), Stigmaphronidae (Cretaceous), Megaspilidae (Early Cretaceous–Recent), and Ceraphronidae (Upper Cretaceous–Recent). Ceraphronoidea + Evanioidea (= Praeaulacidae + Andreneliidae + Gasteruptiidae + Evaniidae) conform the Evaniomorpha, but in these publications, Rasnitsyn has overlooked that due to priority (Leach, 1815 vs. Haliday, 1833) the proper name of his Ceraphronoidea (sensu lato) should be Stephanoidea.

Grimaldi and Engel (2005) include the Ceraphronoidea into the Proctotrupomorpha, because they consider acceptable the apomorphies that Ceraphronoidea shares with other proctotrupomorphs proposed by Basibuyuk and Quicke (1997) and Ronquist et al. (1999). Apart of some character states due to reduction, the former study emphasizes the presence of small, stiff setae opposing the distal hamuli and the lack of secondary hamuli, whereas the last stands out the geniculate antennae, the tubular petiole and the exposed prepectus. After more than three decades of morphological and molecular studies on Hymenoptera, the relationships among the superfamilies of Apocrita remain controversial.

Material and methods

The specimens studied here are from Peñacerrada I (Moraza, Spain), the type locality for the nine specimens studied. They are labelled as MCNA 8754, MCNA 8760, MCNA 8769, MCNA 8789, MCNA 8989, MCNA 9561, MCNA 9576, and MCNA 13030 (with 2 specimens). Except for MCNA 8754

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and MCNA 9576 they are each embedded in polished epoxy resin EPO-TEK 301. The technique for its preparation is explained in Corral et al. (1999).

The specimens were studied under a Leica MZ 9.5 and Leica MS 5 stereomicroscopes, using reflected and transmitted light. Drawings were made using a *camera lucida* attached to the stereomicroscopes. The fossils were photographed by the above first microscope with a Nikon D70 camera attached and a Leica DFC 420 attached to the second, and the measurements were established with the Leica IM1000 software.

The amber-bearing deposits from Moraza-Peñacerrada (northern Spain) are included within the Albian (Early Cretaceous) Escucha Formation, in the Basque Cantabrian Basin. The sedimentary units that contain the amber were deposited in deltaic environments and are always associated with coal or organic-rich layers (Martínez-Torres et al. 2003; Delclòs et al. 2007). During the mid-Cretaceous the amber deposits of the Iberian Peninsula were located at 27–30°N, in the boundary between wet and warm tropical-subtropical climates (Scotese Paleomap Project web: http://www.scotese.com/; Martínez-Delclòs et al. 2004; Haywood et al. 2004).

Apart from the wasps described herein, the fossil assemblage that has been recovered from this amber deposit is dominated by insects, but also inclusions of microorganisms (protists, fungi, etc.), and other arthropods such as crustaceans (Vonk and Schram 2007), arachnids (Penney 2006), and collembolans (see synthesis in Delclòs et al. 2007).

Systematic paleontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Superfamily Ceraphronoidea Haliday, 1833

Family Radiophronidae nov.

Type genus: *Radiophron* nov.

Diagnosis.—Head globular, not extremely flattened, hypognathous, without acute hind vertical margin. Lateral ocelli elongate, separated less than one ocellar distance from the compound eye. Nine flagellomeres in both sexes. Fore wings with wide pterostigma, venation reduced to Rs long and well defined, and C and R veins not fused laying a more or less wide costal cell. Hind coxae flattened and slightly elongate, not reaching completely the dorsum of metasoma, then not obscuring completely the lateral view of propodeum. Hind femur moderately widened medially but not extremely flattened and sub-triangular as in Stigmaphronidae. Tibial spur combination 2-2-2. Hind tibia of normal proportion in respect to tarsi (not half length as in most Stigmaphronidae), slender, moderately widened distally, with tibial spurs not elongate. Six metasomal segments sub-equal in length (apparent first slightly longer) without a reduced first forming a carinated system over the second. Females with short internal ovipositor. Male genitalia exposed except basally in both males available: this might be their normal position because of elongation of gonostyli. Gonostylus long (longer than in other ceraphronoids), paddle shaped, arching, with apex rounded and bearing several setae, narrow and possibly immovably fused with gonocoxae which are much shortened along with volsellae and penis valves. Gonocoxa short, hardly visible in exposed genitalia, toothed digitus apparently present.

Genus *Radiophron* nov.

Type species: *Radiophron ibericus* sp. nov., monotypic.

Etymology: Combination of radio- for the presence of the radial vein in fore wing and -phron for being placed within Ceraphronoidea.

Diagnosis.—Compound eyes occupying more than half lateral side of head. Scape elongate around 5.5 times as long as wide, distally expanded ventrally. First flagellomere shorter than pedicel, almost half as long as second, strongly narrowed basally. Pronotum dorsally covered by mesoscutum. Scutellum elevated, shorter than mesoscutum, not reaching transverse mesonotal suture and posteriorly ending acute and sloping vertical, not covering the dorsal view of propodeum. Fore wing vein Rs+2r-rs arising beyond pterostigmal mid length. Hind trochanter wide, elongate, curved and cylindrical. Metasoma fusiform, wider basally.

Radiophron ibericus sp. nov.

Figs. 1–3.

Etymology: After the place they have been found for first time, the Iberian Peninsula.

Type material: Holotype: MCNA 8754. Female. Specimen preserved in a yellow-brown polished drop of amber of 2.5 × 2 × 1 mm. Well preserved except for a fracture that affects the left hind femur and another fracture that obscures the head view from below. Paratypes: MCNA 8789, MCNA 8989, MCNA 9561, MCNA 9576, MCNA 13030.1, and MCNA 13030.2. Females. Well preserved specimens, all included in translucent dusty amber embedded in polished prisms of epoxy resin (except MCNA 9576).

Type locality: Peñacerrada I, close to Moraza village.

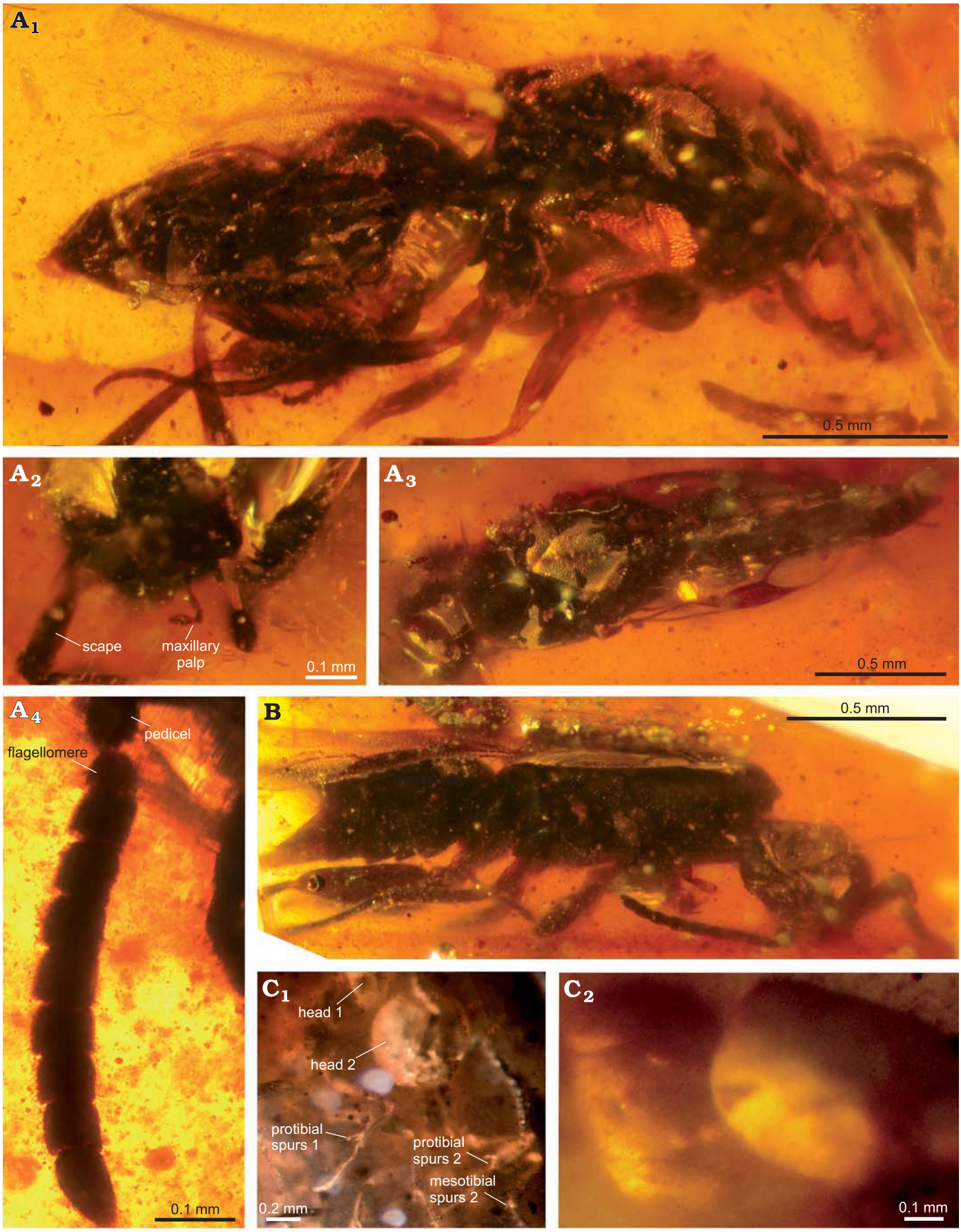
Type horizon: Escucha Formation.

Diagnosis.—As for the genus.

Referred material.—Specimen MCNA 8760 (Figs. 2, 3) is a well preserved but somewhat deformed *Radiophron* male, which lacks just tarsi of left foreleg, mid legs, and left hind leg. It shows very subtle differences with *R. ibericus* sp. nov. females and these differences may be easily due to sexual dimorphism and weak compression, hence this specimen is presented as referred material as it does not seem to have enough differences for placing it in a new species. It differs from females mostly by its more quadrate frontal view of head, with striated ornamentation, with two depressed areas on the frons which can be a result of the amber deformation; flagellomeres more compressed; ratio of hind tarsomeres, from basitarsus, 1: 0.4: 0.3: 0.2: 0.3; gaster dorso-ventrally flattened, with genitalia protruded except very basally, gonostylus weakly arching, ca. 4 times as long as maximal width, sub-apically about 1.5 times as wide as medially, with apex rounded, gonocoxal plates reaching near basal quarter of

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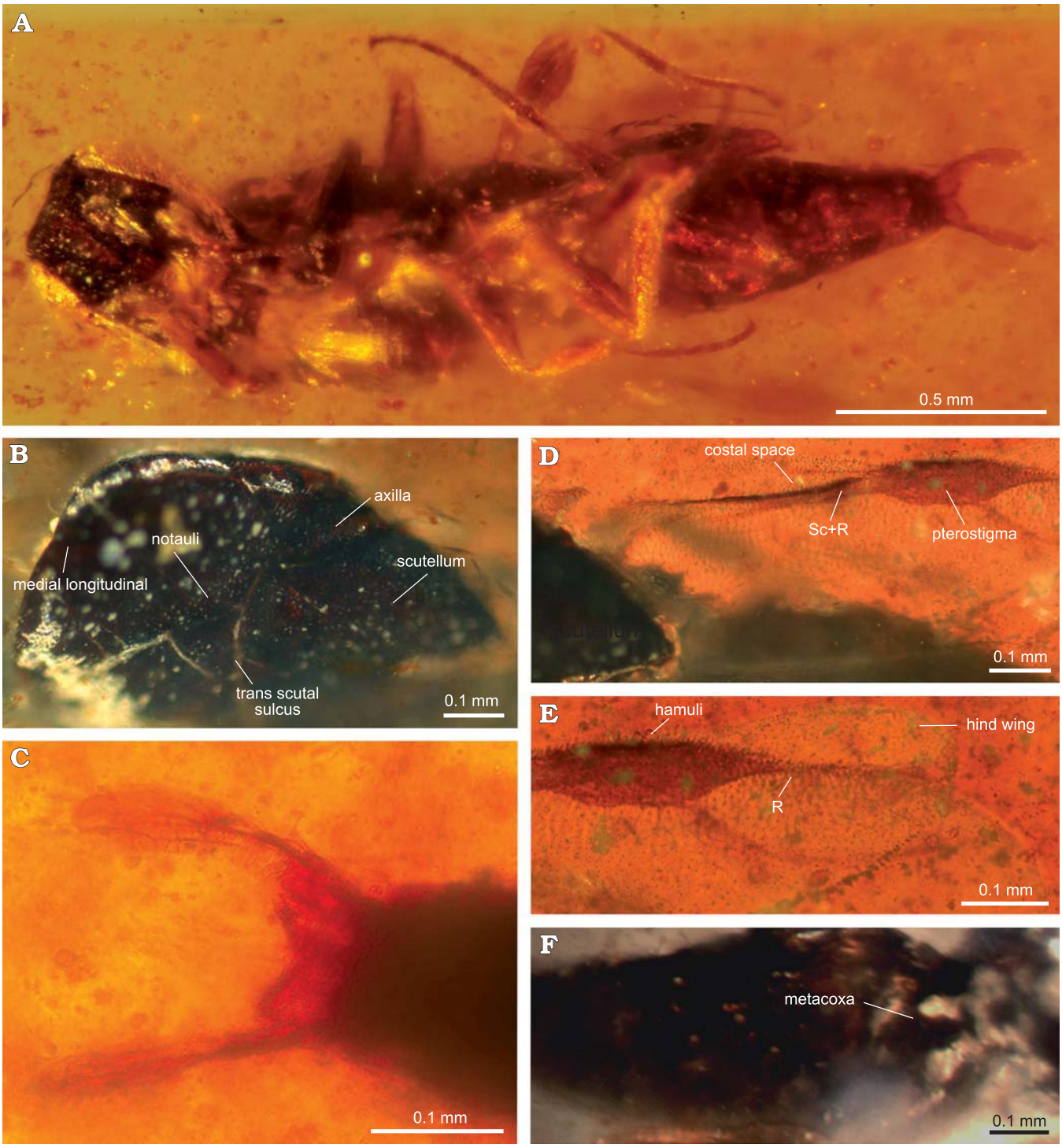


Fig. 2. Ceraphronoid wasp *Radiophron* aff. *ibericus* gen. et sp. nov. MCNA 8760, male; Peñacerrada I, Albian. **A**. Ventral view. **B**. Dorsal view of elevated mesosoma (mesoscutum and scutellum), showing mesoscutum, notauli and trans scutal sulcus, wide axilla and long scutellum with acute posterior margin. **C**. Detail of the protruded genitalia. **D**. Detail of the acute margin of scutellum and the fore wing, with the distal preserved Sc+R up-curved, very wide at its contact with pterostigma and the wide costal space. **E**. Details of fore wing showing part of R distal from pterostigma, Rs+2r-rs up-curved and arising oblique from distal base of pterostigma, and hind wing with three curved hamuli. **F**. Detail of right wide and flattened metacoxa labelled in the middle.

← Fig. 1. Ceraphronoid wasp *Radiophron ibericus* gen. et sp. nov.; Peñacerrada I, Albian. **A**. Holotype MCNA 8754: A_1, lateral view of holotype; A_2, frontal view showing the long and wide scape and the maxillary palp; A_3, dorsal view; A_4, detail of the antenna showing the pedicel elbowed respect scape and the first flagellomere reduced and basally constrained. **B**. MCNA 8789: lateral view showing the wide and flattened metacoxa, with the label situated approximately in the middle of it. **C**. Paratype MCNA 13030: C_1, detail of the two protibial spurs on both specimens and two mesotibial spurs that characterize ceraphronoids (left side of each head labelled as head 1 and head 2); C_2, dorsal view of head 1 showing disposition of ocelli.

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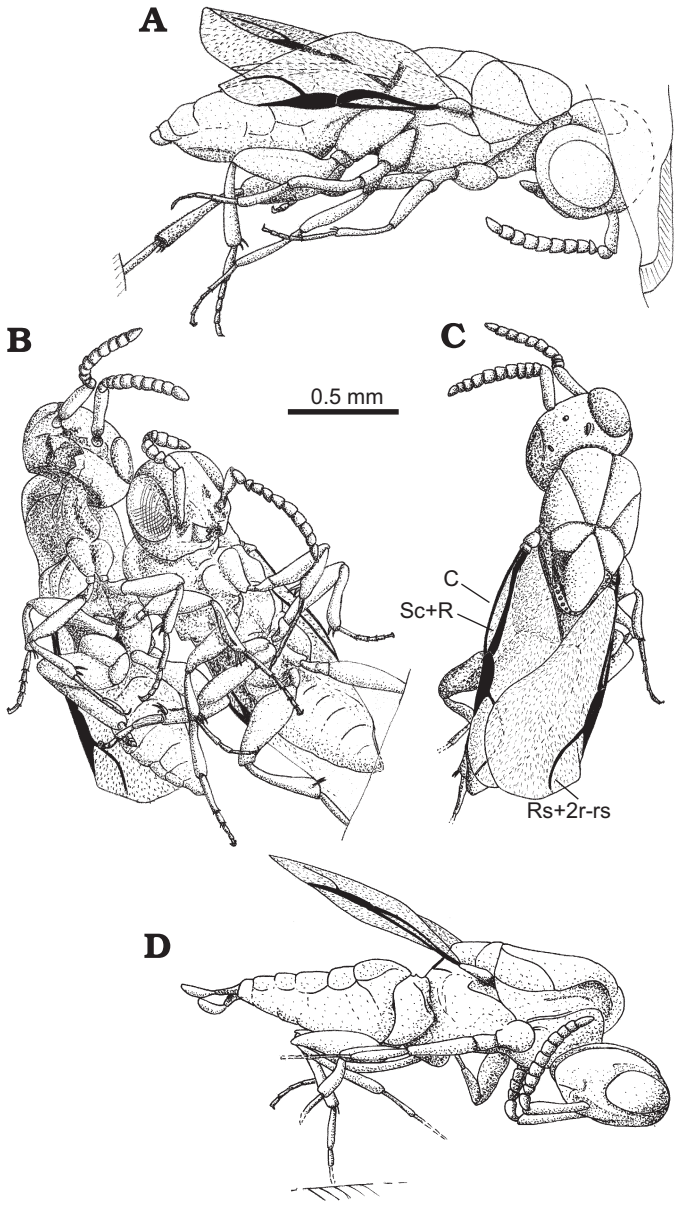


Fig. 3. Camera lucida drawings of *Radiophron ibericus* gen. et sp. nov., and *Radiophron* aff. *ibericus* gen. et sp. nov., male; Peñacerrada I, Albian. **A**. Lateral view of holotype MCNA 8754. **B**. Ventral view of paratypes MCNA 13030.1 and 13030.2 showing tibial spur combination 2-2-2. **C**. Dorsal view of paratype MCNA 13030.1. **D**. Lateral view of *Radiophron* aff. *ibericus* gen. et sp. nov., male, MCNA 8760.

gonostylus, with distal margins meeting at about 120° medially, penis and volsellae not visible, probably very short.

Description.—Female. Body length between 2.2 and 1.68 mm (mean from the 7 females: 1.97 mm). Head with minute punctured sculpture, wider than mesosoma, partially placed under it; concave occiput with evident preoccipital carina. Compound eyes occupying 2/3 of lateral surface of head. Ocelli well distant from each other, lateral ones elongate separated for less than one ocellar length from the compound eye margin and for three ocellar lengths from the circular median ocellus. Antennae elbowed between scape and pedicel; scape with distal half ventrally widened, almost half as long as flagellum and about as long as shorter eye diameter; nine flagellomeres all near-squared, gradually increasing in size except for the first being almost half as long as the second, with constricted base, and for last one being longer than wide, tapered apically. Maxillary palps 6-segmented, elbowed between third and fourth segments.

Mesosoma with mesoscutum and scutellum highly elevated, sloping sub-vertical from scutellar apex toward metasomal articulation, with hind surface somewhat concave, with no teeth or structures seen at the angle. Punctured sculpture over all dorsal and lateral mesosomal sclerites. Pronotum not visible in dorsal view. Mesonotum with medial longitudinal sulcus well impressed, reaching both margins. Notauli present, widely separated at transverse scutal suture. Axillae long and wide, touching antero-medially. Scutellum almost half as long as of mesonotum, anteriorly not reaching transverse mesonotal suture and posteriorly not covering the dorsal view of propodeum.

Wings covered by microtrichia. Fore wing showing thin tubular C and Sc+R quite arched and very wide at contact with pterostigma, leaving a wide costal space. Pterostigma roughly three times as long as wide, semicircular except for the distal 2/5 obliquely truncated. R slightly extending beyond pterostigma, leaving 3r cell not margined at wing anterior margin. Rs+2r-rs arising oblique from the basal inflexion point of curvature of pterostigma, curved with no angle, faintly reaching wing margin. Hind wing with at least one tubular vein (R) basally and three medial hamuli.

Legs moderately setose. Hind coxa flattened and moderately widened, partly covering lateral view of propodeum. Hind trochanter curved, cylindrical, large and wide. Hind femur swollen, laterally slightly flattened, wider in the basal medial part, without row of hard setae either lateral or on ventral distal margin. All tibia slender, subtle widened distally. Tibial spur combination 2-2-2. Tarsomeres with two, anterior and posterior, apical setae, with no comb of harder setae or striated sculpture. Hind tarsal proportions from basitarsus on 1: 0.5: 0.4: 0.3: 0.4. Claw simple.

Metasoma nearly as long as mesosoma, inserted low on propodeum just above coxae; fusiform with rounded base and convex dorsum, six segmented, first one the largest, following ones gradually narrowing, with apical one weakly sclerotized. No spiracles visible.

Geographic and stratigraphic range.—Exclusively from the type locality and type horizon.

Genus *Microcostaphron* nov.

Type species: *Microcostaphron parvus* sp. nov., monotypic.

Etymology: Combination of Microcosta—referring to the evident but very small costal cell that it shows and -phron for being placed within Ceraphronoidea.

Diagnosis.—Head short and wider than mesosoma. Flagellomeres barely longer than wide, sub-equal in length; first flagellomere longer than pedicel, slightly narrowed basally but

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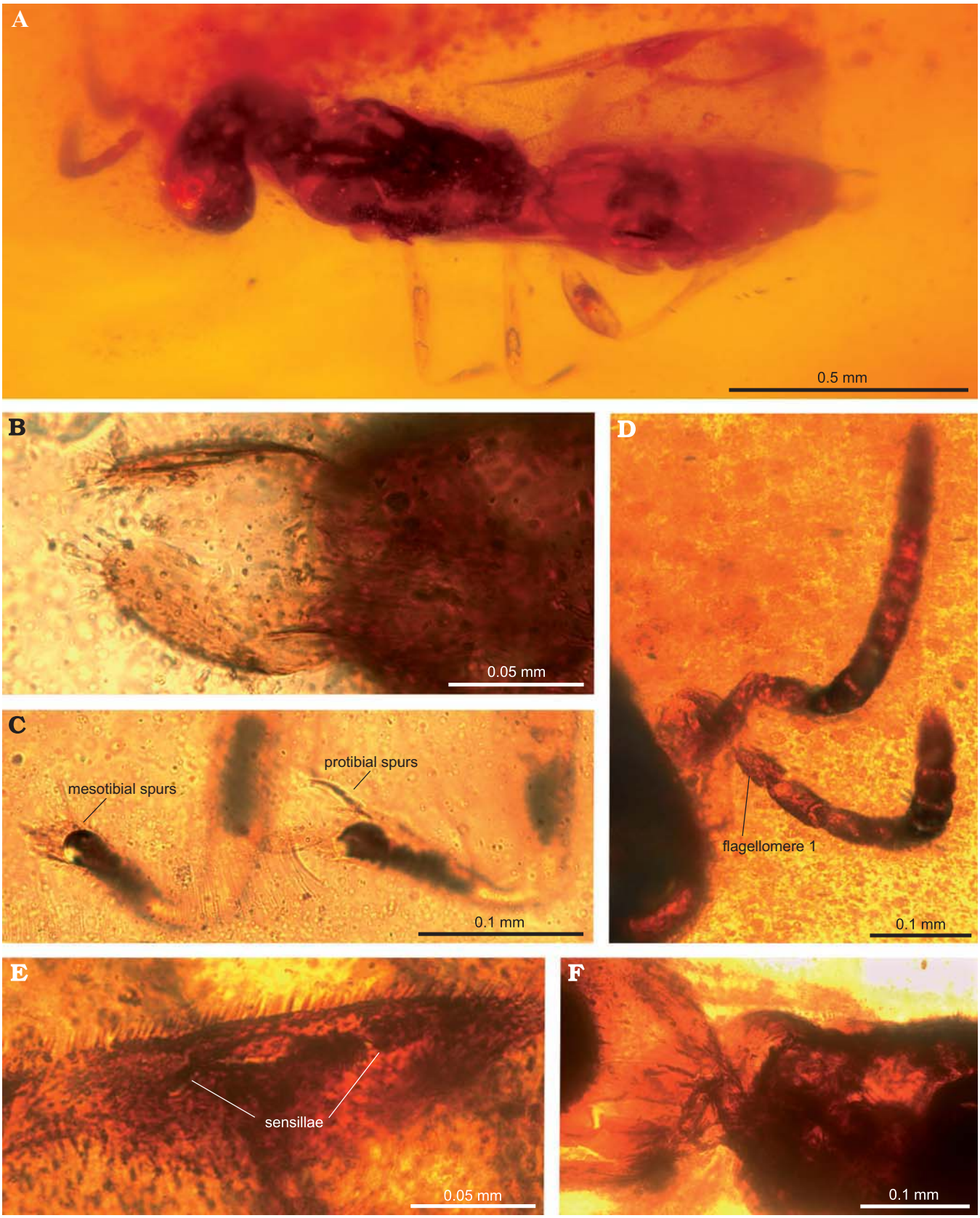


Fig. 4. Ceraphronoid wasp *Microcostaphron parvus* gen. et sp. nov., holotype male MCNA 8769; Peñacerrada I, Albian. **A**. Dorso-lateral view. **B**. Detail of genitalia. **C**. Detail of left pro- and mesotibial spurs, apparently two on each tibia. **D**. Detail of antennae showing relatively elongate, slightly constrained first flagellomere. **E**. Detail of pterostigma with two small distinct structures that may be sensillae. **F**. Detail of the constricted attachment of metasoma to mesosoma.

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not reduced (differing from *Radiophron* gen. nov. and basal stigmaphronids *Elasmophron* and *Libanophron*). Pronotum elongate, apparently as long as mesonotum medially. Medial mesoscutal sulcus not visible (possibly lost). Scutellum almost twice as long as mesoscutum, not covering dorsal view of propodeum but ending more acute than in *Elasmophron*. Fore wing vein C weak or lost, Sc+R weak or absent basally, slightly concave in respect to anterior margin, leaving a thin but distinct membrane representing costal space. Rs+2r-rs arising from pterostigma basal third, clearly angled basally, and more or less equally curved along the rest of the vein. Femora, tibial apical margin and tibial spurs not widened nor enlarged (differentiating from all except *Radiophron* gen. nov., *Elasmophron*, and *Libanophron*). Genitalia protruding, with large arched gonostyli bearing each 6 apical long setae.

Microcostaphron parvus sp. nov.

Figs. 4, 5.

Etymology: From the Latin parvus meaning small, in reference to the small size of the specimen.

Type material: Holotype: MCNA 8769. Male. Specimen preserved in a drop of very clear polished amber of 3 × 2 × 0.9 mm, embedded in a piece of epoxy resin of 8 × 6 × 1 mm. The preservation of the exoskeleton is very translucent which impedes a clear view of some sclerite margins. Tarsomeres are preserved only in the left foreleg.

Type locality: Peñacerrada I, close to Moraza village.

Type horizon: Escucha Formation.

Diagnosis.—As for the genus.

Material.—Only holotype.

Description.—Total body length 1.36 mm excluding genitalia. Head transverse, deeply emarginated behind, with temples very narrow, without carinated margin before occipital carina. Compound eyes covering almost complete lateral surface of head. Ocelli not visible. Flagellum 9 segmented, elbowed between scape and pedicel. Scape longer than pedicel and first flagellomere combined. Flagellomeres slightly longer than wide, sub-equal in size and shape except for the first one somewhat constricted at base, and the last one longer and tapered.

Mesosoma barely longer than metasoma. Pronotum elongate, dorsally visible, not covered by mesoscutum. Mesoscutum short, with faintly impressed notauli seen only posteriorly, apparently wide separated, no visible median mesoscutal sulcus. Scutellum covering slightly less than half the mesosoma length. Mesosoma abruptly declivous slightly beyond scutellar apex, apparently not sculptured. Fore wings with moderately abundant microtrichia, mainly anteriorly near the wing base. Costal vein weakly visible by preservation. Sc+R weakly sclerotized, not visible along basal third, widened at pterostigmal contact. Sc+R slightly curved leaving a thin but distinct costal space between mid length of R and pterostigma. Pterostigma three times as long as high, more or less semi circular, almost as long as Rs, with some distinct structures (possibly 2–5 sensilla). R very short beyond pterostigma. Rs+2r-rs distinctly angled sub-basally, arising from basal third of pterostigma, reaching wing margin very faintly. Hind wings not seen. Metacoxa not well seen but apparently wide and flattened. Metafemur slender, without any marginal or distal row or comb of spines or stiff setae. Pro- and mesotibia each with two thin and short apical spurs. Metatibia narrow, just slightly widened apically, without comb of distal setae (or not preserved).

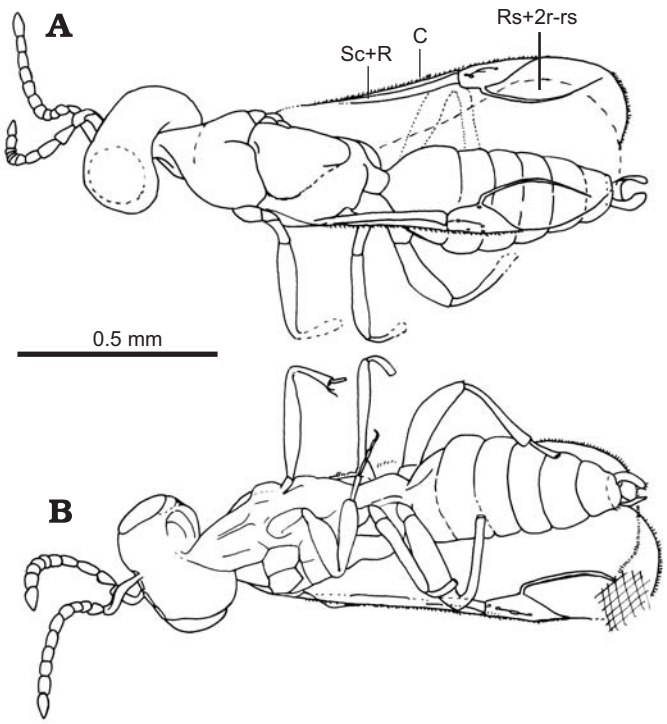


Fig. 5. Camera lucida drawings of *Microcostaphron parvus* gen. et sp. nov., holotype MCNA 8769; Peñacerrada I, Albian. **A**. Dorso-lateral view. **B**. Ventral view.

Metasoma fusiform with first abdominal segment small, short, tube-like. First gastral segment the longest; 2nd to 6th sub-equal in length, gradually narrowing in width. Male genitalia protruded except basally, with gonostylus distinctly arching, about three times as long as wide, of sub-equal width except for rounded apex, with at least six long apical setae. Gonocoxal plates short, with apical margins sub-parallel. Penis and volsellae not well seen, very short if correctly identified, toothed digits probably present.

Geographic and stratigraphic range.—Exclusively from the type locality and type horizon.

Discussion

A cladistic analysis was performed under WinClada (Nixon 2002) and Nona (Goloboff 1997) programs to assess the relationship of the newly proposed family with other ceraphronoids. We used the 22 characters and states recently proposed by Engel and Grimaldi (2009: table 2 and appendix 1) in their study of the Stigmaphronidae, and just coded the new fossils with them (Table 1, Appendix 1). States of characters 7 and 8 as defined by Engel and Grimaldi (2009) were somewhat pro-

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Table 1. Data matrix for cladistic analysis of Ceraphronoidea, taken from Engel and Grimaldi (2009) with additional scoring for *Radiophron ibericus* gen. et sp. nov. and *Microcostaphron parvus* gen. et sp. nov.

Taxon/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
General Proctotrupomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lagynodes sp. (Megaspilidae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Ceraphron sp. (Ceraphronidae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
Allocotidus buesi	1	0	0	2	0	?	1	?	?	?	?	?	?	?	1	1	1	1	0	1	1	0
Allocotidus melpomene	1	0	0	2	0	0	1	1	0	0	1	1	0	0	1	1	1	1	0	1	1	0
Burmaphron prolatum	1	0	1	0	0	1	1	1	0	1	1	1	1	0	1	1	1	1	0	1	1	0
Burmaphron tridentatum	1	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	0	1	1	0
Elasmophron kurthi	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Hippocoon evadne	1	0	0	3	1	0	1	1	0	0	1	1	0	0	?	1	1	1	0	0	1	0
Libanophron astarte	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0
Stigmaphron orphne	1	1	0	0	0	2	1	1	0	0	1	1	0	0	?	1	1	1	0	2	1	0
Tagsmiphron ascalaphus	1	0	0	1	0	2	1	1	1	0	1	1	0	1	?	1	1	1	0	0	1	0
Tagsmiphron canadense	1	0	0	1	0	0	1	1	1	0	1	1	0	2	?	?	?	?	?	?	1	0
Tagsmiphron gigas	1	0	0	0	0	2	1	1	1	0	1	1	0	1	?	1	1	1	0	0	1	0
Tagsmiphron muesbecki	1	0	0	0	0	2	1	1	1	0	1	1	0	1	1	1	1	1	0	0	1	0
Radiophron ibericus gen. et sp. nov.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Microcostaphron parvus gen. et sp. nov.	0	0	0	0	0	0	?	0	0	0	0	0	?	?	?	1	0	0	0	0	1	0

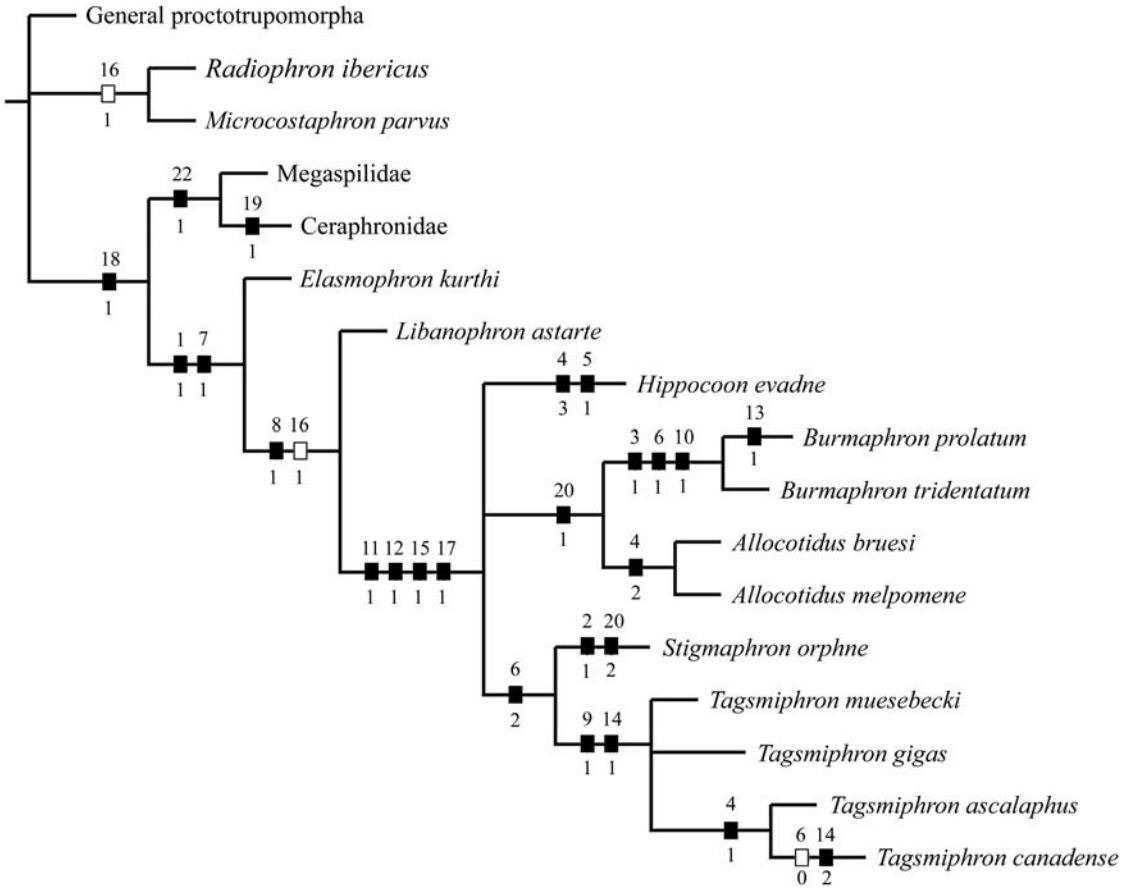


Fig. 6. Cladogram of ceraphronoid relationships including Radiophronidae (most parcimonious tree, L = 29, CI = 0.93, RI = 0.96). Unambiguous apomorphies marked as black circles and reversals as white rectangles. Character number appears above the branch and character state below it.

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blematic when applied to *Radiophron* gen. nov. and *Microcostaphron* gen. nov. Character 7 (metacoxa 0 = slender and short, not covering lateral view of propodeum, or 1 = greatly enlarged, flattened, and covering lateral view of propodeum) was coded as 0 for both genera, though they have weakly enlarged, flattened metacoxa partly covering the lateral view of propodeum but this is much more reduced than in Stigmaphronidae. Similarly for character 8 (metafemur 0 = slender, or 1 = greatly swollen), both genera have the femora only weakly flattened and swollen medially, thus we coded 8:0.

The new analysis was undertaken with characters considered as non-additive, and resulted in a single most parsimonious tree of length 29, CI 0.93 and RI 0.96 (Fig. 6), in which Radiophronidae fam. nov. are basal sister-group to the clade Megaspilidae + Ceraphronidae + Stigmaphronidae. However, the grouping of Radiophronidae is supported only by a homoplastic state 1 of character 16 (posterior border of mesoscutellum pointed) and the lack of synapomorphies for Ceraphronidae, Megaspilidae and Stigmaphronidae sensu Engel and Grimaldi (2009). Unfortunately the structure of the male genitalia, which putatively represents the unique synapomorphy of Radiophronidae, is absent from the matrix by Engel and Grimaldi (2009). A detailed description of this character in male stigmaphronids will be necessary to provide better support for the monophyly of Radiophronidae.

Microcostaphron is synapomorphic in respect to *Radiophron* in having numerous reductions as well as the pronotum much elongate. *Microcostaphron* is plesiomorphic in having the first flagellomere not reduced and Rs+2r-rs angular sub-basally. The angle might mark the place of junction of the vein Rs with the crossvein 2r-rs, a plesiomorphy lost by all other Ceraphronoidea.

Concluding remarks

A new material of ceraphronoid wasps from Albian (Early Cretaceous) Álava Amber, Spain warrants a description of two new species belonging to two new genera. *Radiophron ibericus* is currently represented by eight specimens while *Microcostaphron parvus* is known from the holotype only. The morphological analysis of the material at hand suggests that these fossil wasps form a separate clade among ceraphronoid wasps which is here described as a new family Radiophronidae. We hope that ongoing excavations at the type locality will provide additional material of the two species, especially their male individuals, which would substantiate taxonomic position of the group as interpreted herein. As a future development we also consider using the synchrotron tomography to obtain better images of *M. parvus*. It especially concerns their metacoxas being currently obscured to view and also the unclear sclerite boundaries difficult to discern from fractures and grooves. The new character states would considerably improve the preliminary cladistic analysis which now places the Radiophronidae as basal sister-group of all other ceraphronoids.

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Appendix 1

Characters used in cladistic analysis

Below are the characters and character states used in the cladistic analysis of stigmaphronid relationships. All of the characters were considered non-additive and of equal weight.

1. Body design: 0 = body more gracile, head not tightly fitted to pronotum; 1 = body relatively compact, with hemispherical head fitted to pronotum.
2. Compound eye: 0 = normal, occupying large portion of lateral surface of head (occupying 75% or more of lateral head surface); 1 = reduced, slender, set posteriorly on head, not occupying large portion of head's lateral surface (occupying less than 50% of head width).
3. Preoccipital ridge: 0 = sharply angled and carinate; 1 = with ridge prior to posterior angle.
4. Scape: 0 = slender, elongate, five or more times longer than apical width; 1 = slender, 3–3.5 times as long as wide; 2 = short, about 1.5–2.5 times as long as wide; 3 = exceedingly short, about as long as wide.
5. Funicular articles: 0 = gradually increasing in length, from transverse to longer than wide; 1 = all extremely short, compact, and transverse.
6. Protibial spurs: 0 = two well-developed spurs of approximately equal design; 1 = two spurs, with second drastically reduced and nearly vestigial; 2 = a single protibial spur present.
7. Metacoxa: 0 = slender and short, not covering lateral view of propodeum; 1 = greatly enlarged, flattened, and covering lateral view of propodeum.
8. Metafemur: 0 = slender; 1 = greatly swollen.
9. Row of short, stout spicules on posterior margin of metafemur: 0 = absent; 1 = present.
10. Five to seven long, fine, spicules on distal margin of metafemur: 0 = absent; 1 = present.
11. Metatibia: 0 = slender; 1 = greatly broadened apically.
12. Metatibial spurs: 0 = short, as long as or scarcely longer than metatibial apical width; 1 = greatly elongate, much greater than apical width of metatibia.
13. Metabasitarsus: 0 = as long as or shorter than metafemur; 1 = longer than metafemur.
14. Inner surface of metabasitarsus: 0 = with scattered setae; 1 = with row of short, stout spicules; 2 = with row of distinct spines.
15. Medial line of mesoscutum: 0 = present; 1 = absent.
16. Posterior border of mesoscutellum: 0 = rounded; 1 = pointed.
17. Mesoscutellum: 0 = not obscuring propodeum; 1 = obscuring propodeum.
18. Forewing veins C and Sc+R: 0 = distinct; 1 = fused.
19. Pterostigma: 0 = large, distinct; 1 = reduced, effectively absent.
20. Forewing Rs: 0 = present, well developed; 1 = present, nebulous; 2 = absent.
21. First metasomal segment: 0 = distinct; 1 = forming a short petiole largely obscured by second metasomal segment.
22. Second metasomal segment: 0 = not greatly larger than succeeding metasomal segments and comprising bulk of metasoma; 1 = greatly enlarged relative to succeeding metasomal segments and comprising bulk of metasoma.

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