

A braconid wasp (Hymenoptera, Braconidae) from the Lower Cretaceous amber of San Just, eastern Iberian Peninsula

Sergio Álvarez-Parra¹, Enrique Peñalver², Xavier Delclòs¹, Michael S. Engel^{3,4,5}

1 *Departament de Dinàmica de la Terra i de l'Oceà and Institut de Recerca de la Biodiversitat (IRBio), Facultat de Ciències de la Terra, Universitat de Barcelona, c/ Martí i Franquès s/n, 08028, Barcelona, Spain* **2** *Instituto Geológico y Minero de España-CSIC, c/ Cirilo Amorós 42, 46004, Valencia, Spain* **3** *Division of Entomology, Natural History Museum, University of Kansas, 1501 Crestline Drive – Suite 140, Lawrence, Kansas 66045-4415, USA* **4** *Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA* **5** *Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA*

Corresponding author: Sergio Álvarez-Parra (sergio.alvarez-parra@ub.edu)

Academic editor: Kees van Achterberg | Received 11 March 2022 | Accepted 22 April 2022 | Published 30 May 2022

<http://zoobank.org/079C1F77-A3AA-4158-AE53-5F510C8FA0BE>

Citation: Álvarez-Parra S, Peñalver E, Delclòs X, Engel MS (2022) A braconid wasp (Hymenoptera, Braconidae) from the Lower Cretaceous amber of San Just, eastern Iberian Peninsula. ZooKeys 1103: 65–78. <https://doi.org/10.3897/zookeys.1103.83650>

Abstract

Braconid parasitoid wasps are a widely diversified group today, while their fossil record from the Mesozoic is currently poorly known. Here, we describe *Utrillabracon electropteron* Álvarez-Parra & Engel, **gen. et sp. nov.**, from the upper Albian (Lower Cretaceous) amber of San Just in the eastern Iberian Peninsula. The holotype specimen is incomplete, although the forewing and hind wing venation are well preserved. The new taxon is assigned to the subfamily †Protorhyssalinae (Braconidae) and, based on characteristics of the wing venation, seems to be closely related to *Protorhyssalus goldmani* Basibuyuk & Quicke, 1999 and *Diorhyssalus allani* (Brues, 1937), both from Upper Cretaceous ambers of North America. We discuss the taxonomy of the Cretaceous braconids, considering †Seneciobraconinae as a valid subfamily. We also comment on possible relationships within †Protorhyssalinae, although a phylogenetic analysis is necessary. Additionally, a checklist is included of braconids known from Cretaceous ambers.

Keywords

Albian, fossil, Ichneumonoidea, Protorhyssalinae, Spanish amber, taxonomy, wasp diversity, wing venation

Introduction

Braconidae are the second largest family of Hymenoptera in terms of species numbers (Chen and van Achterberg 2019), trailing just behind the closely related family, Ichneumonidae. Like ichneumonids, braconids are parasitoid wasps, with their larvae developing within or externally on other insects, typically Coleoptera, Diptera, and Lepidoptera, but actually encompassing a considerable breadth of hosts from aphids to other wasps, and even adult stages (e.g., Euphorinae) (Wharton 1993). Given that braconids attack the immatures of many agriculturally important pest species, they have been heavily employed in sustainable pest management programs throughout the world (e.g., Nomano et al. 2015).

Braconids belong to the superfamily Ichneumonoidea, which comprises the extant families Ichneumonidae, Braconidae, and Trachypetidae (Quicke et al. 2020), along with the extinct †Praeichneumonidae, a monogeneric family including five species known from Early Cretaceous compression fossils (Rasnitsyn 1983, 1990; Kopylov 2012). A putative fifth group, †Ichneumonimidae (Rasnitsyn 1975), has subsequently been considered to belong to Trigonalidae (Rasnitsyn 1988), while the Trachypetidae has been recently restored as a non-cyclostome braconid subfamily (Jasso-Martínez et al. 2022a, 2022b). The fossil record of Ichneumonoidea is most diverse in Cenozoic deposits but extends well into the Early Cretaceous, with Mesozoic fossils representing early diverging lineages of both Ichneumonidae and Braconidae, several of which have been difficult to place phylogenetically or to even confirm as monophyletic (Kopylov et al. 2021; Spasojevic et al. 2021; Viertler et al. 2022).

One notable example of these early lineages is the braconid subfamily †Protorhyssalinae, a group of parasitoid wasps almost exclusively known by amber inclusions from the Albian to the Campanian (Li et al. 2021). Braconidae are currently represented by 21 genera and 22 species in Cretaceous ambers (Table 1), besides other specimens preserved as compressions in Cretaceous rocks (Belokobylskij 2012). Only two braconid species have been previously reported from Cretaceous Spanish amber (Ortega-Blanco et al. 2009, 2011) (Fig. 1). Furthermore, other specimens of the family were found in lower Miocene compression outcrops from the eastern Iberian Peninsula (Peñalver and Martínez-Delclòs 2000; Álvarez-Parra and Peñalver 2019). Here, we describe a new genus and species of fossil wasp belonging to the subfamily †Protorhyssalinae included in amber from the upper Albian San Just in the eastern Iberian Peninsula. Although the specimen is incomplete, the wings are extraordinarily well preserved and allow for its proper placement and characterization relative to other protorhyssalines. We provide a description of the new species and compare it with the previously known genera of †Protorhyssalinae. In addition, we append comments on the diversity of the subfamily and putative phylogenetic groups among this assemblage of wasps.

Table 1. Checklist of species of Braconidae (Hymenoptera, Ichneumonoidea) from Cretaceous ambers. The two species marked with an asterisk need taxonomic revision. For Cretaceous compression fossils see Belokobylskij (2012).

Subfamily	Genus and species	Locality	Age	Reference
Aphidiinae	<i>Archephedrus stolamissus</i> Ortega-Blanco, Bennett, Delclòs, & Engel, 2009	Peñacerrada I, Spain	late Albian	Ortega-Blanco et al. (2009)
Brachistinae	" <i>Neoblacus</i> " (= <i>Blacus</i>) <i>facialis</i> Brues, 1937 *	Cedar Lake, Canada	Campanian	Brues (1937)
Euphorinae	" <i>Pygostolus</i> " <i>patriarchicus</i> Brues, 1937 *	Cedar Lake, Canada	Campanian	Brues (1937)
†Megalyrhyssalinae	<i>Megalyrhyssalus clavicornis</i> Belokobylskij & Jouault, 2021	Hukawng Valley, Myanmar	early Cenomanian	Belokobylskij and Jouault (2021)
†Protobraconinae	<i>Rhetinorhyssalites emersoni</i> Engel, Thomas, & Alqarni, 2017	Sayreville, USA	Turonian	Engel et al. (2017); Chen et al. (2021b)
	<i>Chainochora syntoma</i> Chen & van Achterberg, 2021	Hukawng Valley, Myanmar	early Cenomanian	Chen et al. (2021a)
	<i>Kleistochora dolichura</i> Chen & van Achterberg, 2021	Hukawng Valley, Myanmar	early Cenomanian	Chen et al. (2021a)
	<i>Protobracon robusticauda</i> Chen & van Achterberg, 2021	Hukawng Valley, Myanmar	early Cenomanian	Chen et al. (2021b)
	<i>Tibialobracon compressicornis</i> Chen & van Achterberg, 2021	Hukawng Valley, Myanmar	early Cenomanian	Chen et al. (2021b)
†Protorhyssalinae	<i>Diorhyssalus allani</i> (Brues, 1937)	Cedar Lake, Canada	Campanian	Brues, (1937); Engel (2016); Chen et al. (2021b)
	<i>Protorhyssalus goldmani</i> Basibuyuk & Quicke, 1999	Sayreville, USA	Turonian	Basibuyuk et al. (1999)
	<i>Protorhyssalodes arnaudi</i> Perrichot, Nel, & Quicke, 2009	Cadeuil, France	early Cenomanian	Perrichot et al. (2009); Chen et al. (2021b)
	<i>Archaeorhyssalus subsolanus</i> Engel, 2016	Hukawng Valley, Myanmar	early Cenomanian	Engel and Wang (2016)
	<i>Burmabracon gracilens</i> Li, Shih, & Ren, 2021	Hukawng Valley, Myanmar	early Cenomanian	Li et al. (2021)
	<i>Burmabracon grossus</i> Li, Shih, & Ren, 2021	Hukawng Valley, Myanmar	early Cenomanian	Li et al. (2021)
	<i>Protorhyssalopsis perrichoti</i> Ortega-Blanco, Delclòs, & Engel, 2011	Peñacerrada I, Spain	late Albian	Ortega-Blanco et al. (2011)
	<i>Utrillabracon electropteron</i> Álvarez-Parra & Engel, gen. et sp. n.	San Just, Spain	late Albian	This paper
†Seneciobraconinae	<i>Seneciobracon novalatus</i> Engel & Huang, 2018	Hukawng Valley, Myanmar	early Cenomanian	Engel et al. (2018)
<i>Incertae sedis</i>	<i>Aenigmabracon capdoliensis</i> Perrichot, Nel, & Quicke, 2009	Cadeuil, France	early Cenomanian	Perrichot et al. (2009)
	<i>Pyramidibracon clypeatus</i> Chen & van Achterberg, 2021	Hukawng Valley, Myanmar	early Cenomanian	Chen et al. (2021b)
	<i>Rhetinorhyssalus morticinus</i> Engel, 2016	Hukawng Valley, Myanmar	early Cenomanian	Engel (2016)
	<i>Stephanorhyssalus longiscapus</i> Belokobylskij & Jouault, 2021	Hukawng Valley, Myanmar	early Cenomanian	Belokobylskij and Jouault (2021)

Materials and methods

The amber material reported here comes from the San Just amber-bearing outcrop (Teruel Province, Aragón, Spain). The site is located near the Utrillas Municipality, in the Aliaga Sub-basin within the Maestrazgo Basin (Fig. 1). More than 30 amber-

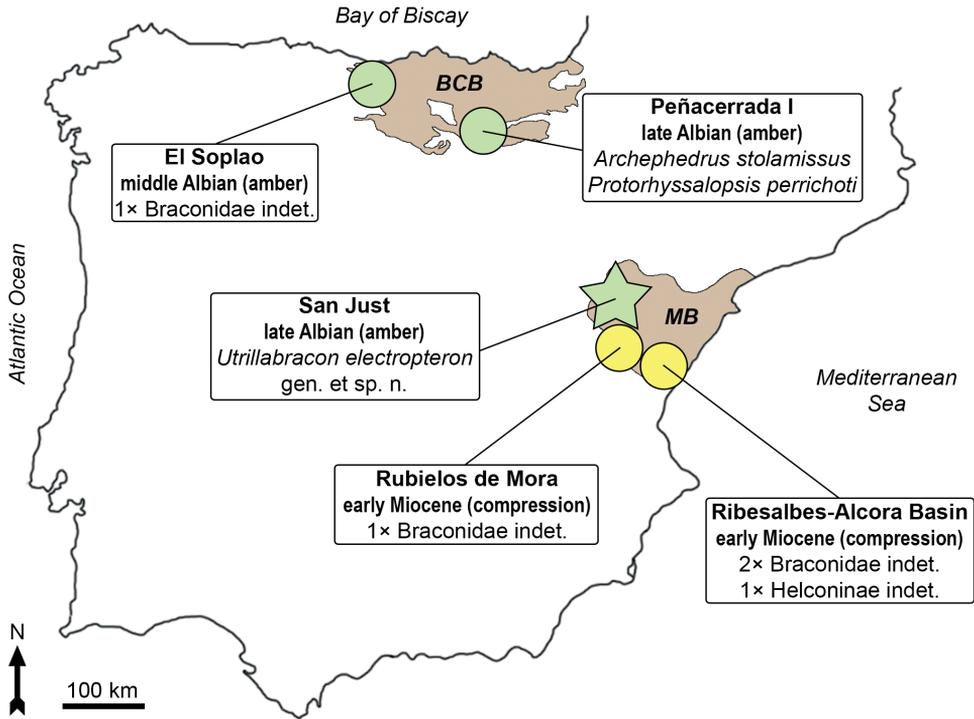


Figure 1. Map of the Iberian Peninsula showing the location of the amber and compression outcrops that have yielded braconid wasps. Basque-Cantabrian (BCB) and Maestrazgo (MB) basins are represented. The type locality the studied specimen is indicated with a star. The specimens from El Soplao and Rubielos de Mora are undescribed to date.

bearing outcrops have been reported in this basin, although only four of them have yielded bioinclusions (Álvarez-Parra et al. 2021). Stratigraphically, the San Just section has been assigned to the Escucha Formation (Peñalver et al. 2007). The amber-rich level is composed of grey-black marls with a high content of organic matter, charcoal, and fusinite and has been interpreted as a freshwater swamp plain (Peñalver et al. 2007; Villanueva-Amadoz et al. 2010). The site was dated as middle–earliest upper Albian based on palynological evidence (Villanueva-Amadoz et al. 2010). A new palynological study constrains the dating to the upper Albian (Eduardo Barrón pers. comm.). San Just is the type locality of 26 arthropod species (including the new species here described) and the Hymenoptera are represented by nine species in eight families (Santer et al. 2022). The amber piece was recovered during an excavation in 2012 (Government of Aragón permit 119/10-11-2012). The original amber piece was divided in four epoxy preparations to better examine the syninclusions. This process followed the methodology of Corral et al. (1999). The specimen was photographed and drawn using an Olympus CX41 compound microscope, with an attached digital camera sCMEX-20 and a camera lucida. Photographs were made using the software

ImageFocusAlpha v. 1.3.7.12967.20180920 and the figures were prepared using Photoshop CS6. Venational nomenclature is based on Huber and Sharkey (1993) and Ortega-Blanco et al. (2009). The specimen is deposited in the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis), Teruel, Spain. The fossil notation “MAP” corresponds to the number at the Museo Aragonés de Paleontología, while “SJE2012” is the field number.

Systematic paleontology

Family Braconidae Nees von Esenbeck, 1811

Subfamily †Protorhyssalinae Basibuyuk, Quicke, & van Achterberg, 1999

Protorhyssalinae Basibuyuk, Quicke, & van Achterberg, 1999: 211. Type genus: *Protorhyssalus* Basibuyuk & Quicke in Basibuyuk et al. (1999), by original designation.

Comments. Herein we restore the traditional concept of †Protorhyssalinae as recognized by Basibuyuk et al. (1999) and Chen and van Achterberg (2019). Belokobylskij and Jouault (2021) proposed a classification in which virtually all Cretaceous braconids are thrown into a paraphyletic group, rendering †Protorhyssalinae a meaningless grade. Admittedly, restoring †Protorhyssalinae still leaves the group paraphyletic but at least removes the more obviously derived groups and thereby narrows the challenge as to the affinities of the remaining genera. Nonetheless, while Belokobylskij and Jouault (2021) advocated for such a paraphyletic assemblage, they used plesiomorphic features along with autapomorphies to establish the subfamily †Megalyrhyssalinae. Unfortunately, †Megalyrhyssalinae is poorly justified and could be merely an autapomorphic form of the same protorhyssaline grade. By their own reasoning, they should have either not established such a subfamily or further divided †Protorhyssalinae to resolve the paraphyly. Under their conception of †Protorhyssalinae, †Megalyrhyssalinae would be a junior synonym. For now, we recognize the following subfamilies: †Protorhyssalinae, †Seneciobraconinae (*Seneciobracon*), and †Megalyrhyssalinae (*Megalyrhyssalus*), noting that the last may not be sufficiently justified but may well be worth considering once the full phylogeny of the genera comprising these groups is elucidated. Until such time it seems that further alterations of the subfamilial system in the absence of a cladistic framework would be unwarranted.

Included genera and species. *Archaeorhyssalus subsolanus* Engel, 2016; *Burmabracon gracilens* Li, Shih, & Ren, 2021; *B. grossus* Li, Shih, & Ren, 2021; *Diorhyssalus allani* (Brues, 1937); *Protorhyssalodes arnaudi* Perrichot, Nel, & Quicke, 2009; *Protorhyssalopsis perrichoti* Ortega-Blanco, Delclòs, & Engel, 2011; *Protorhyssalus goldmani* Basibuyuk & Quicke, 1999; and *Utrillabracon electropteron* Álvarez-Parra & Engel, gen. et sp. nov. *Cretorhyssalus brevis* Belokobylskij, 2012, *Magadanobracon rasnitsyni* Belokobylskij, 2012, and *M. zherikhini* Belokobylskij, 2012, known from compression fossils, were putatively assigned to †Protorhyssalinae *sensu* Belokobylskij (2012).

***Utrillabracon* Álvarez-Parra & Engel, gen. nov.**

<http://zoobank.org/C6FE19C1-A5D0-4780-9860-F611198EF09C>

Type species. *Utrillabracon electropteron* Álvarez-Parra & Engel, sp. nov.

Diagnosis. Forewing with margin bearing setae; pterostigma 4 × longer than wide; 1Rs relatively long and curved; r-rs oblique, arising medially from pterostigma; r-rs several times longer than abscissa of M between 2Rs and m-cu; marginal cell reaching wing apex; rs-m nebulous; elongate, five-sided second submarginal cell, 3 × longer than wide; 1M and m-cu of similar length; m-cu distinctly postfurcal; 2m-cu absent; cu-a slightly postfurcal and orthogonal. Hind wing with margin bearing setae; R1 distally widened with several hamuli beyond its apex; Sc + R not aligned with Rs; 2Cu present. Pretarsal claws present, without preapical tooth; arolium wide.

Etymology. The generic name is a combination of Utrillas, municipality where the San Just amber outcrop is located, and *Bracon* Fabricius, 1804, type genus of the family Braconidae. The gender of the name is masculine.

***Utrillabracon electropteron* Álvarez-Parra & Engel, sp. nov.**

<http://zoobank.org/59B73E2C-0514-4DA4-8A87-ABF61D6EF2A8>

Fig. 2

Material. Holotype, MAP-7819 (SJE2012 49-04), sex unknown, from San Just amber. The holotype is largely preserved as the forewings and hind wings. Some parts of the head, an antenna, and a leg are next to the wings. Undetermined cuticular fragments are visible near the wings. Deposited in the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis) in Teruel, Spain. Syninclusions include three other hymenopterans (probable serphitid, platygastriid, and stigmaphronid wasps). The holotype is prepared isolated in an epoxy prism of 20 × 15 mm.

Locality and horizon. San Just amber-bearing outcrop, Utrillas, Teruel, Spain; Maestrazgo Basin, Escucha Formation, upper Albian (Peñalver et al. 2007).

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

Description. Head deformed and incomplete as preserved (Fig. 2A, B); antenna partially preserved with 11 flagellomeres covered by setae, multiporous plate sensilla not visible; only distal two maxillary palpomeres preserved, covered by fine setae. Forewings and venation rather complete (Fig. 2C), forewing base not preserved, more than 1.31 mm long and 0.53 mm in its maximum width, margin bearing setae; C + Sc + R fused anterobasally, extending along wing margin to pterostigma; pterostigma 4 × longer than wide (0.33 mm vs 0.08 mm); elongate marginal cell, 3 × longer than wide (0.57 mm vs 0.19 mm), reaching wing apex; 1Rs relatively long and curved; Rs + M slightly sinuous; first submarginal cell 2 × longer than wide (0.31 mm vs 0.15 mm), pentagonal; 2Rs slightly sinuous; r-rs oblique, arising medially from pterostigma, 0.08 mm long; 3Rs extending nearly straight until wing margin, 0.55 mm long; r-rs several times longer than abscissa of M between 2Rs and m-cu; 1M curved, 2 × longer

than 1Rs (0.14 mm vs 0.07 mm); 2M straight, 0.38 mm long; almost straight 3M, disappearing before wing margin; rs-m nebulous, 0.13 mm long; elongate, pentagonal second submarginal cell, 3 × longer than wide (0.38 mm vs 0.13 mm); trapezoidal third submarginal cell, 0.31 mm long; first discal cell almost 2 × longer than wide (0.21 mm vs 0.12 mm); m-cu distinctly postfurcal (absence of a vein 2Rs + M), 0.12 mm long; lacking 2m-cu; elongate second discal cell, 0.63 mm long; cu-a (nervulus) slightly postfurcal (therefore presence of an exceptionally short 1Cu_a), 0.06 mm long, perpendicular to 1Cu and A; 1Cu nearly straight, 0.14 mm long; 2Cu strongly curved basally separating 2Cu_a (0.05 mm long) and 2Cu_b, latter curved and directed towards wing margin (but without meeting margin); first subdiscal cell 2 × longer than wide (0.13 mm vs 0.07 mm); elongate and narrow second subdiscal cell; A tubular and nearly straight; 1a and 2a not visible. Hind wings and venation rather complete

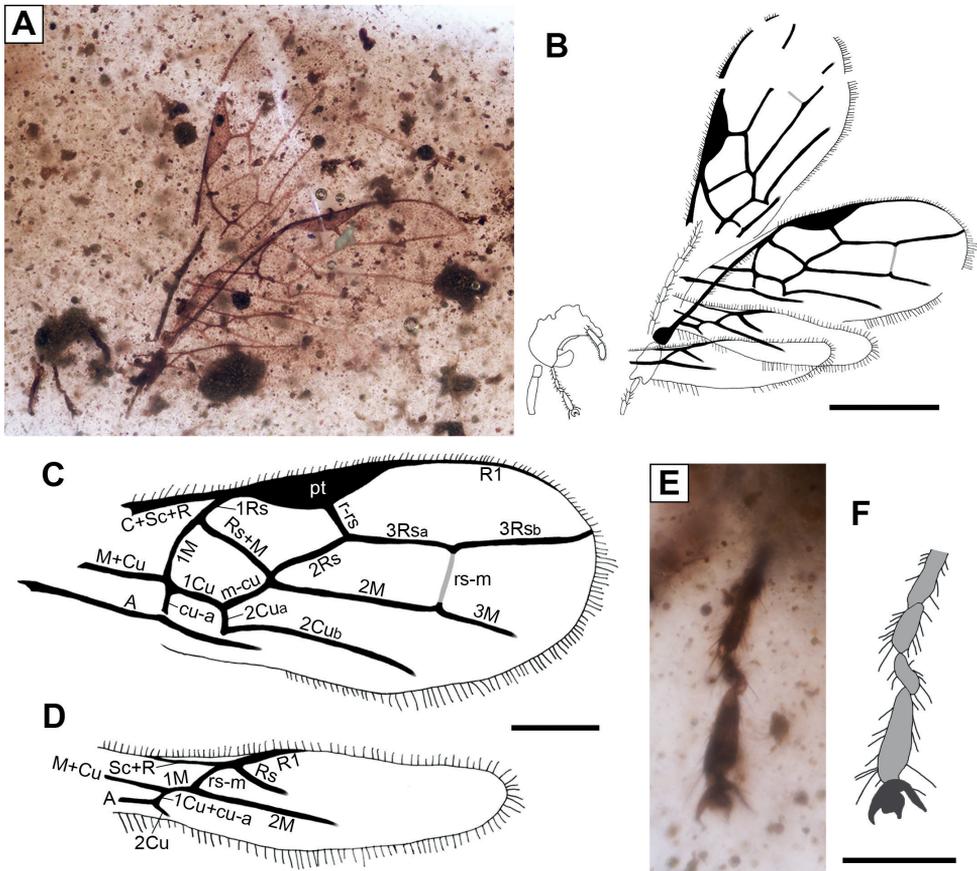


Figure 2. *Utrillabracon electropteron* Álvarez-Parra & Engel, gen. et sp. nov. (Braconidae, †Protorhyssalinae) from the upper Albian amber-bearing outcrop of San Just, specimen MAP-7819 (SJE2012 49-04). **A, B** photograph and drawing of preserved remains, both to the same scale **C** forewing venation **D** hind wing venation **E, F** photograph and drawing of tarsus and pretarsus, both to the same scale. Abbreviation: pt = pterostigma. Scale bars: 0.5 mm (**A, B**); 0.2 mm (**C, D**); 0.1 mm (**E, F**).

(Fig. 2D), hind wing base not preserved, more than 0.94 mm long and 0.23 mm at its maximum width, margin bearing setae; Sc + R fused anterobasally; R1 distally widened with several hamuli beyond its apex; Sc + R not aligned with Rs; 1M short, 0.05 long; rs-m oblique, 0.07 mm long; Rs and M ending as nebulous veins before margin; 1Cu + cu-a inclivitous, 0.03 mm long; short 2Cu, not contacting wing margin. Two fragments of legs visible: a partial femur and a tarsus; four distal tarsomeres preserved covered by fine setae (Fig. 2E, F), tarsomere III 0.06 mm long, tarsomere IV 0.04 mm long, tarsomere V 0.08 mm long; pretarsus with paired claws, preapical tooth absent, arolium wide.

Etymology. The specific epithet is a combination of the Greek ἤλεκτρον (*élektron*), meaning, “amber”, and πτερόν (*ptéron*), meaning, “winged creature”, and referring to the fact that the holotype is mainly preserved by the wings in amber.

Discussion

The newly reported San Just amber wasp can be assigned to Braconidae quite easily owing to the characteristic wing venation: Rs + M present and 2m-cu absent in the forewing and rs-m proximal to bifurcation of R1 and Rs in the hind wing (Huber and Sharkey 1993; Belokobylskij and Jouault 2021). The absence of 2m-cu in the forewing also serves to exclude the fossil from the plesiomorphic †Praeichneumonidae. Additionally, the Trachypetinae (formerly as family Trachypetidae) have rs-m distal to the separation of R1 and Rs (Quicke et al. 2020), and therefore the current fossil also does not accord with the circumscription of this group. Although many have noted that braconid wing venation can be quite variable, the current fossil from San Just cannot be ascribed to any other clade and is quite readily attributable to Braconidae. In fact, several Cretaceous braconids possess 2m-cu in the forewing, such as *Aenigmabracon capdoliensis* Perrichot, Nel, & Quicke, 2009 (subfamily *incertae sedis*), *Stephanorhysalus longiscapus* Belokobylskij & Jouault, 2021 (subfamily *incertae sedis*), and species of the subfamily †Eoichneumoninae, all of which likely retain this trait symplesiomorphically (Belokobylskij and Jouault 2021). Furthermore, some living species of the subfamilies Apozyginae, Doryctinae, and Rhyssalinae (all of crown-Braconidae) possess 2m-cu in the forewing (Tobias and Belokobylskij 1983), while some species of a few subfamilies of Ichneumonidae lack this vein (Tobias 1963). All of these cases are easily identified as secondary reappearances of the crossvein or “atavisms” based on the phylogenetic placement of the taxa in question (Belokobylskij and Jouault 2021).

The presence of a pentagonal (five-sided) second submarginal cell in the forewing and vein 2Cu in the hind wing indicates that *Utrillabracon electropteron* is currently best assigned to the subfamily †Protorhysalinae (Basibuyuk et al. 1999; Chen et al. 2021b), despite the fact that this group, even in its restricted sense, may be paraphyletic. Indeed, the overall venation of *Utrillabracon* accords broadly with that of †Protorhysalinae (Basibuyuk et al. 1999). The pentagonal second submarginal cell in the forewings is likely to be plesiomorphic in braconids. The other braconid subfamilies

with a Cretaceous record, such as Aphidiinae, †Seneciobraconinae, †Megalyrhyssalinae, and †Protobraconinae, lack 2Cu in the hind wing (Belokobylskij and Jouault 2021; Chen et al. 2021b). Several extant braconid subfamilies have 2Cu in the hind wing (Perrichot et al. 2009; Belokobylskij and Jouault 2021), and interestingly they are phylogenetically placed basal to all other crown-braconids (Apozyginae) or to the derived non-cyclostome lineage (Acampsohelconinae, Agathidinae, Meteorideinae, and Sigalphinae) (Chen and van Achterberg 2019). Furthermore, this character is also present in some †Eoichneumoninae (Braconidae), and in the ichneumonoid groups Trachypetinae (Braconidae), †Praeichneumonidae, and Ichneumonidae (Belokobylskij and Jouault 2021). Therefore, it is probable that the presence of 2Cu in the hind wing is symplesiomorphic across all of these lineages (Perrichot et al. 2009; Belokobylskij and Jouault 2021). The †Eoichneumoninae possess 2m-cu in the forewings (like the †Praeichneumonidae and the vast majority of Ichneumonidae) (Belokobylskij and Jouault 2021; Chen et al. 2021b), and quite unlike *U. electropteron*.

The San Just fossil may be easily distinguished from the two unplaced Canadian Late Cretaceous amber species “*Neoblacus*” (= *Blacus*) *facialis* Brues, 1937 and “*Pygostolus*” *patriarchicus* Brues, 1937. Both of these species need revision and likely do not belong to the genera to which Brues assigned them (Antropov et al. 2014; Chen et al. 2021b). Nonetheless, both are sufficiently known as to differentiate them from *U. electropteron*. The species *N.* (= *B.*) *facialis* lacks Rs + M and rs-m in the forewing (vs present), r-rs arises before the middle of the pterostigma and is perpendicular to the costal margin (vs inclivitous and arising pterostigmal midlength), and cu-a is distinctly postfurcal (vs slightly postfurcal) (Brues 1937). The pterostigma of *U. electropteron* seems to be similar to that of *N.* (= *B.*) *facialis*, as in both species it is 4 × longer than wide (Brues 1937). “*Pygostolus*” *patriarchicus* has a triangular pterostigma with basal and apical margins of equal length (vs pterostigma long and narrow), and cu-a postfurcal in the forewing (Brues 1937). The *incertae sedis* braconids *A. capdoliensis* and *S. longiscapus* differ from *U. electropteron* in the presence of 2m-cu and cu-a postfurcal in the forewing (Perrichot et al. 2009; Belokobylskij and Jouault 2021). *Pyramidibracon chypeatus* Chen & van Achterberg, 2021 and *Rhetinorhyssalus morticinus* Engel, 2016 are currently not assigned to a subfamily and differ from *U. electropteron* in several characters, such as cu-a strongly inclivitous in the forewing, Sc + R aligned with Rs, and both lack 2Cu in the hind wing (Engel 2016; Chen et al. 2021b).

Considering those genera currently assigned to †Protorhyssalinae, *U. electropteron* can be differentiated from them as summarized below. *Archaeorhyssalus subsolanus* lacks 1Rs (vs present), has a distinct 2Rs + M (vs absent), and m-cu antefurcal and contacting Rs + M (vs not contacting) in the forewing (Engel and Wang 2016). *Burmabracon gracilens*, *B. grossus*, and *Protorhyssalopsis perrichoti* have Sc + R aligned with Rs in the hind wing (vs not aligned), aside from a slew of further differences (Li et al. 2021; Ortega-Blanco et al. 2011). *Protorhyssalodes arnaudi* has cu-a distinctly postfurcal with 1Cu_a as long as cu-a (vs cu-a slightly postfurcal) in the forewing and also Sc + R aligned with Rs in the hind wing (Perrichot et al. 2009). The wing venation of *U. electropteron* is quite similar to that of *Protorhyssalus goldmani* and *Diorhyssalus allani* (Brues 1937; Basibuyuk et al. 1999; Engel 2016). *Utrillabracon electropteron*

shares with *P. goldmani* the marginal cell reaching the wing apex, vein m-cu postfurcal, and cu-a slightly postfurcal in the forewing, while differing in the length of the second submarginal cell (shorter in *P. goldmani*) and the length of r-rs in comparison to the abscissa of M between 2Rs and m-cu (similar length in *P. goldmani* and several times longer in *U. electropteron*) (Basibuyuk et al. 1999). Both species have Sc + R not aligned with Rs in the hind wing (Basibuyuk et al. 1999). In general, the venation of *U. electropteron* seems to be closest to that of *D. allani* (Brues 1937; Engel 2016). Particularly, the lengths of the second submarginal cell and r-rs (several times longer than the abscissa of M between 2Rs and m-cu) are similar in both, and they also have m-cu postfurcal (Brues 1937; Engel 2016). The characters present in *U. electropteron* that differ from *D. allani* are 1Rs curved (vs shorter and straight), rs-m nebulous (vs sclerotized), and cu-a orthogonal and slightly postfurcal (vs inclivitous and somewhat more postfurcal) (Brues 1937; Engel 2016). The hind wing of *D. allani* is poorly known (Engel 2016). Therefore, despite the similar venation of the San Just species with *D. allani*, we prefer to assign it to a new genus, as we think that the anatomical differences cannot be associated with variability between species. Furthermore, the San Just species and *D. allani* are separated by more than 20 Myr (Albian to Campanian), and a vast geographical distance (Iberian Peninsula vs western Canada).

Based on the similarities of the wing venations of *U. electropteron*, *P. goldmani*, and *D. allani*, it is possible that they were closely related. These three taxa may form a group within †Protorhyssalinae, supported by the following characters: 1Rs present, pterostigma long and narrow, r-rs arising medially from pterostigma, m-cu distinctly postfurcal, cu-a slightly postfurcal (1Cu_a shorter than cu-a) in the forewing, and Sc + R not aligned with Rs in the hind wing. The latter character is tenuous for *D. allani*, as the hind wings are poorly documented (Brues 1937; Engel 2016). Nonetheless, it is probable that the hind wing of *D. allani* also had 2Cu, based on the other anatomical similarities with *P. goldmani* and *U. electropteron*. A revision of the holotype of *D. allani* or the discovery of new specimens of the same morphotype may demonstrate the presence of 2Cu (and Sc + R not aligned with Rs) for the hind wing, thus corroborating its placement to †Protorhyssalinae. *Archaeorhyssalus subsolanus* has m-cu antefurcal, a distinctive character among protorhyssalines, and it may be that this genus belongs to a more derived clade between the generally plesiomorphic †Protorhyssalinae and the more derived †Seneciobraconinae. We refrain, however, from establishing another monogeneric subfamily for this genus until such time as more critical cladistic work has been undertaken. *Burmabracon gracilens*, *B. grossus*, *P. arnaudi*, and *P. perrichoti* share Sc + R aligned with Rs in the hind wing, a character that could be a potential apomorphy of a group formed by these four species. In any case, these groupings are based solely on observations of wing venation and a phylogenetic analysis incorporating larger suites of data is necessary to resolve monophyly (or lack thereof) for †Protorhyssalinae, relationships among the constituent groups, as well as the placement of the various extinct subfamilies among early diverging Braconidae. Basibuyuk et al. (1999) noted that the subfamily †Protorhyssalinae lacks apomorphies, and it is likely that it will be discovered to be a grade (Engel 2016; Chen and van Achterberg 2019), necessitating the removal of some genera to other or even new subfamilies (e.g., *Archaeorhyssalus*).

An interesting breadth of early braconid diversity is documented from Cretaceous amber inclusions and compression fossils (Table 1). Nonetheless, this diversity is trivial by comparison to the overwhelming diversity of present-day Braconidae (Chen and van Achterberg 2019). This may be the result of a Late Cretaceous diversification of the family, with little diversity present prior to this time. This may be partly the case as an incredible diversity of new potential hosts for braconids were appearing during the Late Cretaceous and into the Paleogene owing to the rise of several flower-associated insects at the time (Labandeira and Li 2021). However, there is likely also a considerable taphonomic bias against the capture and preservation of early fossil Braconidae (Martínez-Delclòs et al. 2004). Their typically diminutive size means that preservation in sediments requires exceptionally fine grains in order to have sufficient fidelity for their proper identification as braconids and despite the rich number of wasps included in amber, Cretaceous braconids are rare. This could be owing to the fact that braconids have little reason to be near resin flows except in the case of seeking or emerging from a host that was somehow present on or in trees exuding resins. Certainly, the family was present and widespread during the Cretaceous owing to their occurrence in deposits spanning Canada to Myanmar, and so the combination of potentially low abundances, lower than present species diversity, typically small body size necessitating exceptional preservational conditions, and biases away from resin-producing sources may account for their rarity. If this is the case, then it would also render challenging any direct exploration of their earliest history as fossils would likely continue to be rare.

Acknowledgements

We thank the Museo Aragonés de Paleontología (Fundación Conjunto Paleontológico de Teruel-Dinópolis) for the loan of the material reported herein. We are grateful to the Dirección General de Patrimonio Cultural of the Government of Aragón (Spain) for the permission to excavate in the San Just outcrop, and to Rafael López del Valle for the preparation of the amber piece. We also thank Sergey Belokobylskij, two anonymous reviewers, and the subject editor Kees van Achterberg for their generous and helpful comments that improved the manuscript. This study is a contribution to the project CRE CGL2017-84419 funded by the Spanish AEI/FEDER and UE. S.Á.-P. is grateful for support from the Secretaria d'Universitats i Recerca de la Generalitat de Catalunya (Spain) and the European Social Fund (2021FI_B2 00003).

References

- Álvarez-Parra S, Peñalver E (2019) Palaeoentomological study of the lacustrine oil-shales of the lower Miocene San Chils locality (Ribesalbes-Alcora Basin, Castellón province, Spain). *Spanish Journal of Palaeontology* 34(2): 187–203. <https://doi.org/10.7203/sjp.34.2.16093>
- Álvarez-Parra S, Pérez-de la Fuente R, Peñalver E, Barrón E, Alcalá L, Pérez-Cano J, Martín-Closas C, Trabelsi K, Meléndez N, López Del Valle R, Lozano RP, Peris D, Rodrigo A,

- Sarto i Monteys V, Bueno-Cebollada CA, Menor-Salván C, Philippe M, Sánchez-García A, Peña-Kairath C, Arillo A, Espílez E, Mampel L, Delclòs X (2021) Dinosaur bonebed amber from an original swamp forest soil. *eLife* 10: e72477. <https://doi.org/10.7554/eLife.72477>
- Antropov AV, Belokobylskij SA, Compton SG, Dlussky GM, Khalaim AI, Kolyada VA, Kozlov MA, Perfilieva KS, Rasnitsyn AP (2014) The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the insect limestone (Late Eocene) of the Isle of Wight, UK. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 104(3–4): 335–446. <https://doi.org/10.1017/S1755691014000103>
- Basibuyuk HH, Rasnitsyn AP, van Achterberg K, Fitton MG, Quicke DLJ (1999) A new, putatively primitive Cretaceous fossil braconid subfamily from New Jersey amber (Hymenoptera, Braconidae). *Zoologica Scripta* 28(1–2): 211–214. <https://doi.org/10.1046/j.1463-6409.1999.00006.x>
- Belokobylskij SA (2012) Cretaceous braconid wasps from the Magadan Province of Russia. *Acta Palaeontologica Polonica* 57(2): 351–361. <https://doi.org/10.4202/app.2010.0120>
- Belokobylskij SA, Jouault C (2021) Two new striking braconid genera (Hymenoptera: Braconidae) from the mid-Cretaceous Burmese amber. *Proceedings of the Geologists' Association* 132(4): 426–437. <https://doi.org/10.1016/j.pgeola.2021.04.003>
- Brues CT (1937) Superfamilies Ichneumonoidea, Serphoidea, and Chalcidoidea. In: Carpenter FM (Ed.) *Fossil Insects in Canadian Amber*. University of Toronto Studies, Geological Series 40: 27–44.
- Chen XX, van Achterberg C (2019) Systematics, phylogeny, and evolution of braconid wasps: 30 years of progress. *Annual Review of Entomology* 64(1): 335–358. <https://doi.org/10.1146/annurev-ento-011118-111856>
- Chen HY, van Achterberg C, Hong P (2021a) Two new genera of Protobraconinae (Hymenoptera, Braconidae) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research* 126: e104914. <https://doi.org/10.1016/j.cretres.2021.104914>
- Chen HY, van Achterberg C, Pang H, Liu JX (2021b) Three new genera of Braconidae (Hymenoptera) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research* 118: e104669. <https://doi.org/10.1016/j.cretres.2020.104669>
- Corral JC, López Del Valle R, Alonso J (1999) El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. *Estudios del Museo de Ciencias Naturales de Álava* 14: 7–21.
- Engel MS (2016) Notes on Cretaceous amber Braconidae (Hymenoptera), with descriptions of two new genera. *Novitates Paleontologicae* 15(15): 1–7. <https://doi.org/10.17161/np.v0i15.5704>
- Engel MS, Wang B (2016) The first Oriental protorhyssaline wasp (Hymenoptera: Braconidae): A new genus and species in Upper Cretaceous amber from Myanmar. *Cretaceous Research* 63: 28–32. <https://doi.org/10.1016/j.cretres.2016.02.012>
- Engel MS, Thomas JC, Alqarni AS (2017) A new genus of protorhyssaline wasps in Raritan amber (Hymenoptera, Braconidae). *ZooKeys* 711: 103–111. <https://doi.org/10.3897/zookeys.711.20709>
- Engel MS, Huang D, Cai C, Alqarni AS (2018) A new lineage of braconid wasps in Burmese Cenomanian amber (Hymenoptera, Braconidae). *ZooKeys* 730: 75–86. <https://doi.org/10.3897/zookeys.730.22585>

- Huber JT, Sharkey MJ (1993) Structure. In: Goulet H, Huber JT (Eds) Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada, Ottawa, 13–59.
- Jasso-Martínez JM, Quicke DLJ, Belokobylski SA, Santos BF, Fernández-Triana JL, Kula RR, Zaldívar-Riverón A (2022a) Mitochondrial phylogenomics and mitogenome organization in the parasitoid wasp family Braconidae (Hymenoptera: Ichneumonoidea). *BMC Ecology and Evolution* 22(1): e46. <https://doi.org/10.1186/s12862-022-01983-1>
- Jasso-Martínez JM, Santos BF, Zaldívar-Riverón A, Fernandez-Triana J, Sharanowski BJ, Richter R, Dettman JR, Blaimer BB, Brady SG, Kula RR (2022b) Phylogenomics of braconid wasps (Hymenoptera, Braconidae) sheds light on classification and the evolution of parasitoid life history traits. *Molecular Phylogenetics and Evolution* 107452: e107452. <https://doi.org/10.1016/j.ympev.2022.107452>
- Kopylov DS (2012) New species of Praeichneumonidae (Hymenoptera, Ichneumonoidea) from the lower Cretaceous of Transbaikalia. *Paleontological Journal* 46(1): 66–72. <https://doi.org/10.1134/S0031030112010078>
- Kopylov DS, Zhang Q, Zhang HC (2021) The Darwin wasps (Hymenoptera: Ichneumonidae) of Burmese amber. *Palaeoentomology* 4(6): 592–603. <https://doi.org/10.11646/palaeoentomology.4.6.8>
- Labandeira CC, Li L (2021) The history of insect parasitism and the Mid-Mesozoic Parasitoid Revolution. In: De Baets K, Huntley JW (Eds) The evolution and fossil record of parasitism: Identification and macroevolution of parasites. Springer, Topics in Geobiology 49(11): 377–533. https://doi.org/10.1007/978-3-030-42484-8_11
- Li L, Shih C, Yang J, Wang L, Li D, Ren D (2021) New amber record of Braconidae (Insecta: Hymenoptera) from the mid-Cretaceous of Myanmar. *Cretaceous Research* 124: e104794. <https://doi.org/10.1016/j.cretres.2021.104794>
- Martínez-Delclòs X, Briggs DE, Peñalver E (2004) Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203(1–2): 19–64. [https://doi.org/10.1016/S0031-0182\(03\)00643-6](https://doi.org/10.1016/S0031-0182(03)00643-6)
- Nees von Esenbeck CG (1811) Ichneumonides Adsciti, in genera et familias divisi. *Magazin Gesellschaft Naturforschender Freunde zu Berlin* 5: 1–37.
- Nomano FY, Mitsui H, Kimura MT (2015) Capacity of Japanese *Asobara* species (Hymenoptera; Braconidae) to parasitize a fruit pest *Drosophila suzukii* (Diptera; Drosophilidae). *Journal of Applied Entomology* 139(1–2): 105–113. <https://doi.org/10.1111/jen.12141>
- Ortega-Blanco J, Bennett DJ, Delclòs X, Engel MS (2009) A primitive aphidiine wasp in Albian amber from Spain and a Northern Hemisphere origin for the subfamily (Hymenoptera: Braconidae: Aphidiinae). *Journal of the Kansas Entomological Society* 82(4): 273–282. <https://doi.org/10.2317/JKES0812.08.1>
- Ortega-Blanco J, Delclòs X, Engel MS (2011) A protorhyssaline wasp in Early Cretaceous amber from Spain (Hymenoptera: Braconidae). *Journal of the Kansas Entomological Society* 84(1): 51–57. <https://doi.org/10.2317/JKES100728.1>
- Peñalver E, Martínez-Delclòs X (2000) Insectos del Mioceno Inferior de Ribesalbes (Castellón, España). *Hymenoptera. Treballs del Museu de Geologia de Barcelona* 9: 97–153.
- Peñalver E, Delclòs X, Soriano C (2007) A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretaceous Research* 28(5): 791–802. <https://doi.org/10.1016/j.cretres.2006.12.004>

- Perrichot V, Nel A, Quicke DLJ (2009) New braconid wasps from French Cretaceous amber (Hymenoptera, Braconidae): Synonymization with Eoichneumonidae and implications for the phylogeny of Ichneumonoidea. *Zoologica Scripta* 38(1): 79–88. <https://doi.org/10.1111/j.1463-6409.2008.00358.x>
- Quicke DLJ, Austin AD, Fagan-Jeffries EP, Hebert PD, Butcher BA (2020) Recognition of the Trachypetidae stat. n. as a new extant family of Ichneumonoidea (Hymenoptera), based on molecular and morphological evidence. *Systematic Entomology* 45(4): 771–782. <https://doi.org/10.1111/syen.12426>
- Rasnitsyn AP (1975) Hymenoptera Apocrita of Mesozoic. *Transactions of the Palaeontological Institute Academy of Sciences of the USSR* 147: 1–134. [In Russian]
- Rasnitsyn AP (1983) Ichneumonoidea (Hymenoptera) from the lower Cretaceous of Mongolia. *Contributions of the American Entomological Institute* 20: 259–265.
- Rasnitsyn AP (1988) An outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* 22(1): 115–145. <https://doi.org/10.1080/00305316.1988.11835485>
- Rasnitsyn AP (1990) Hymenoptera. In: Ponomarenko AG (Ed.) *Late Mesozoic insects of Eastern Transbaikalian*. *Transactions of the Palaeontological Institute Academy of Sciences of the USSR* 239: 177–205. [In Russian]
- Santer M, Álvarez-Parra S, Nel A, Peñalver E, Delclòs X (2022) New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea). *Cretaceous Research* 133: e105128. <https://doi.org/10.1016/j.cretres.2021.105128>
- Spasojevic T, Broad GR, Sääksjärvi IE, Schwarz M, Ito M, Korenko S, Klopstein S (2021) Mind the outgroup and bare branches in total-evidence dating: A case study of pimply Darwin wasps (Hymenoptera, Ichneumonidae). *Systematic Biology* 70(2): 322–339. <https://doi.org/10.1093/sysbio/syaa079>
- Tobias VI (1963) Ichneumonidae (Hymenoptera) with a venation type in the fore wings which resembles that in Braconidae. *Zoologicheskij Zhurnal* 42: 1513–1522. [In Russian with English summary]
- Tobias VI, Belokobylskij SA (1983) Aberrant wing venation in Braconidae (Hymenoptera) and its significance in study of the phylogeny of the family. *Entomologicheskoe Obozrenie* 62: 341–347. [In Russian]
- Viertler A, Klopstein S, Jouault C, Spasojevic T (2022) Darwin wasps (Hymenoptera, Ichneumonidae) in Lower Eocene amber from the Paris basin. *Journal of Hymenoptera Research* 89: 19–45. <https://doi.org/10.3897/jhr.89.80163>
- Villanueva-Amadoz U, Pons D, Diez JB, Ferrer J, Sender LM (2010) Angiosperm pollen grains of San Just site (Escucha Formation) from the Albian of the Iberian Range (northeastern Spain). *Review of Palaeobotany and Palynology* 162(3): 362–381. <https://doi.org/10.1016/j.revpalbo.2010.02.014>
- Wharton RA (1993) *Bionomics of the Braconidae*. *Annual Review of Entomology* 38(1): 121–143. <https://doi.org/10.1146/annurev.en.38.010193.001005>