

Revision of 18 ichneumonid fossil species (Hymenoptera, Ichneumonidae) highlights the need for open nomenclature in palaeontology

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Abstract

The fossil record of Darwin wasps (Ichneumonidae) is extremely understudied relative to their enormous extant diversity, with only around 300 species described. Moreover, the taxonomic placement of many of the fossils is based on an outdated classification system. We here revise 18 ichneumonid fossils, all described before the most comprehensive revision of ichneumonid classification by Henry Townes. After a careful reinterpretation of character evidence, we leave the original placement of only five fossils, while expressing uncertainty about the placement of two of them, *Pimpla? seyrigi* Theobald and *Polysphincta? inundata* Brues, by following the principles of open nomenclature. In addition, we move *Parapimpla rhenana* Theobald, 1937 **stat. rev.** from Pimplinae to Ctenopelmatinae. We describe a new phygadeuontine genus to accommodate two fossils previously described in Pimplinae, *Armadilleon morticinus* (Brues) **gen. et comb. nov.** and *A. petrorum* (Brues) **gen. et comb. nov.** Finally, we change the genus and, almost always, the subfamily placement for ten fossils: *Hallocinetus? arvernus* (Piton) **comb. nov.**, *Dimophora? longicornis* (Theobald) **comb. nov.**, *Dimophora? wickhami* (Cockerell) **comb. nov.**, *Lycorina? indura* (Theobald) **comb. nov.**, *Acerataspis? revelata* (Brues) **comb. nov.**, *Hypsicera? solidata* (Brues) **comb. nov.**, *Orthocentrus? mortuaria* (Brues) **comb. nov.**, *Zagryphus tilloyi* (Theobald) **comb. nov.**, *Lithoserix antiquus* (Saussure) **comb. nov.** and *Monoblastus? senilis* (Brues) **comb. nov.** Our revision highlights the need for the re-interpretation of perhaps a majority of ichneumonid fossils and for widely adopting the open nomenclature framework. This framework allows uncertainty in fossil classification to be expressed in an intuitive and explicit manner, which contributes to alleviating misinterpretation of the palaeontological literature, for instance in phylogenetic dating studies.

Key Words

compression fossils, Darwin wasps, dating, Florissant Formation, fossil record, Palaeogene, taphonomy

Introduction

Darwin wasps constitute the largest family of parasitoid wasps, with currently more than 25,000 species described and many more awaiting discovery. They attack immature stages of holometabolous insects and spiders and, by controlling their populations, fulfill a crucial role in nearly all terrestrial ecosystems. Their fossil record dates back to the late Jurassic, although the first unequivocal representatives

of extant subfamilies are from the late Palaeocene, so after the K-Pg boundary (Kopylov 2009). The first molecular dating study of Ichneumonidae (Spasojevic et al. 2021) recovered a Jurassic origin of crown group ichneumonids, a result that implies ghost ranges of at least 45 million years for the extant subfamilies. However, the associations of the Mesozoic ichneumonid fossils, which have been classified in extinct subfamilies, currently remain uncertain, as they show many similarities with some extant subfamilies

(Kopylov 2010; McKellar et al. 2013). In any case, the fossil record of ichneumonids appears very patchy. Also later periods, such as the Palaeocene and the early Eocene, are represented by only very few described ichneumonid fossils. A pronounced incompleteness of the fossil record and thus long ghost ranges are common in insects (Rasnitsyn 2000; Ronquist et al. 2012), which only fossilize under rather rare conditions. However, there is an additional explanation for the poverty of the Darwin wasp fossil record: it is drastically understudied, with around 300 described fossil species in contrast to the 25,000 extant species (Yu et al. 2016; PaleoBioDB 2020). Ichneumonid fossils simply have not attracted much attention by palaeoentomologists (Khalaim 2008; Kopylov 2010; Kopylov et al. 2010, 2018; Antropov et al. 2014; Spasojevic et al. 2018a, 2018b; Klopstein 2021; Meier et al. 2022; Viertler et al. 2022), and extensive undescribed material of this family is present in numerous fossil collections at museums worldwide.

Even among the described fossil ichneumonids, much work remains to be done. Of the 302 known fossils, more than half were described before Henry Townes published his seminal genus-level treatments of the family (Townes 1969a, 1969b, 1970, 1971) in which he profoundly revised the genus and subfamily classification; any work from before that date thus reflects an outdated taxonomy. Unfortunately, the great majority of ichneumonid fossils have not been revised since their original description (Yu et al. 2016). Their current taxonomic placement is thus not reliable, which greatly diminishes their use for informing molecular dating studies and distorts our understanding of the evolutionary history of the group. For example, a recent review of the ten described ichneumonid species from the Green River Formation overturned the placement of four of them, while noting considerable uncertainty in the placement of the remaining ones (Spasojevic et al. 2018b).

We here make a modest contribution to improving the interpretation of the ichneumonid fossil record by redescribing and carefully illustrating 18 ichneumonid fossil species that have been described between 1910 and 1940 (Saussure 1852; Brues 1910; Cockerell 1919; Théobald 1937; Piton 1940). These fossils are from the Palaeocene Menat Formation (one species), the Late Eocene Florissant shales (12 species), the Early Oligocene Kleinkembs locality (three species), and the Late Oligocene locality in Aix-en-Provence (three species). For the majority of the revised fossils, we suggest new genus and often subfamily placement. We describe a new genus, *Armadilleon* gen. nov., for two species with remarkable sculpture. Moreover, we apply open nomenclature to express placement uncertainty and discuss its usefulness in communication with scientists outside the palaeontological community.

Materials and methods

Information about fossil ichneumonids was first obtained through the EDNA fossil insect database (Mitchell 2013: <https://fossilinsectdatabase.co.uk>), with stratum names

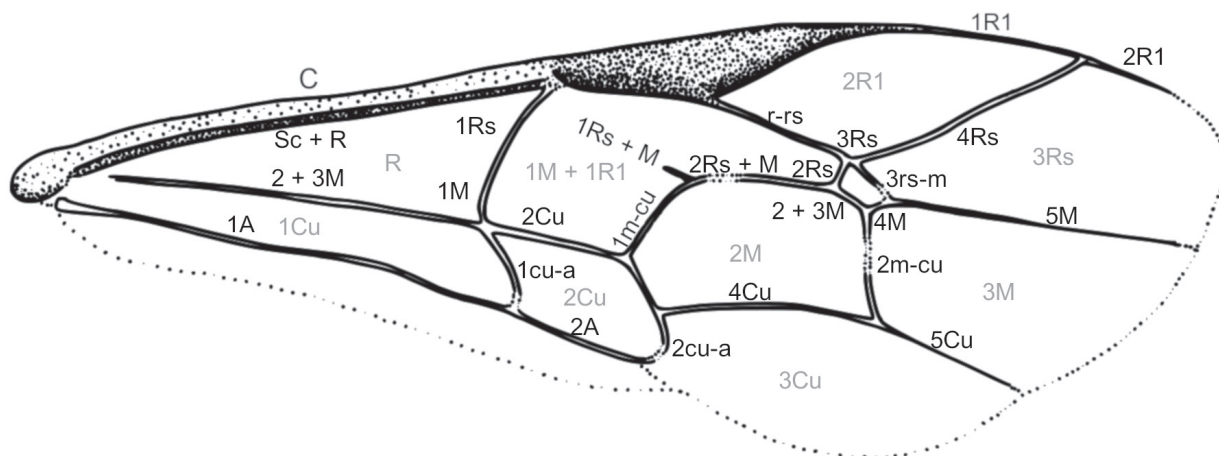
and current age estimates taken from the Paleobiology Database accessed through Fossil works (<http://fossilworks.org>). We mostly chose fossils described in one of the subfamilies of the informal but monophyletic Pimpliformes group of subfamilies (Gauld 1985; Klopstein et al. in press; Wahl 1986), but also from some other ichneumonid subfamilies. Those fossils were originally chosen for inferring the absolute age of Pimpliformes in a total-evidence dating analysis (Spasojevic et al. 2021), which revealed that a redescription and/or revision of most of them is necessary. Most fossil types could not be sent to us by mail because of restrictions by the institutions, in which cases we either visited the corresponding museums to study the type specimens or obtained high-resolution photographs. The redescribed fossils are from the Palaeontology collection at the Muséum National d'Histoire Naturelle in Paris, France (**MNHN.F**: Menat, Aix-en-Provence), the Museum of Comparative Zoology in Harvard, USA (**MCZ**: Florissant Formation), the University of Colorado Museum of Natural History in Boulder, USA (**UCM**: Florissant Formation), and the Natural History Museum in Basel, Switzerland (**NMBA**: Kleinkembs).

For the redescriptions, we followed the morphological nomenclature in Broad et al. (2018), except for wing venation characters, which follow Spasojevic et al. (2018b) (Fig. 1). If a character is visible only in the holotype or paratype, this is indicated with a #h or #p, respectively, or by the specimen numbers in the case of several paratypes or non-type specimens. Metasomal tergites and sternites are numbered and abbreviated as T1, T2, etc. and S1, S2, etc., respectively. Measurements were taken in ImageJ (Abramoff et al. 2004). Unless stated otherwise, measurements reflect the length-to-width ratio of the structure mentioned, such as pterostigma, hind femur, or T2. Ovipositor length was measured as the entire visible length of the ovipositor, and it is also expressed in relation to the length of the hind tibia or, if the hind tibia was not preserved or incomplete, to the length of the metasoma. If more than one specimen was used for measurements, the value of the holotype follows in brackets after the recorded range.

Our interpretations of the characters visible in the fossils are represented both in the descriptive text and in the form of a drawing created by overlaying high-resolution photographs of holotypes and sometimes also paratypes in Adobe Photoshop CC v. 14.2. Thicker lines are used to indicate outlines of body structures, thinner lines show characters inside these outlines, and uncertain interpretations (mostly where lines were extrapolated between clearly visible portions) are represented as dotted lines. Conspicuous sculpture of the cuticle, which in some cases was preserved in great detail, is shown in grey.

To express uncertainty in the taxonomic placement of the fossils, we made use of the open nomenclature framework (Matthews 1973; Sigovini et al. 2016), a system that has been proposed to complement the International Code of Zoological Nomenclature (Ride et al. 1999; Ferraris and Eschmeyer 2000). Following this framework, we put

A



B

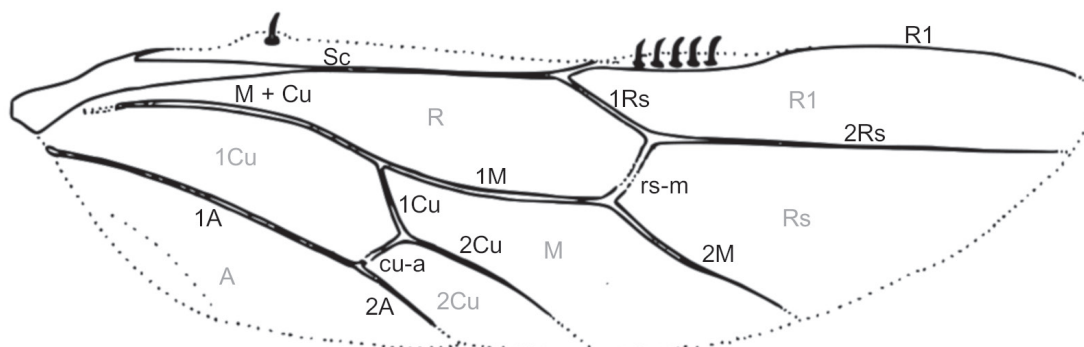


Figure 1. Wing venation nomenclature in ichneumonids. **A.** Fore wing; **B.** Hind wing. The nomenclature follows Spasojevic et al. (2018b). Figure modified after Spasojevic et al. (2018b) and Klopstein and Spasojevic (2019). Names of wing veins are given in black and of wing cells in grey.

a question mark behind an uncertain generic or subfamily placement (Spasojevic et al. 2018b; Viertler et al. 2022) and, in one case where the subfamily placement could not be established, we labelled the subfamily placement of the fossil as incertae subfamiliae.

Results

We here redescribe 18 fossil species described before 1941. The classification of most species had to be revised, with eleven out of 18 now placed in a different subfamily and twelve in a different genus (Table 1). Considerable uncertainty remains, especially for the less well-preserved fossils. For all but one species, placement in the family Ichneumonidae is unambiguous given the fore wing venation, especially the combined discocubital cell and complete 2m-cu, and the long, multi-segmented antennae. We thus only discuss the evidence for family placement if these characters are not clearly visible. The exception is *Lycorina? indura* (Theobald, 1937) comb. nov., for which wing venation is not preserved and family placement is thus ambiguous (for further details, see under that species). The fossil taxa are sorted alphabetically by subfamily and genus in which we have placed them, which in some cases deviates strongly from their original placement.

Acaenitinae? Förster, 1869

Hallocinetus? Viktorov, 1962

Hallocinetus? arvernus (Piton, 1940) comb. nov.

Fig. 2

**Phaenolobus arvernus* Piton, 1940

Material. *Holotype* (part only, MNHN.F.A57301) examined at MNHN.F.

Stratum. Menat Formation, Puy-de-Dôme, France. Late Palaeocene (Thanetian), 58.7–55.8 Ma.

Description. Sex unknown. Holotype in lateral view, rather poorly preserved, with head, outline of mesosoma and partial metasoma, partial fore wing and outline of hind legs. Body length ~10 mm.

Dark brown including wing venation, legs and posterior part of metasoma lighter brown or reddish.

Head rather large and high, compound eye about 0.7–0.8× head height in lateral view. Antennae incomplete, scape rather short. **Mesosoma** rather short, without any details preserved. **Fore wing** 7.2 mm; areolet obliquely quadrate and strongly petiolate, 2 + 3M longer than 4M; 1cu-a meeting M + Cu nearly opposite of 1M & 1Rs; 3Cu a bit longer than 2cu-a; cell 2R1 3.2× longer than wide; 2m-cu without bullae in posterior half, potentially with

Table 1. List of fossils treated and summary of taxonomic changes. Eleven subfamily and 12 generic classifications have changed (*Xylonomus* is variously treated as a subgenus or junior synonym of *Xorides* and is thus not included in this count).

New placement				Original placement		Provenance	
Subfamily	Genus	Species	Author	Subfamily	Genus	Formation	Epoch
Acaenitinae	<i>Hallocinetus?</i>	<i>arvernus</i>	(Piton, 1940)	Acaenitinae	<i>Phaenolobus</i>	Menat	Late Palaeocene
Cremastinae	<i>Dimophora?</i>	<i>longicornis</i>	(Theobald, 1937)	Campopleginae	<i>Nemeritis</i>	Aix-en-Provence	Late Oligocene
Cremastinae	<i>Dimophora?</i>	<i>wickhami</i>	(Cockerell, 1919)	Pimplinae	<i>Theronia</i>	Florissant	Late Eocene
Metopiinae	<i>Acerataspis?</i>	<i>revelata</i>	(Brues, 1910)	Pimplinae	<i>Pimpla</i>	Florissant	Late Eocene
Metopiinae	<i>Hypsicera?</i>	<i>solidata</i>	(Brues, 1910)	Orthocentrinae	<i>Camaratops</i>	Florissant	Late Eocene
Orthocentrinae	<i>Orthocentrus</i>	<i>defossus</i>	Brues, 1910	Orthocentrinae	<i>Orthocentrus</i>	Florissant	Late Eocene
Orthocentrinae	<i>Orthocentrus?</i>	<i>mortuaria</i>	(Brues, 1910)	Pimplinae	<i>Polysphincta</i>	Florissant	Late Eocene
Phygadeuontinae	<i>Armadilleon</i>	<i>morticinus</i>	(Brues, 1910)	Pimplinae	<i>Pimpla</i>	Florissant	Late Eocene
Phygadeuontinae	<i>Armadilleon</i>	<i>petrorum</i>	(Brues, 1910)	Pimplinae	<i>Polysphincta</i>	Florissant	Late Eocene
Pimplinae	<i>Lithoserix</i>	<i>antiquus</i>	(Saussure, 1852)	Pimplinae	<i>Pimpla</i>	Aix-en-Provence	Late Oligocene
Pimplinae	<i>Lithoserix</i>	<i>williamsi</i>	Brown, 1986	Pimplinae	<i>Lithoserix</i>	Florissant	Late Eocene
Pimplinae?	<i>Pimpla?</i>	<i>seyrigi</i>	Theobald, 1937	Pimplinae	<i>Pimpla</i>	Kleinkembs	Early Oligocene
Pimplinae	<i>Polysphincta?</i>	<i>inundata</i>	Brues, 1910	Pimplinae	<i>Polysphincta</i>	Florissant	Late Eocene
Lycorininae?	<i>Lycorina?</i>	<i>indura</i>	(Theobald, 1937)	Pimplinae	<i>Pimpla</i>	Kleinkembs	Early Oligocene
Tryphoninae	<i>Monoblastus?</i>	<i>senilis</i>	(Brues, 1910)	Pimplinae	<i>Pimpla</i>	Florissant	Late Eocene
Tryphoninae	<i>Zagryphus</i>	<i>tilloyi</i>	(Theobald, 1937)	Diplazontinae	<i>Promethes</i>	Aix-en-Provence	Late Oligocene
Xoridinae	<i>Xorides</i>	<i>sejugatus</i>	(Brues, 1910)	Xoridinae	<i>Xylonomus</i>	Florissant	Late Eocene
Ctenopelmatinae	<i>Parapimpla</i>	<i>rehana</i>	Theobald, 1937	Pimplinae	<i>Parapimpla</i>	Kleinkembs	Early Oligocene

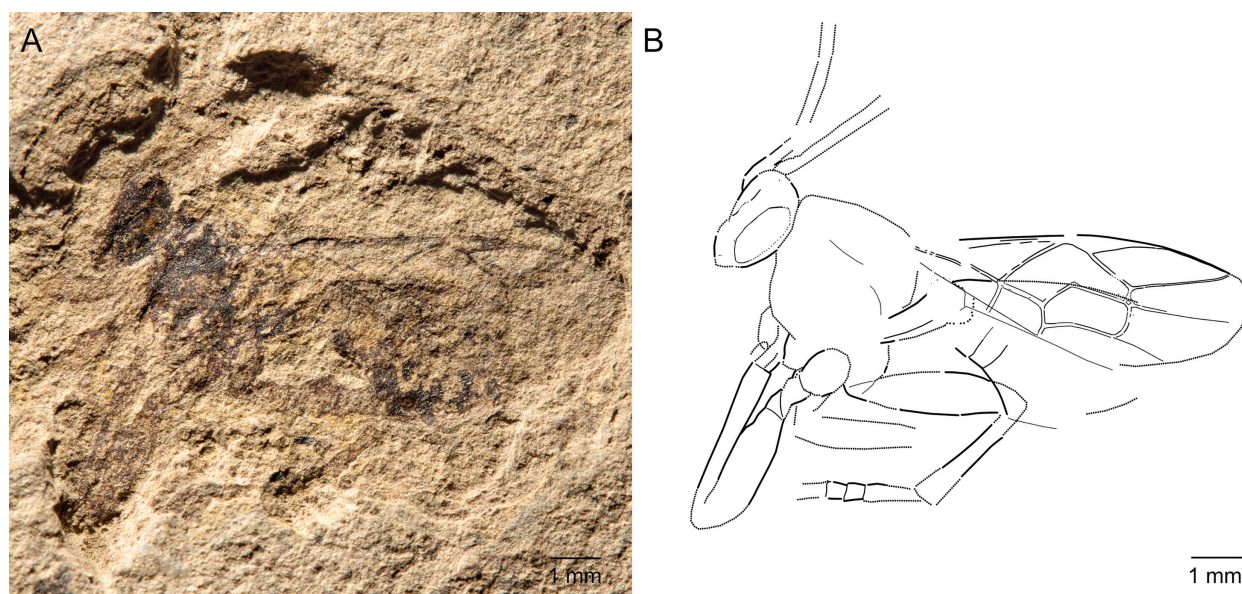


Figure 2. *Hallocinetus? arvernus* (Piton, 1940) comb. nov. **A.** Photograph of the holotype obtained from MNHN.F; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

one or two bullae in anterior half. **Hind legs** rather stout; femur 3.5×, tibia 5.2× longer than wide; hind tarsi with first segment much longer than second and third, which are about as long as wide. **Metasoma** with T1 elongate, probably with a dorso-lateral carina; sternites rather well sclerotized; tip not well preserved.

Interpretation. This is a rather poorly preserved fossil, from which not many characters can be discerned. Comparing the holotype and its high-resolution photograph with the drawing in the original description (p. 228, fig. 94, Piton 1940), we found that the latter shows a considerable amount of artistic freedom. The antennae are drawn as very short and apically expanded, while they are incomplete and parallel-sided in the fossil. The head

shows a beak-like structure not discernible clearly in the fossil and unknown in extant representatives of the subfamily, and the small eyes appear around 0.5× as long as the head length in profile, compared to 0.7–0.8× in the fossil. The areolet is depicted as being open, while we found it to be closed and strongly petiolate in the fossil. The tarsi of the fore and hind legs appear complete with claws present in the drawing, while at most the first tarsal segments are visible in the fossil. The femora of all legs are much thinner in the drawing than in the fossil, and the drawing of the posterior half of the fore wing, which largely overlaps the metasoma, contains veins not found in any ichneumonid wasp. Piton also drew the elongate-triangular hypopygium typical for the subfamily

Acaenitinae; we are more cautious, noting that the apical part of the metasoma is too poorly preserved to draw conclusions about the shape of the hypopygium. Additional characters that could help subfamily placement, such as the shape of T1 and position of its spiracle, the propodeal carination and length of the ovipositor are indiscernible. The general habitus of the fossil, especially the shape of the metasoma in profile and stout legs, does resemble Acaenitinae, but in a rather vague fashion. Other characters are somewhat at odds with this placement, although not completely so. For instance, most Acaenitinae have 2m-cu with two bullae, one in the anterior and one in the posterior half, which would disagree with the fossil; however, some genera in former Acaenitini, such as *Hieroceryx* Tosquinet, 1896 and *Prosacron* Townes, 1971, have both bullae in the anterior half and separated by a very short tubular part of the vein. Moreover, *Phaenolobus* and *Phorotrophus* Saussure, 1892 can in fact have a single bulla, in the former located in the dorsal half of 2m-cu. However, all former Acaenitini have an open areolet, while a closed and petiolate areolet occurs only in the former tribe Coleocentrini, which has turned out paraphyletic with respect to the former Acaenitini (Wahl and Gauld 1998; Quicke et al. 2009; Klopstein et al. 2019; Spasojevic et al. 2021). The characters for generic placement within the former Coleocentrini, such as the shape of the clypeus, size and shape of the hypopygium and modifications on tarsal claws (Townes 1971) are not visible in the fossil. Since we also have no character evidence for placing the fossil in a different subfamily, we tentatively place it in *Hallocinetus* Viktorov, 1962, to which it superficially resembles in the shape of the anterior margin of the mesoscutum and stout and large hind legs. However, we acknowledge the uncertainty in its placement by placing a question mark after the genus and subfamily names.

Cremastinae Förster, 1869

Dimophora? Förster, 1869

Dimophora? *longicornis* (Theobald, 1937), comb. nov.

Fig. 3

**Nemeritis longicornis* Theobald, 1937

Material. *Holotype* (part only, MNHN.F.B24398) examined at MNHN.F.

Stratum. Aix-en-Provence, Bouche-du-Rhône, France. Late Oligocene (Chattian), 28.4–23.0 Ma.

Description. Female. Lateral aspect of head, most of both antennae, mesosoma, both fore wings, part of fore and hind legs, and metasoma including ovipositor with sheaths preserved. Body length ~5.3 mm.

Mostly black in colour, with some reddish colouration on metasoma and dark brown to orange-brown legs, wing veins brown.

Head rather short, with eyes not clearly outlined but might be rather prominent. **Antennae** with scape and pedicel short, with at least 24 flagellomeres, but tips broken.

Mesosoma not well preserved; mesoscutum conspicuously elongate, notauli probably present, as is epicnemial carina and probably posterior transverse carina of mesosternum; propodeum evenly rounded, carination unclear given bad preservation. **Fore wings** 3.1 mm, well preserved; pterostigma broad triangular (3.1×) with light base; areolet closed, quadrate and a bit oblique; cell 2R1 (radial cell) short (2.5×), ending rather distant from tip of the wing; 2m-cu quite short, forming inner angle greater than 90° with 4Cu, with a single broad bulla; 1cu-a meeting M + Cu opposite of 1M & 1Rs; 3Cu shorter than 2cu-a; vein 1M & 1Rs a bit bowed; r-rs shorter than 2Cu. **Legs** partially preserved; fore coxa, trochanters, base of femur preserved, dark

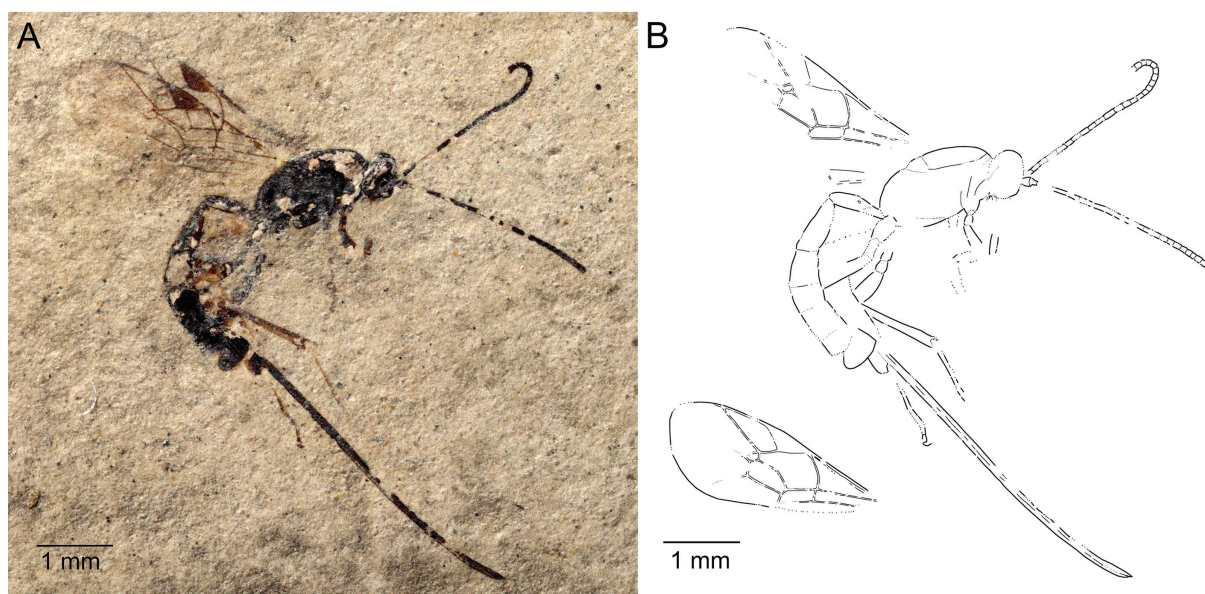


Figure 3. *Dimophora*? *longicornis* (Theobald, 1937) comb. nov. **A.** Photograph obtained from MNHN.F; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

brown; mid leg weakly indicated; hind legs both partially preserved, including elongate hind coxa; hind femur apparently toothless, dimensions unclear, dark brown or orange (the latter colouration might come from overlaying sternites instead); hind tibia very long and slender (10×), brown on anterior, orange on posterior half, potentially showing a deep emargination at apex indicative of spurs present in membranous area separate from tarsus (unique character for Cremastinae, but interpretation in fossil not unequivocal); tarsi elongate, one partial claw might show pecten, but interpretation rather uncertain. **Metasoma** compressed from T3 or T4, mostly black, with reddish colouration on laterotergite 2 and partly on T3 and T4; T1 petiole-shaped, narrow and long (4.7×), probably with glymma, spiracle slightly behind middle; T2 as long as T1, laterotergite might be indicated by red colouration; T3 and following shorter, T7 quite long, not distinctly shorter than T6. Ovipositor preserved with sheaths, very long, 4.4 mm, about 3.3× as long as hind tibia, a bit bowed downwards towards tip.

Interpretation. The reason that we have covered this species, which was originally described in the genus *Nemeritis* (Campopleginae), is a remark by Theobald in the original description (Theobald 1937) that this species could be identical with *Pimpla renevieri* Meunier, 1903, which was later repeated by Menier et al. (2004) when he compiled a list of fossil ichneumonids. Based on this list, Yu and Horstmann (Yu et al. 2012, 2016) catalogued *N. longicornis* as a synonym of *P. renevieri*. We could not cover the latter species because the type could not be located. But we studied the former and concluded that several characters support a placement in the subfamily Cremastinae: the narrow T1 in the shape of a petiole, compressed metasoma, fore wing with a short and wide pterostigma and cell 2R1, 3Cu shorter than 2cu-a, hind tibia very long and slender, ovipositor much longer than metasoma. The first set of characters are also present in Campopleginae, but the broad pterostigma and, to a lesser extent, very long ovipositor point to Cremastinae. Given the large and only slightly oblique areolet, the fossil might belong to the genus *Dimophora*, but crucial characters for generic placement such as the thyridiae are unfortunately not visible. The affinity of the fossil with *Dimophora* was also supported in the recent total-evidence dating analysis (see supplementary file S12 in Spasojevic et al. 2021), which however included only limited sampling of Cremastinae and Campopleginae. We therefore remove it from synonymy with *P. renevieri* and tentatively place it in the genus *Dimophora*.

Cremastinae Förster, 1869

***Dimophora*? Förster, 1869**

***Dimophora*? *wickhami* (Cockerell, 1919), comb. nov.**

Fig. 4

**Theronia wickhami* Cockerell, 1919

Material. Photograph examined of the holotype (part, PALE-3915 and counterpart, #UCM8604), obtained from the MCZ and UCM, respectively.

Stratum. Wilson Ranch, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 My.

Description. Female. Rather well-preserved fossil. Part with dorsal and posterior aspect of head, antennae almost complete, mesosoma including propodeum and details of propodeal carination, weak impressions of fore wings with only few veins visible, incomplete hind legs, and dorsal aspect of metasoma with ovipositor and ovipositor sheaths. Counterpart with ventral aspect of head with antennae showing flagellomeres, mesosoma, weakly but almost completely preserved impressions of fore wings, partial mid and almost complete hind legs, and ventral aspect of metasoma with ovipositor sheaths. Body length 8.5 mm.

Dark brown on head, mesosoma and first metasomal segment, lower part of face possibly lighter coloured (but could be artefactual), antennae lighter brown, wing venation very light, legs and metasoma from T2 or T3 orange.

Head with parallel-sided inner eye margins; mandibles with two teeth; clypeal sulcus weakly developed; occipital carina strong and probably complete and evenly rounded dorsally. **Antennae** 5.4 mm, with scape a bit longer than wide and pedicel short; with about 31 flagellomeres, these transverse except for most basal ones. **Mesosoma** showing deep median sternal groove, probably complete epicnemial and complete posterior transverse carina of mesosternum. Metapleuron with submetapleural carinae shown as two longitudinal lines; propodeum with complete propodeal carination. **Fore wing** 5.9 mm, with large and slightly oblique areolet, vein 2m-cu meeting M close to its outer corner (4M very short), number of bullae unclear; 1cu-a meeting M + Cu opposite of 1M and inclivous; 3Cu about as long as 2cu-a; cell 2R1 2.6× longer than wide. **Legs** rather slender; hind femur 3.6×, hind tibia 6.2× longer than wide, without ventral tooth. **Metasoma** slender, apical segments compressed; T1 petiolate, narrow at base and expanded from about mid-length; S1 reaching to about 0.65 of length of T1, probably with laterotergites parallel and not meeting ventrally at midline; T2 about 2.2× longer than basally wide, with narrow laterotergite visible; following tergites transverse; hypopygium inconspicuous. Ovipositor 1.5 mm, around 1.7× as long as hind tibia, straight, enclosed by sheaths.

Interpretation. The petiolate T1 excludes the subfamily Pimplinae and thus the genus *Theronia*, and the compressed metasoma and complete posterior transverse carina of mesosternum carina point to either Campopleginae or Cremastinae. The clypeus separated from the lower face by a groove and the rather stout fore wing cell 1M+1R1 point to the latter. Within Cremastinae, the large areolet is reminiscent of *Dimophora*, even though it is slightly oblique. A recent revision of the Australian members of the genus (Klopfstein 2016) expanded the generic definition to also include larger representatives, with fore wing lengths of up to 7.1 mm found. As the areolet does not entirely match extant *Dimophora* and characters excluding some other genera in the subfamily are not visible, we tentatively place the fossil in this genus. It can be distinguished from all extant representatives of the genus

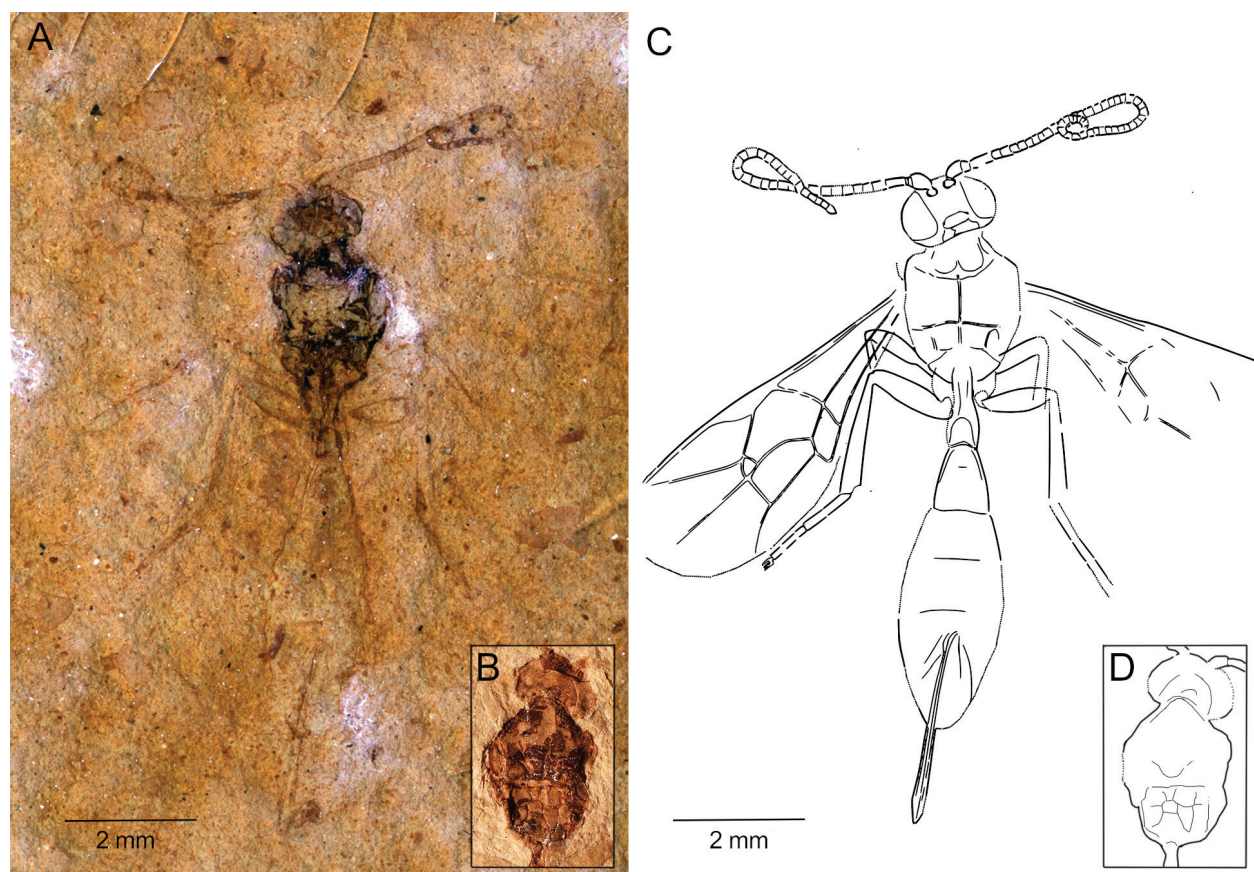


Figure 4. *Dimophora? wickhami* (Cockerell, 1919) comb. nov. **A.** Photograph of the counterpart of the holotype obtained from the UCM; **B.** Photograph of the propodeum from the part of the holotype obtained from the MCZ; **C.** Our interpretative drawing of the counterpart; **D.** our interpretative drawing of the propodeum of the part. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

by fore wing vein 2m-cu originating close to the distal end of the areolet, from *D. antiqua* (Brues 1910; also from the Florissant shales) by the larger areolet and less stout fore wing, from *D. fumipennis* (Theobald 1937; Oligocene of Aix-en-Provence) by the hyaline wings and longer ovipositor, and from the here revised *D.? longicornis* by the much shorter ovipositor, more slender pterostigma and different coloration.

Metopiinae Förster, 1869

Acerataspis? (Uchida, 1934)

Acerataspis? revelata (Brues, 1910), comb. nov.

Fig. 5

**Pimpla revelata* Brues, 1910

Material. Photographs examined of the holotype (#PALE-2158, referred to as #h) and of another specimen (#PALE-2159), which Brues (1910) placed tentatively in the same species, but expressing doubts; obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Sex unknown in holotype, second specimen is a female; we support the notion that the two

specimens belong to the same species and base our description on both of them. Holotype showing ventral aspect; specimen #PALE-2159 in lateral (head and mesosoma) and dorsolateral (metasoma) aspect. Holotype with part of head, base of antennae, mesosoma, fore and most of hind wings, partial hind leg and segments on to partial five of metasoma. Specimen #PALE-2159 with head, almost complete antennae, mesosoma, fore wings, hind legs including tarsi and complete metasoma. Body length 9 mm (#PALE-2159).

Fragments of dark colouration on most of body including T1, T2–T5 with orange or reddish colouration and lighter hind margins.

Head with face apparently protruding (#PALE-2159), eyes smaller than usual in ichneumonids. **Antennae** with scape short and ovoid (#h), with more than 30 mostly transverse flagellomeres (#PALE-2159). **Mesosoma** rather short, with rather high and short pronotum with strong epomia; mesopleuron with strong but probably interrupted epicnemial carina curving anteriorly at mid height of pronotum (#PALE-2159), complete ventrally and dipping into medial sternal groove (#h); at least mesosternum, mesopleuron and metapleuron covered in strong and very dense punctures (#h). Propodeum with pleural carina complete (#PALE-2159), remaining carination unclear but probably with some portion of apical transverse

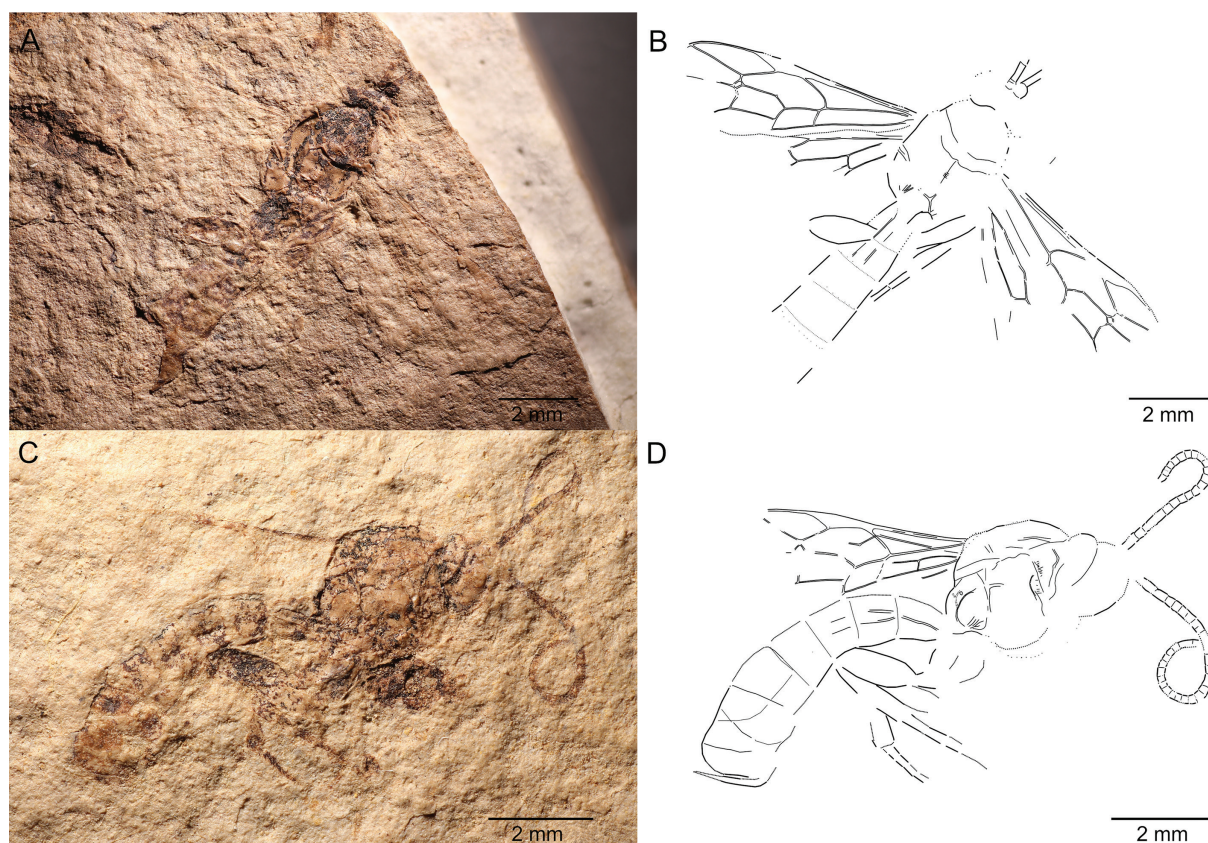


Figure 5. *Acerataspis? revelata* (Brues, 1910), comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the holotype; **C.** Photograph of the paratype obtained from the MCZ; **D.** Our interpretative drawing of the paratype. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

and lateral longitudinal carina present (#PALE-2159); metapleuron rather high, with several diagonal carinulae starting at lower hind corner of metapleuron (visible in both specimens, in #h on both sides from ventral). **Fore wing** 6.4 mm (#PALE-2159 5.0 mm), with areolet oblique-quadrate and strongly petiolate; pterostigma 4.5× longer than wide; cell 2R1 of average proportions (3×); vein 2m-cu with strong curve and one wide bulla anteriorly; 1cu-a meeting M + Cu far distally of 1M; 3Cu a bit longer than 2cu-a; 1M distinctly curved at base. **Hind wing** with cell 1Cu rather narrow and with subparallel sides; vein 1Rs a bit longer than rs-m; 1Cu about 1.5 times longer than cu-a. **Hind legs** with femur short and thick (#p 2.7×); hind tibia (#p 4.5×) with strong spines on outer side, mostly lightly coloured with dark base and apex (#PALE-2159). **Metasoma** rather short and stout; T1–T3 with two subparallel dorsal carinae; last tergites and last sternite enlarged; short ovipositor indicated, probably not much longer than metasoma height at apex (#PALE-2159).

Interpretation. Brues (1910) interpreted the holotype as showing a dorsal aspect, which probably led him to miss some crucial characters. The stout body, protruding face, short flagellomeres, and carinae on T1–T3 place these fossils in the subfamily Metopiinae. The extant genus *Acerataspis* seems a good match in terms of tergite

carination, carinulae low on metapleuron and closed areolet, but the latter is much larger in the extant species and the antenna much more elongate; we thus place it in this genus with a question mark.

Metopiinae Förster, 1869

Hypsicera? Latereille, 1829

Hypsicera? solidata (Brues, 1910), comb. nov.

Fig. 6

**Camerotops solidatus* Brues, 1910

Material. Photographs of the holotype (part only, #PALE-2239) obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Female. Holotype in ventro-lateral view, with nearly complete antennae, outline of head, details of mesosoma, one fore wing, partial fore and mid and nearly complete hind legs, and metasoma with ovipositor sheaths. Body length 6.1 mm.

Black or dark brown on head, mesosoma and T1, dark brown on antennae, red on hind legs and T2 until end of metasoma, orange on fore and mid legs; wing venation very light.

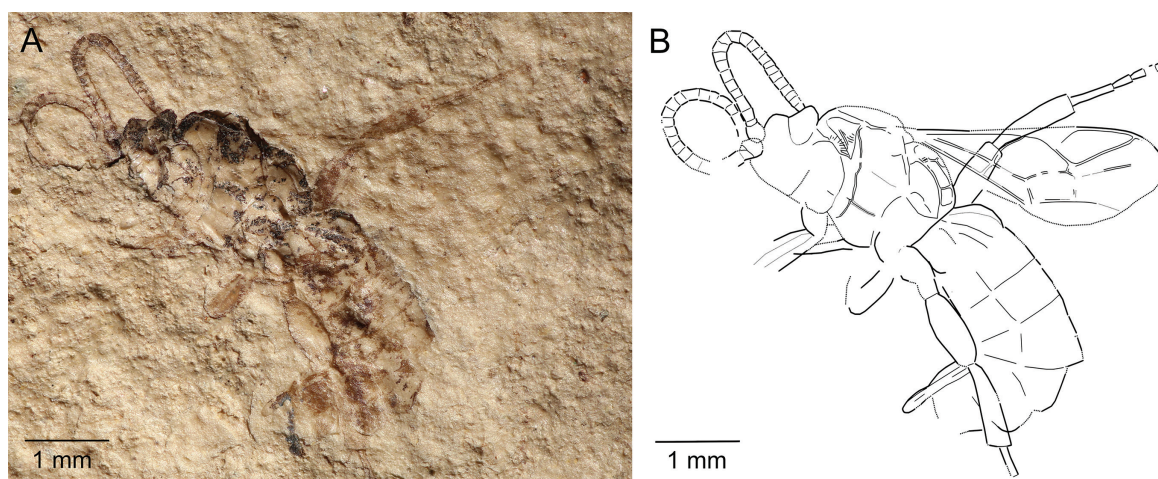


Figure 6. *Hypsicera? solidata* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

Head with face bulging, eye rather small (if interpreted correctly). **Antennae** stout, with about 23 flagellomeres; scape about $1.1\times$ as long as wide; first flagellar segments subquadrate, following transverse. **Mesosoma** short and compact; pronotum with long epomia and parallel wrinkles; mesopleuron with epicnemial carina strong and reaching at least to half the height of the pronotum, probably more; with deep mesosternal scrobe and possibly indication of sternaulus (which could be an artefact), and with very closely spaced, parallel wrinkles on most of its surface. Metapleuron large, higher than wide; propodeum rather short, with pleural, lateral longitudinal, and a low-sitting posterior and probably also anterior transverse carina complete, delimiting areas; median longitudinal carina unclear. **Fore wing** 3.0 mm, with areolet probably open; 1cu-a meeting 2Cu at same position as 1M; cell 2R1 short ($2.1\times$). **Legs** very stout, hind femur $2.5\times$ and hind tibia $3.7\times$ as long as wide. **Metasoma** short, with both strongly sclerotized tergites and at least partial sternites; T1 about $1.6\times$ longer than wide, expanding towards apex, with distinct longitudinal lines which probably represent the median dorsal and dorsolateral carinae; T2 and following transverse; T6 and T7 of about same length as previous ones. **Ovipositor** short, around 1 mm long, and around as long as hind tibia, internal portion longer than sheaths.

Interpretation. The bulging face, long malar space, short flagellar segments and thickened legs indicate either Metopiinae or the *Orthocentrus* genus-group of Orthocentrinae. Brues (Brues 1910) placed the specimen in the latter, but the short scape and the presence of a clear epomia and costula clearly point to the former. Brues also stated that the “abdomen flaked off in the specimen” and did not make a decision about the sex; we note that the ovipositor sheaths are clearly visible, even though its base is crossed by a hind leg. Within Metopiinae, the placement is more difficult, but *Hypsicera* and *Exochus* Gravenhorst, 1829 seem a good match given the similarity of the propodeal carination, bow in 1M of the fore

wing and long T7. If we interpreted the head correctly, the small eyes and the bulging of the face closer to the antennal sockets correspond more to *Hypsicera*. However, the longer and stouter ovipositor sheaths indicate *Exochus*, while the fore wing venation is typical for *Exochus* and only rarely seen in *Hypsicera*. Thus, even though we place the fossil in *Hypsicera*, this placement should be seen as preliminary with *Exochus* as a valid alternative.

Orthocentrinae Förster, 1869

Orthocentrus Gravenhorst, 1829

**Orthocentrus defossus* Brues, 1910

Fig. 7

Material. Photographs of the holotype (part only, #2238) obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Probably female. Holotype in ventro-lateral view with metasoma bent under the body, with nearly complete antennae, head, mesosoma, both fore and one hind wing and nearly complete hind legs. Overlapping metasoma, legs and fore wing make interpretation partially difficult. Hairs on wings and hind legs very well preserved. Body length 8.2 mm.

Black or dark brown on head, mesosoma and T1; dark brown on antennae, base of hind coxa, hind femur and outer side of hind tibia, red on remainder of hind legs and T2 until end of metasoma; wing venation dark brown to orange.

Head with face bulging, eye rather small, malar space very long and with a deep groove. **Antennae** stout, with at least 20 flagellomeres, scape elongate, $1.8\times$ as long as wide. **Mesosoma** short and stout; pronotum with a short lower part of epomia and parallel wrinkles posteriorly, which are mirrored on mesopleuron; epicnemial carina might be present ventrally (or this is the impression of a fore coxa). Metapleuron rather high, with what seems like

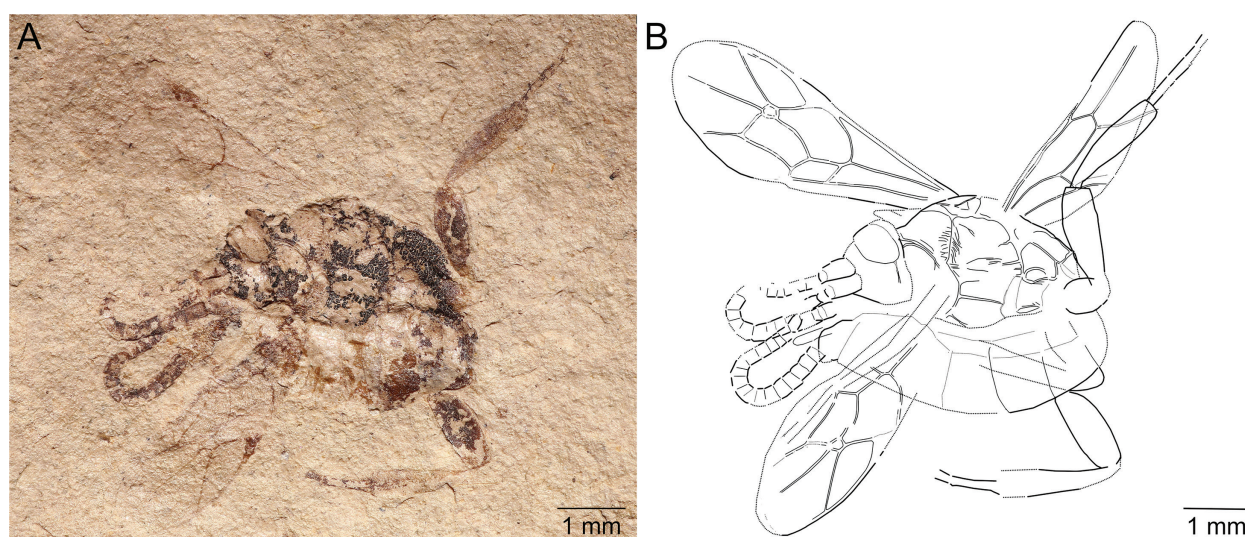


Figure 7. *Orthocentrus defossus* (Brues, 1910) **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations

strong juxacoxal carina visible on both sides; propodeum with pleural and a low apical transvers carina visible, remainder unclear. **Wings** evenly hairy, fore wing 4.5 mm, with areolet rather large and pentagonal, receiving 2m-cu close to its outer corner, 4M thus very short; 1cu-a meeting 2Cu distinctly after 1M; 3Cu a little shorter than 2cu-a; cell 2R short and stout (2.6×). Hind wing with 1Cu almost 4× longer than 1cu-a, 2Cu rather weak, 1Rs somewhat longer than rs-m. Hind **legs** rather stout, femur 2.5× and tibia 4.5× longer than wide. **Metasoma** poorly preserved, but last segments seemingly compressed and tergites transversal. **Ovipositor** sheaths about as long as height of tip of metasoma.

Interpretation. We agree with the original placement of this species. Despite the difficulties in interpreting the ventral part of the mesosoma and the metasoma, the characters visible on the head and wings allow confidence in placing this species in the *Orthocentrus* genus-group of Orthocentrinae. Character evidence for this placement are the bulging face, long malar space, and shortened antennae with

an elongate scape. Within the group, only *Orthocentrus* contains species with such a large, pentagonal areolet, and the malar groove and 1cu-a meeting 2Cu distinctly after 1M are a further good match with this genus.

Orthocentrinae Förster, 1869

Orthocentrus? Gravenhorst, 1829

Orthocentrus? *mortuaria* Brues, 1910, comb. nov.

Fig. 8

**Polysphincta mortuaria* Brues, 1910

Material. Photographs of the holotype (part, #PALE-2134) obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Female. Holotype in lateral view, with head and a few segments of antennae, mesosoma, fore

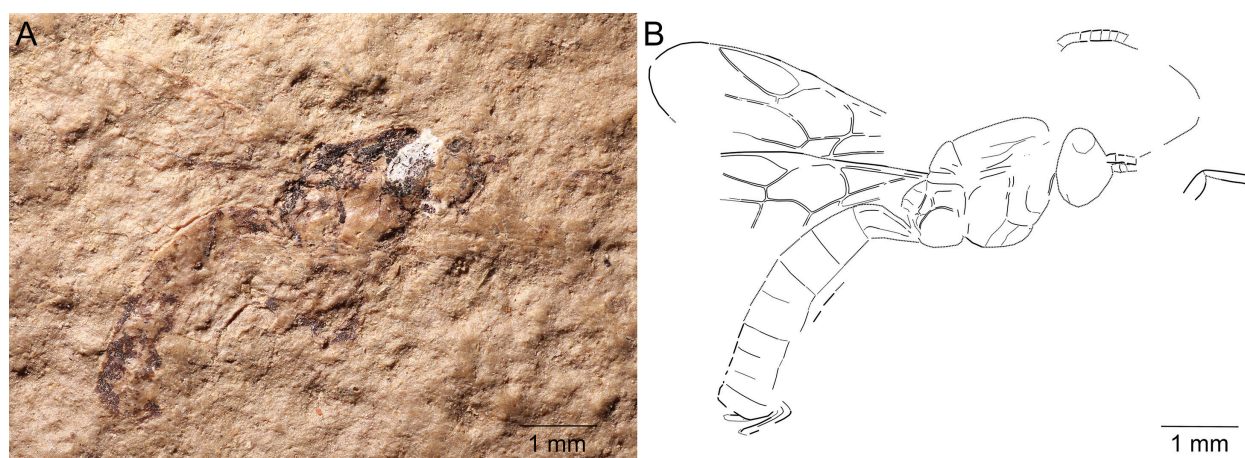


Figure 8. *Orthocentrus*? *mortuaria* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

wings, and metasoma with ovipositor, all rather poorly preserved; legs and hind wings missing. Body length 6.3 mm.

Head light brown, mesosoma black with light brown portions, metasoma mostly light brown on T1–T3, remainder dark brown (the light brown colouration could actually be a preservation artefact: it shows different sculpture and its texture is repeated on the rock outside the body).

Head with face bulging below antennal sockets, with eye very small, with very long malar space. **Antennae** more than 3.9 mm, incompletely preserved. **Mesosoma** rather short, poorly preserved, unclear if with epicnemial carina. Propodeum with pleural carina and lateral longitudinal carina, maybe also with posterior transverse carina. **Fore wing** 4.1 mm, rather short and stout, with areolet open and vein 2Rs longer than 3M; vein 1cu-a strongly inclivous meeting M + Cu clearly distally of 1M; cell 2R1 only 2.9× longer than wide. **Metasoma** compressed from about fourth segment; T1 short and tapering towards base, with latero-median carinae converging on basal half, parallel on apical half; T2 and following tergites transverse. Ovipositor 0.5 mm.

Interpretation. The bulging face with small eyes and long malar space are only found in Metopiinae and Orthocentrinae, and wing venation and ovipositor shape point to the latter. Given the size, 1cu-a meeting M + Cu clearly distally of 1M, and possible presence of the lateral portion of the epicnemial carina, *Orthocentrus* is the best guess, but the poor preservation of the fossil precludes a certain placement.

Phygadeuontinae Förster, 1869 (*sensu* Santos (2017))

Armadilleon gen. nov.

<http://zoobank.org/63B3D98F-89CF-4CAE-B2EE-3AE254F5649E>

Type species. *Armadilleon morticinus* (Brues 1910).

Etymology. This genus is named after the heavily armoured armadillo due to its unique, heavy sculpture.

Diagnosis. The placement within the subfamily Phygadeuontinae is evident from the strong and long sternaulus, which posteriorly ends above the mid-height of the hind coxa, the probably pentagonal areolet, T1 in the shape of a petiole, and the ovipositor clearly protruding from the metasomal apex and without a dorsal subapical notch. In strong and wavy structure on the mesosoma, *Armadilleon* resembles several described phygadeuontine genera, such as *Astomaspis* Förster, 1869 and *Bentyra* Cameron, 1905 from the subtribe Chiroticina, *Diaglyptidea* Viereck, 1913 and *Acrolyta* Förster, 1869 from Acrolytina, and *Brachypimpla*, Strobl 1902 from the subtribe Mastrina; it also resembles some undescribed tropical phygadeuontines with similar sculpture (Mabel Alvarado pers. comm.). In the fore wing venation, propodeal carination, clypeus shape in the profile and shape of the ovipositor, *Armadilleon* is very similar to *Brachypimpla*, but it differs from it in the more extensive longitudinal striate sculpture on the mesosoma that is additionally

present on the mesoscutum, anterior half of the propodeum and gena, absent notauli and lack of ramulus in the fore wing, stouter legs, and the flatter T1 in the profile. In addition, *Armadilleon* has longer metasoma as the posterior tergites are exposed, while they are retracted below each other in *Brachypimpla*. However, our interpretation of the metasoma should be regarded with caution, as the tergites might have been pushed out and distributed evenly during the preservation process.

Description. **Head** above and possibly on front with conspicuous, nubby sculpture. **Mesosoma** with mesoscutum with strong and dense punctures, which fuse into parallel carinae towards the posterior end; mesopleuron and propodeum nearly completely covered with strong striae forming wavy patterns; sternaulus on mesopleuron strong, reaching almost to its end. Propodeum with strong carinae enclosing area petiolaris, areal lateralis, area basalis, and at least first and second lateral areas. **Fore wing** areolet pentagonal. **Metasoma** with T1 broad at apex and strongly tapering towards the narrow base, humped around middle and thus forming a petiole and postpetiole. **Ovipositor** clearly protruding from metasoma by about the length of the hind tibia, without a dorsal notch.

Circumscription. *Armadilleon* includes *A. morticinus* and *A. petrorum*, both from the Oligocene Florissant formation.

Armadilleon morticinus (Brues, 1910), comb. nov.

Fig. 9

**Pimpla morticina* Brues, 1910

Material. Photographs examined of the holotype (#PALE-2156) and paratype (#PALE-2157) females (parts only), obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. **Holotype** and **paratype** (both females) very well preserved, including carination and sculpture of mesosoma, with fore wings, partial hind wings, some almost complete legs and ovipositor including sheaths. Both holotype and paratype with remains of dark colouration on most body parts, but overall, colouration not well preserved; metasoma possibly orange or red from T2 (#p, somewhat uncertain). Body length 10.4 mm (#p 10.1 mm).

Head short, only partly preserved, one lateral ocellus and strong sculpture on frons visible (#h). **Antennae** rather stout, scape about 1.6 times longer than wide, pedicel short, about 24 flagellomeres, basal ones subquadrate, becoming quadrate and transverse towards apex (#h). **Mesosoma** strongly sculptured; pronotum about 0.7× as long as high, with longitudinal rugae and with epomia strong, angled forward above; mesoscutum with strong punctures, in posterior half increasingly arranged in longitudinal lines; notauli absent; scutellum and post-scutellum slightly convex; mesopleuron with very strong

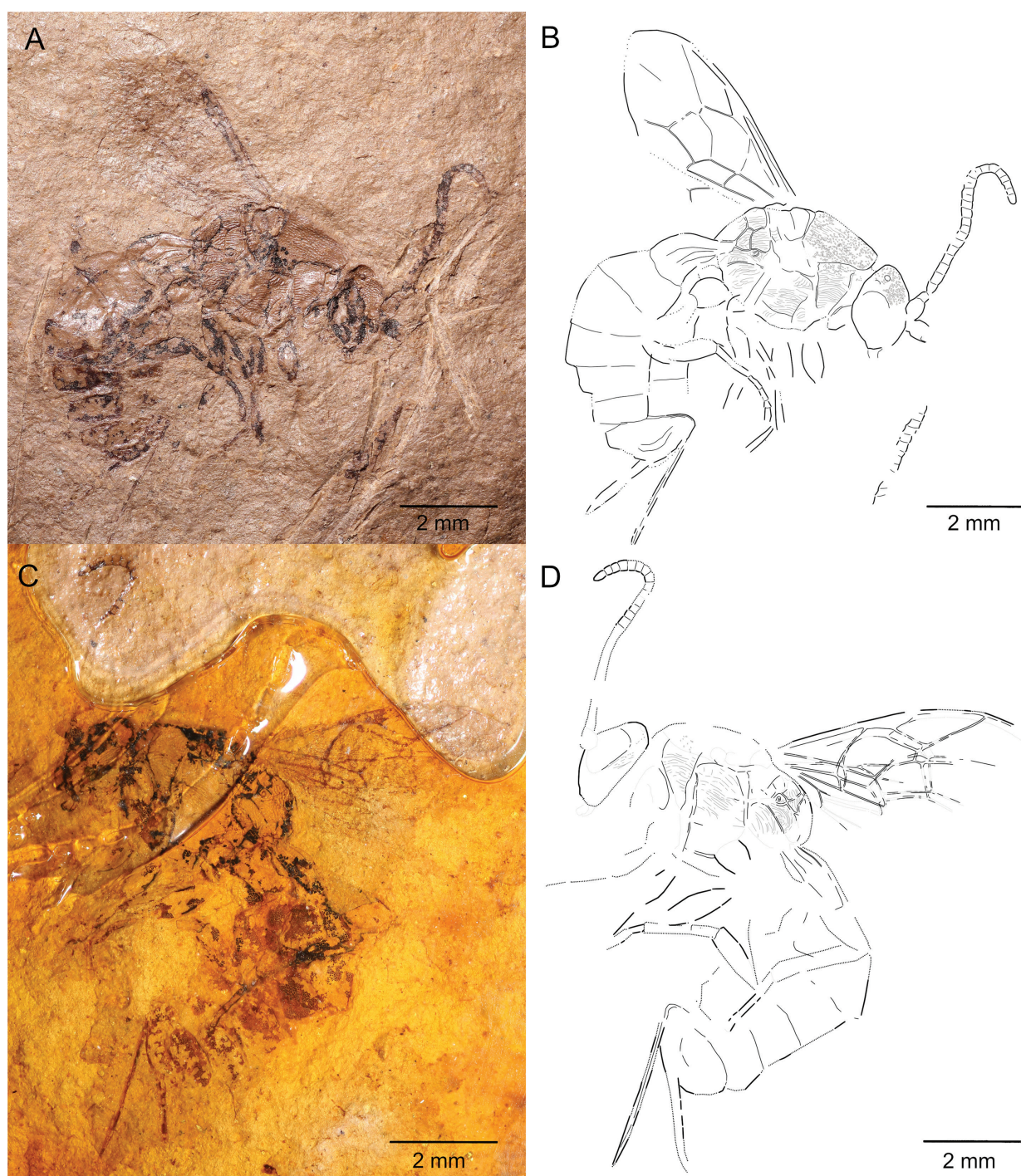


Figure 9. *Armadilleon morticinus* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the holotype; **C.** Photograph of the paratype obtained from the MCZ; **D.** Our interpretative drawing of the paratype. Thicker black lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations. Grey lines and circles show conspicuous sculpture of the cuticle.

and conspicuous longitudinal carinae forming wave-like patterns; sternaulus strong and reaching posterior end in sinusoid curve; epicnemial carina long and curving towards front end of mesopleuron at around mid-height of pronotum. Propodeum with all three lateral, three pleural and petiolar areas enclosed by carinae, basal area and areola fused (or basal area very short); pleural carina

complete; propodeal spiracle slightly elliptic; propodeum covered by strong rugae forming wavy patterns, unpunctured. **Fore wing** 5.2 mm (#p 5.3 mm), venation only partially preserved, brown or dark brown; areolet probably closed and pentagonal (cf. #p); 1cu-a meeting M + Cu opposite of 1M; 3Cu a bit longer than 2cu-a; hind wing reconstruction difficult. **Legs** rather stout, hind leg with

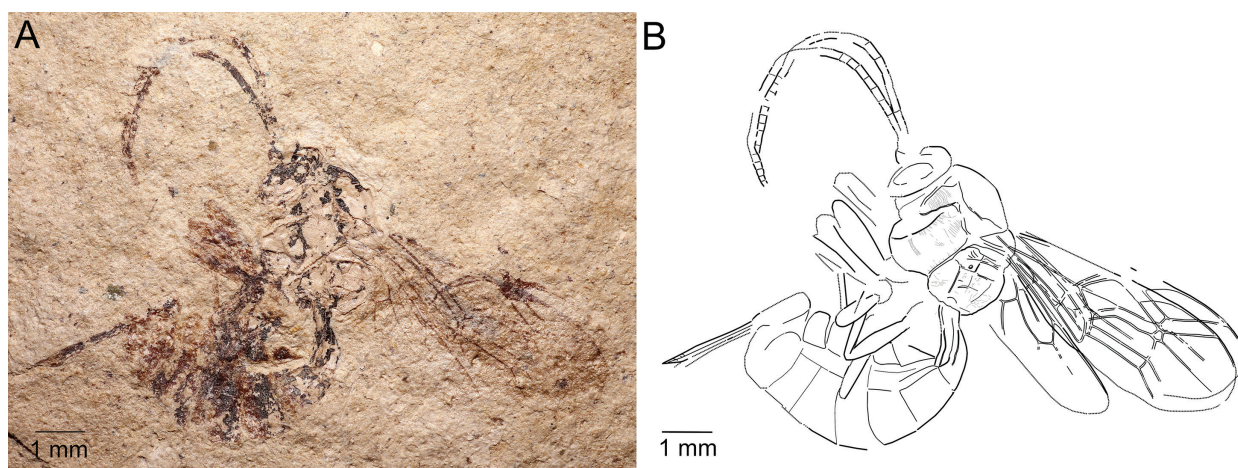


Figure 10. *Armadilleon petrurum* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil. Thicker black lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations. Grey lines and circles show conspicuous sculpture of the cuticle.

femur less than $3\times$ longer than wide. **Metasoma** dorso-ventrally depressed or with apical segments somewhat compressed; T1 broad posteriorly, but strongly narrowed towards base, forming petiole, $1.6\times$ as long as apically wide; latero-median and dorso-lateral carinae present on entire length; T2 and following transverse; T7 not much shorter than T6. **Ovipositor** 2.8 mm (#p 3.2 mm); ovipositor sheaths about 1.6 mm (#p 1.7 mm), as long as hind tibia; ovipositor straight, parallel-sided, without dorsal subapical notch, with weak nodus and potentially some ridges apically on lower valve (#p).

Interpretation. For subfamily placement and genus diagnosis, see description of the genus above. For distinguishing features from the other species in the genus, *A. petrurum*, see under that species.

Armadilleon petrurum (Brues, 1910), comb. nov.

Fig. 10

**Polysphincta petrurum* Brues, 1910

Material. Photographs of the holotype (part, #PALE-2136) obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Female. Holotype in lateral view with nearly complete antennae, partial head, mesosoma detailing sculpture, both fore and hind wings, at least parts of all legs, and metasoma with ovipositor with sheaths. Body length 9.2 mm.

Mostly black, antennae and wing venation dark brown, T2 and following with broad, reddish apical bands, legs orange to dark brown.

Head very short, eyes of normal dimensions. **Antennae** 6.6 mm, with at least 24 (probably about 32) flagellomeres, basal segments elongate, apical segments transverse. **Mesosoma** with strong sculpture; pronotum with epomia strong

and with numerous longitudinal wrinkles especially along hind margin which continue on mesopleuron; epicnemial carina complete to about mid-height of pronotum; sternaulus long and strong, with transverse carinulae; sculpture of mesopleuron dominated by longitudinal carinulae on much of its surface. Metanotum rather short and high, with some carinulae visible on lower part. Propodeum with pleural carina, indications of lateral and lateromedian longitudinal carinae, anterior transverse and at least lateral portions of posterior transverse carinae, with rugulo-punctate sculpture between the carinae. **Wings** evenly and densely hairy; fore wing 5.8 mm, with pentagonal areolet; 2m-cu probably with a single bulla; 1cu-a meeting M + Cu opposite of 1M; cell 2R1 $3.0\times$ longer than wide. Hind wing with 1Rs longer than rs-m and 1Cu longer than Cu-a; M + Cu probably strongly curved in apical half. **Legs** somewhat hard to tease apart, but of rather average dimensions; hind femur $4.5\times$ longer than wide. **Metasoma** seems somewhat compressed towards apex; T1 clearly elongate and petiolate, with strong lateral and dorsolateral carinae, remaining tergites transverse; sternites rather strongly sclerotized; hypopygium short and inconspicuous. Ovipositor 2.2 mm, $0.4\times$ as long as metasoma, straight and parallel-sided, its ventral valve with indications of oblique ridges close to apex, without dorsal subapical notch.

Interpretation. The conspicuous sculpture visible on the propleuron, mesoscutum, mesopleuron and propodeum, together with the subfamily characteristics (strong sternaulus, petiolate T1 and pentagonal areolet), firmly place this species in the new genus *Armadilleon*. Additional similar features between the current and the type species of the genus, *A. morticinus*, include the short head, carination of propodeum, and ovipositor length and shape. The two species differ by the shape of the antennae, which are much stouter in *A. morticinus*, the different colouration of the metasomal tergites, and fore wing vein 1cu-a meeting M + Cu somewhat distally of 1M in the type species and opposite of 1M in *A. petrurum*.

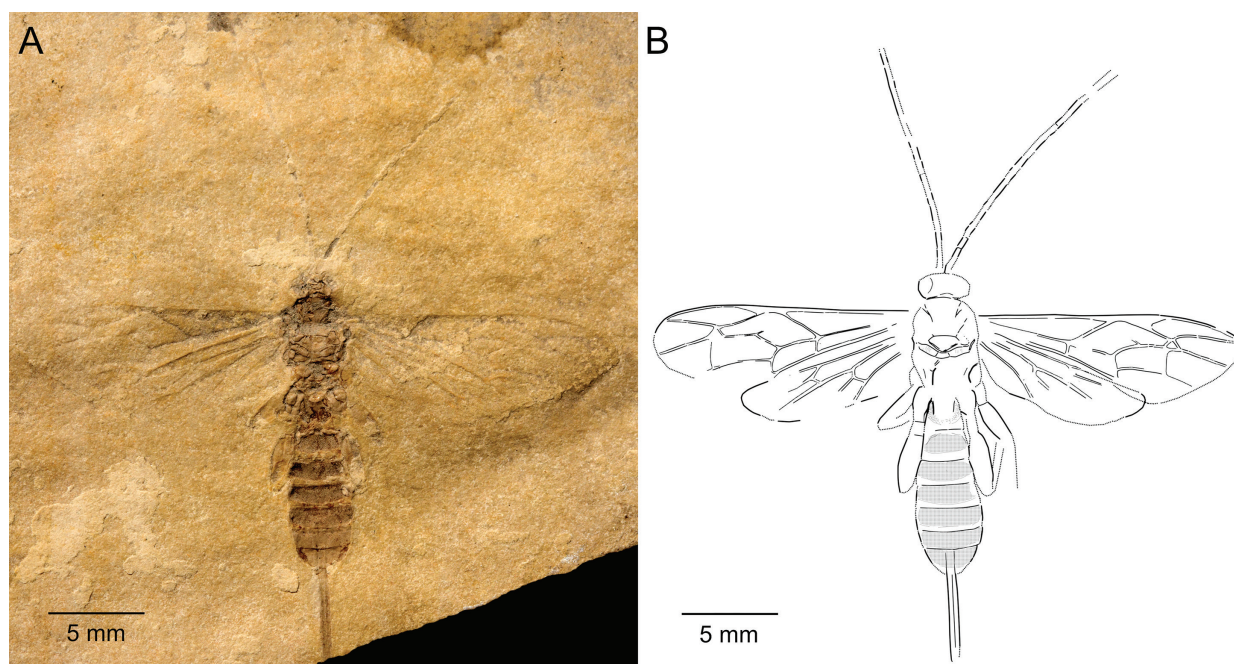


Figure 11. *Lithoserix antiquus* (Saussure, 1852) comb. nov. **A.** Photograph of the holotype obtained from MNHN.F; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, dotted lines represent uncertain interpretations and grey surface indicates sculpture of the cuticle. Grey areas show conspicuous sculpture of the cuticle.

Pimplinae Wesmael, 1845

Lithoserix Brown, 1986

Lithoserix antiquus (Saussure, 1852), comb. nov.

Fig. 11

**Pimpla antiqua* Saussure, 1852

(*Pimpla antiquus* Saussure according to Theobald, 1937)

Material. Specimen databased as ‘holotype’ (part and counterpart, Am 21 / #MNHN.F.B24391-1 and Am 21 2 / #MNHN.F.B24391-2) examined (but see notes under Interpretation) at MNHN.F, from where its photographs were also obtained.

Stratum. Aix-en-Provence, Bouche-du-Rhône, France. Late Oligocene (Chattian), 28.4–23.0 Ma.

Description. Female. Part showing dorsal view with almost complete antennae, partial head, mesosoma with both fore and hind wings, partial mid and hind legs, and metasoma including detailed sculpture and ovipositor sheaths except tip. Counterpart with negative impression of wings, ventral aspect of mesosoma, while metasoma shows a mix of a ventral aspect and what we interpreted as the inner sides of the tergites, where the sternites were weakly sclerotized, ovipositor sheaths complete. Body length 15.2 mm.

Brown, wing veins dark brown where colour is preserved, legs and hind margins of tergites orange.

Head only partially preserved, rather short; **Antennae** at least 13.7 mm, segment boundaries not discernible. **Mesosoma** preservation patchy; notauli present on about basal third; scutellum rather short, might be bounded by

carinae; axillary trough with transverse wrinkles; metanotum short. Propodeum with pleural carina and at least lateral longitudinal carinae complete, anterior transverse carinae probably present, remainder unclear. **Fore wing** 13.9 mm, with areolet almost triangular with outer vein longer than inner vein, 4Rs a little bowed at base and apex; 1cu-a meeting M + Cu opposite of 1M, 3Cu about as long as 2cu-a; ramulus longer than twice the width of the surrounding veins; cell 2R1 4.6× longer than wide. Hind wing with 1Rs longer than rs-m and 1Cu clearly shorter than cu-a. **Legs** rather stout, hind femur 3.5× longer than wide. **Metasoma** with T1 quadrate, only slightly narrowed towards base, with dorsal longitudinal carinae distinct on basal half and far away from each other, with parallel carinulae and some punctures along outer margins and towards lateromedian transverse impressions in posterior half; T2–T7 transverse, with a band along hind margin smooth, remainder strongly and densely punctate; T2 with oblique grooves cutting off anterolateral corners, maybe with thyridiae sunken. Ovipositor 4.7 mm, 0.5× as long as metasoma, straight and parallel sided, rather robust.

Interpretation. The specimen covered here was described by Theobald (1937), who stated that it was close but not identical to the holotype described by Saussure (1852), and that he could not find the latter. The drawing in the original description (plate 23, fig. 5 in Saussure 1852) indeed shows a different outline of the rock where the fossil is placed in, and Theobald mentions several differences especially in the wing venation. However, there are multiple lines of evidence that the present specimen might indeed represent the holotype, most of all the

remarkable similarity of the positioning of the body of the specimen, including the exact angle between the antennae and positions of the legs. We thus suspect that this is indeed the holotype of *P. antiqua*, and that either Saussure took the artistic liberty to draw a more generous outline of the rock, or it was trimmed to a smaller size later on.

The species was transferred to Braconidae by Aubert (1967) without any comment, and thus listed as “Species incertae sedis”, in the world catalogue (Yu et al. 2012). It clearly belongs to the family Ichneumonidae, given the venation in fore and hind wings, and to the subfamily Pimplinae given the triangular areolet, hind wing 1Cu shorter than cu-a, quadrate T1, long ovipositor, and sculpture of the metasoma. The carinae on the propodeum, long ramulus and broad smooth bands apically on the tergites preclude a placement in the genus *Pimpla* as it is defined today (Gauld et al. 2002). However, in all the afore-mentioned characters, it is very similar to the only species placed in the Eocene genus *Lithoserix* Brown, *L. williamsi* (Brown 1986) from the Florissant formation. We thus transfer it to this genus; see there for details on the differences to other genera. *Lithoserix antiquus* can be distinguished from *L. williamsi* by the much shorter ovipositor, shorter mesoscutum and the dorsal carinae on T1 extending to less than the mid-length of the tergite.

Pimplinae Wesmael, 1845

Lithoserix Brown, 1986

**Lithoserix williamsi* Brown, 1986

Fig. 12

Material. Photograph examined of the holotype (part, #UCM31179), obtained from the UCM.

Stratum. Old Scudder Pit, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 My.

Description. Female. Part showing dorsal view including partially preserved antennae, partial head, mesosoma preservation rather patchy, with right fore wing partial and complete left fore and hind wings, partial mid and hind legs, and metasoma including ovipositor sheaths and ovipositor except tip. Body length 22 mm.

Brown, wing veins dark brown where colour is preserved, femora and posterior half of tergites darker brown, posterior half of tergites possibly darker than anterior.

Head, with complete occipital carina straight to evenly rounded or slightly dipped medially. **Antennae** at least 14 mm long, first few segments probably short, only slightly longer than wide. **Mesosoma** with notauli strongly impressed, converging and extending past half of mesoscutum; scutellum borders unclear, might be displaced posteriorly and visible as small triangular structure or

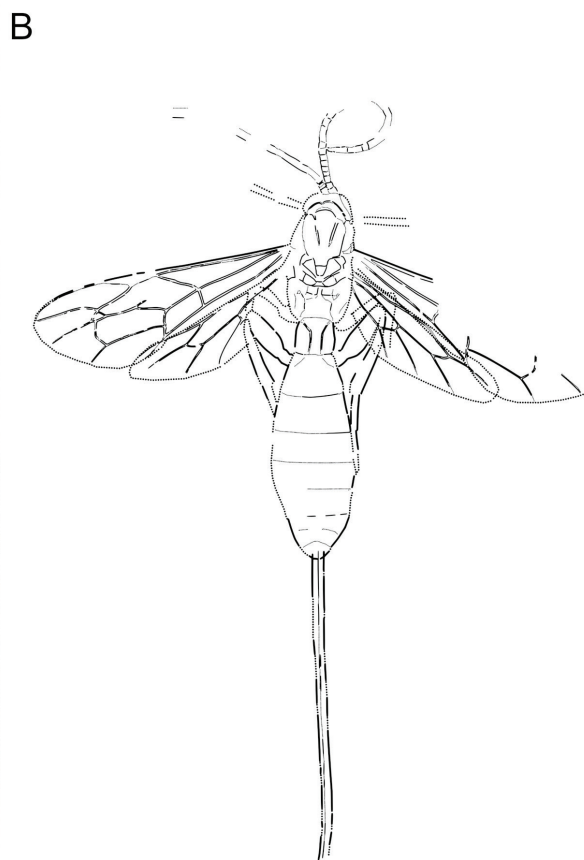


Figure 12. *Lithoserix williamsi* (Brown, 1986) comb. nov. **A.** Photograph of the holotype obtained from the UCM; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

larger and broken around middle; metanotum visible, of regular size. Propodeum with carinae difficult to interpret, but at least with complete lateral longitudinal carinae, anterior portion of median longitudinal carinae, anterior transverse carina and some indication of pleural carinae; spiracle small and oval. **Fore wing** 16.5 mm, with areolet almost triangular, 2 + 3M longer than 4M; 4Rs clearly bowed at base; 1cu-a meeting M + Cu opposite of 1M, 3Cu slightly longer than 2cu-a; ramulus longer than twice the width of the surrounding veins; cell 2R1 4.3× longer than wide. Hind wing with 1Rs longer than rs-m and 1Cu clearly shorter than cu-a. **Legs** rather stout, hind femur around 3.4× longer than wide. **Metasoma** with T1 quadrate, only slightly narrowed towards base, with dorsal longitudinal carinae parallel to each other and almost reaching or reaching posterior margin of tergite; T2 subquadrate with oblique grooves cutting off anterolateral corners; T3–T7 transverse. **Ovipositor** at least 19 mm long, at least 3.5× as long as hind tibia, straight and parallel sided, rather robust.

Interpretation. Described originally in the symphytan family Siricidae, this taxon was moved to the tribe Ephialtini in Pimplinae more recently (Kasparyan and Rasnitsyn 1992). It clearly belongs to Ichneumonidae based on the wing venation. A quadrate areolet and 2m-cu evenly curved outwards, with two bullae, quadrate T1 with lateromedian longitudinal carinae and long ovipositor, clearly support the placement of the genus in Pimplinae. Tribal placement is in fact not unequivocal, as some Delomeristini genera also show as much resemblance to *Lithoserix* as the ephialtine *Dolichomitus* Smith, 1877 mentioned by Kasparyan and Rasnitsyn (1992). The presence of a transverse carina in the anterior part of the propodeum is unusual for Pimplinae and can be seen only in *Xanthopimpla* Saussure, 1892 (Pimplini) some Theroniini and, in a very reduced form, in *Delomerista* Förster, 1869 (Delomeristini). In fact, the presence of rather extensive carination on the propodeum is rather reminiscent of Delomeristini, although this is probably the plesiomorphic state in the subfamily (Kopylov et al. 2018). To distinguish between Delomeristini and Ephialtini, the tarsal claws would need to be examined, which are not preserved in either of the two specimens currently attributed to the genus. In any case, the long ramulus and short flagellar segments are unique for *Lithoserix*, which we suggest to keep without tribal assignment in Pimplinae.

Pimplinae? Wesmael, 1845

***Pimpla*? Fabricius, 1804**

***Pimpla*? *seyrigi* Theobald, 1937**

Fig. 13

**Pimpla seyrigi* Theobald, 1937

Material. **Holotype** (part F1322/1 and counterpart F1322/2) examined at the NMBA.

Stratum. Kleinkembs, Pays de Bade, Haut-Rhin, France. Early Oligocene (Rupelian), 33.9–28.4 Ma.

Description. Sex unknown. Dorsal aspect of head (part), fairly complete antennae, mesosoma, almost complete fore wings and one nearly complete and one partial hind wing, partial hind legs, and metasoma present. Body length ~9.3 mm.

Mainly black, dark brown on wing veins, antennae and most of tergites, those with light end margins, legs lighter brown.

Head seemingly elongate with long gena, rather than representing front view, given that antennae insert at the anterior edge. **Antenna** almost as long as body, 1.25× longer than fore wing, with more than 34 flagellomeres, evenly tapered from middle to apex. **Mesosoma** not well preserved, with no details discernible. **Fore wing** 6.6 mm; areolet closed, somewhat petiolate anteriorly and almost triangular, with vein 2m-cu meeting 3M almost at outer corner; 2m-cu bowed outwards, probably with two bullae; 1cu-a meeting M + Cu clearly distally of 1M, 3Cu clearly longer than 2cu-a; cell 2R1 2.5× longer than wide. **Hind wing** with cell R conspicuously narrow, vein 1Rs a bit longer than rs-m; cell 1Cu broad with vein M + Cu bowed; 1Cu only about half as long as cu-a. **Legs** not well preserved; hind legs rather elongate; hind tibia 6.4× as long as wide. **Metasoma** with T1 parallel-sided, 1.7× longer than broad; T2 and following tergites transverse; each tergite except for T1 with a light band apically which from T4 becomes narrower medially until it is cut into two lateral spots. **Ovipositor** not discernible.

Interpretation. The taxonomic affinity of this fossil is very difficult to discern. The elongate, tapering antennae and shape of the metasoma point to Ctenopelmatinae, but some Pimplinae cannot be ruled out. In addition, the wide quadrate areolet and outwards curved 2m-cu are rarely seen in Ctenopelmatinae, but they are quite common in Pimplinae. Given the poor preservation of the mesosoma, many important characters cannot be observed. As we cannot decide on the subfamily placement, removing the fossil from Pimplinae and labelling it as incertae subfamiliae would require description of a new genus based on the insufficient character evidence. We thus take a conservative approach, leaving the fossil within the genus *Pimpla*, but emphasizing the uncertainty in this placement by adding a question mark behind both the genus and subfamily name.

Pimplinae Wesmael, 1845

***Polysphincta* Gravenhorst, 1829**

***Polysphincta*? *inundata* Brues, 1910**

Fig. 14

**Polysphincta inundata* Brues, 1910

Material. Photographs of the holotype (part only, #PALE-2135) obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. **Female.** **Holotype** in lateroventral view, with one nearly complete and one partial antenna,

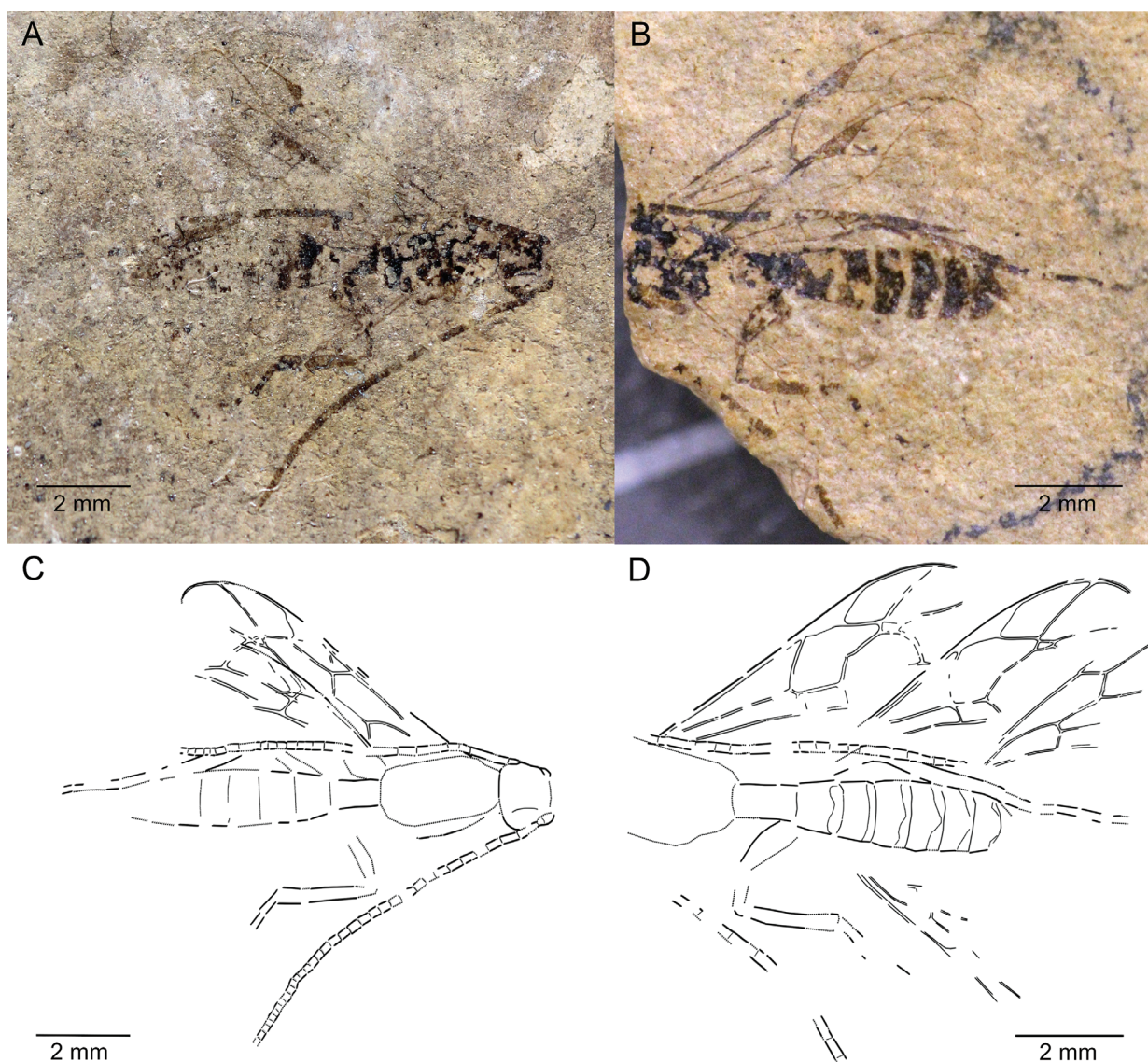


Figure 13. *Pimpla? seyrigi* (Theobald, 1937), comb. nov. **A.** Photograph of the part and **B.** Counterpart of the holotype of taken at the NMBA; **C, D.** Corresponding interpretative drawings. In the drawings, thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

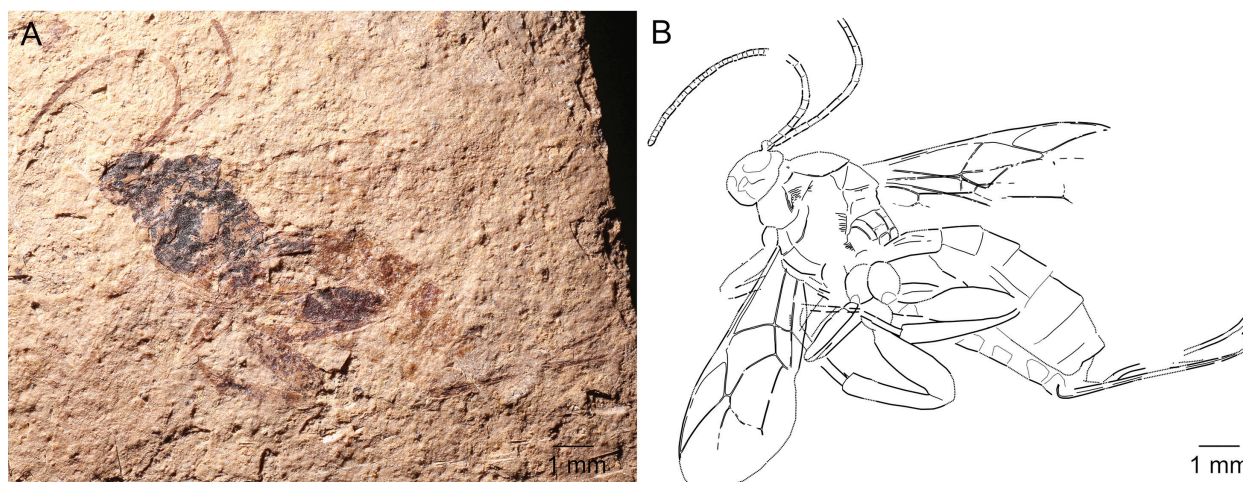


Figure 14. *Polysphincta? inundata* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

head, mesosoma showing some carinae and sculpture, nearly complete fore wings and one partial hind wing, hind legs strongly and mid and fore legs weakly outlined, metasoma complete with ovipositor with sheaths. Body length 10.1 mm.

Black or dark brown on head, mesosoma and T1, antennae and remaining metasoma orange, hind legs dark brown at least on femur and apex of hind tibia, other legs probably orange.

Head rather short, poorly preserved but outline of eyes partially indicated. **Antennae** 7.1 mm, with more than 39 (probably around 43) flagellomeres, basal segments longer than wide, from about mid length transverse, scape short. **Mesosoma** rather stout, with epomia present on pronotum; mesopleuron with epicnemial carina curved forward around mid-height of pronotum, with fine longitudinal carinulae at least in front of mesepimeron. Propodeum with pleural, lateral and lateromedian longitudinal carinae seemingly complete, with indication of low posterior transverse carina and maybe also part of anterior transverse carina. **Fore wing** 6.8 mm; areolet open, vein 2 + 3M twice as long as 2Rs; 1cu-a meeting 2Cu at the same position as 1M; cell 2R1 rather long, $3.6 \times$ as long as wide. Hind wing with vein 1Rs much longer than rs-m; 1Cu about as long as cu-a (but a bit difficult to see). **Legs** rather stout; hind femur $3.0 \times$ and hind tibia $7 \times$ as long as wide. **Metasoma** mostly dorsoventrally depressed and somewhat compressed towards apex, with T1 a bit elongate and nearly parallel sided, with what are probably latero-median and dorso-lateral carinae; T2 and following tergites transverse. **Ovipositor** 3.8 mm, $1.6 \times$ as long as hind tibia, upcurved at apex, seemingly tapering from about middle to apex; ovipositor sheaths parallel-sided.

Interpretation. Members of the *Polysphincta* group of genera are koinobiont ectoparasitoids of spiders and have a unique ovipositor, which is expanded at the base and again around mid-length, from where it evenly tapers into a narrow point. The state of the ovipositor in *P. inundata* seems consistent with this description, but this is somewhat unclear, despite the in general very good preservation of this fossil. Alternatively, if our interpretation of the ovipositor is wrong and there is not a median swelling, it would point to *Clistopyga* Gravenhorst, 1829, a sister genus of the polysphinctines. The fact that we cannot see any paired swellings, impressions or raised areas on tergites, which are typical for many but not all polysphinctines, speaks also more for *Clistopyga*. However, the propodeal carination never occurs in *Clistopyga*, and although it is reduced in most extant members of the polysphinctines, with at most longitudinal carinae present, the posterior transverse carina occurs in some genera, e.g., *Sinarachna* Townes, 1960, *Acrodactyla* Haliday, 1838 and *Zatypota* Förster, 1869. These genera, however, have shorter ovipositors without the upcurved tip. Because we cannot find a convincing alternative placement for the fossil, we leave it in the current genus but express uncertainty in its placement.

Lycorininae? Cushman & Rohwer, 1920

Lycorina? Holmgren, 1859

Lycorina? indura (Theobald, 1937), comb. nov.

Fig. 15

**Pimpla indura* Theobald, 1937

Material. *Holotype* (part #1323/1 and counterpart #1323/2) examined at the NMBA.

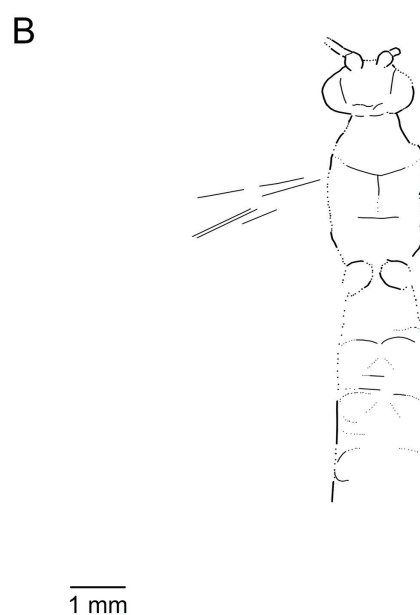
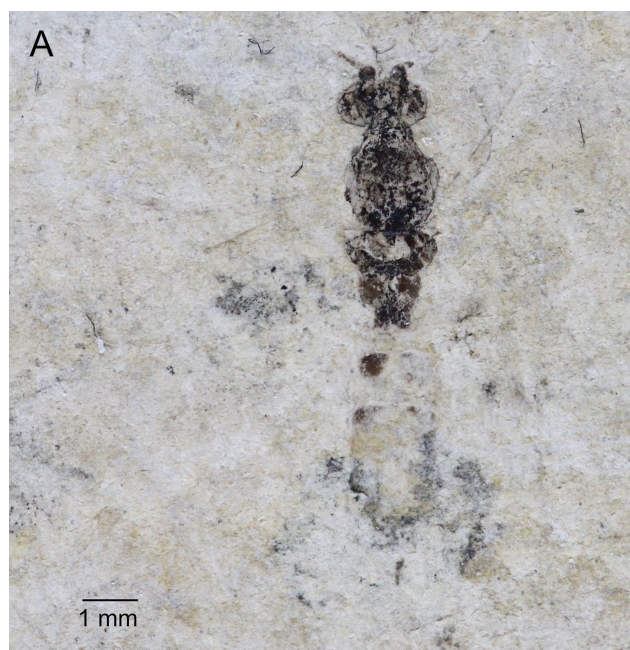


Figure 15. *Lycorina? indura* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from NMBA; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

Stratum. Kleinkembs, Pays de Bade, Haut-Rhin, France. Early Oligocene (Rupelian), 33.9–28.4 Ma.

Description. Sex unclear. Ventral aspect (see ‘Interpretation’ below) of head, base of antenna, mesosoma, base of fore wing, and T1–T4 of metasoma partly preserved. Body length ~9 mm.

Mostly dark brown in colour, with some light colouration on mesosoma and with metasoma mostly light-coloured, with base of T1 and paired dark markings on top of rounded swellings on T2 to T4.

Head rather short, with prominent eyes and clypeus and mandibles indicated. **Antennae** with scape and pedicel short, flagellar segments not discernible. **Mesosoma** not well preserved, with epicnemial carina complete at least ventrally; apparent constriction after mesoscutum probably due to lighter colouration on mesepimeron. Propodeum quite short. **Wings** very poorly preserved, but counterpart showing base of one fore wing with C, Sc + R, M + Cu on the left side in their normal position and Sc + R and M + Cu on the right side folded over, with 1cu-a meeting M + Cu opposite of 1M. **Legs** not preserved, but reddish-brown hind coxae visible in front of T1. **Metasoma** with broad T1, 0.8× as long as broad; T2 0.8×, T3 0.7× as long as wide; T2–T4 with paired, rounded swellings which bear traces coarse punctuation; diagonal grooves obvious on T2 and indicated on T1 and T3, transverse impressions unclear; remainder of metasoma not preserved.

Interpretation. The interpretation of this fossil was difficult given the poor preservation. Some of the interpretation hinges upon the question of whether it shows its ventral or dorsal aspect. Theobald (Theobald 1937) concluded that he was looking at a dorsal aspect, that the mesosoma was “clearly segmented”, and that he saw the three ocelli. However, we believe that the transverse line across the thorax represents the epicnemial carina, followed by the longitudinal mesosternal scrobe. Additional evidence for a ventral view is what we interpret as the two hind coxae lying in front of T1. Instead of very much enlarged ocelli, we think that the three light parts on the head represent the clypeus and mandibles. This interpretation is also in better agreement with the position of the antennae, which would be very low on the head if we were looking at a dorsal aspect. The metasoma is still interpreted as showing the tergites, but from inside; the sternites are usually so weakly sclerotized in ichneumonids that they are missing in fossils.

Overall, this fossil is badly preserved, with only the base of one fore wing visible and most of the mesosoma squashed so that no carination is discernible. The lack of complete fore wing venation makes even the family association seem uncertain; however, all the visible features correspond very well to ichneumonids, especially when comparing ventral view to other ichneumonid fossils (e.g., see the holotype of *Acerataspis? revelata* Brues). Several unusual features are very clearly visible, especially the diagonal grooves on T2 and paired dark swellings with strong punctuation on T2 and T3.

There are only a few ichneumonids with such strong diagonal grooves on the tergites: the tribe Glyptini in the subfamily Banchinae, some genera in Pimplinae, and the members of the subfamily Lycorininae. Only in the pimpline genus *Xanthopimpla* and in some *Lycorina* do the diagonal grooves come together with a light colouration of the metasoma and two basal swellings, which are then often black-marked as in the fossil. In *Xanthopimpla*, however, the grooves are closer to the anterior margin; if dark markings are present on T2, they are usually part of the medial swollen area and thus lie behind the diagonal grooves, which does not seem to be the case in this fossil. Furthermore, *Xanthopimpla* species have a yellow or orange mesosoma, although there is a recently described *Xanthopimpla* species from the Fur Formation with a dark mesoscutum (Klopfstein 2021). The subfamily Lycorininae matches much more closely with the same arrangement of carinae and markings found in extant species, the mesosoma often dark and the rather short scapus. This subfamily comprises only the genus *Lycorina*, which shows the basal part of the median longitudinal carinae on the propodeum, even though this state is somewhat equivocal in the fossil. We thus transfer the species to *Lycorina* in the subfamily Lycorininae but mark it with a question mark given the poor preservation.

Tryphoninae Shuckard, 1840

Monoblastus? Hartig, 1837

Monoblastus? senilis (Brues, 1910), comb. nov.

Fig. 16

**Pimpla senilis* Brues, 1910

Material. Photographs of the holotype (part only, #PALE-2160) obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Female. Holotype in lateral to ventro-lateral view, with head, base and tip and some intermediate segments of antennae, mesosoma, fore and nearly complete hind wings, hind legs, metasoma and ovipositor with sheaths. Body length 8.0 mm.

Colouration unclear, as with irregular dark and lighter patches on head, mesosoma and metasoma which are probably a preservation artefact but with what looks more real orange colouration on parts of pronotum, last sternites and legs. Hind tibia with apex darkened. Tergites of metasoma with apical third to half of lighter colour.

Head with rather long gena, thus almost globular in shape. **Antennae** 6.2 mm, with more than 30 (probably about 45) flagellomeres, tapering strongly on last third of its length, with basal segments longer than wide and apical segments transverse. **Mesosoma** stout; pronotum probably with strong epomia; mesoscutum rather short, maybe with notauli, with short carinulae on outer side; mesosternum with deep medial sternal groove with

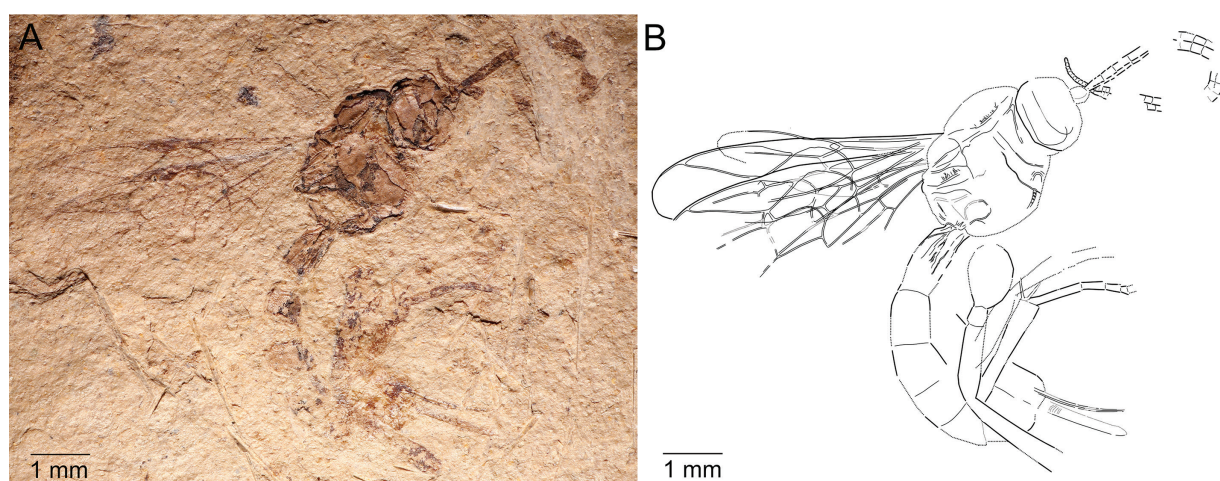


Figure 16. *Monoblastus? senilis* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

transverse carinulae; epicnemial carina curved and reaching up to about mid-height of mesopleuron. Propodeum short, not well preserved, with pleural and submetapleural and probably additional carination present. **Fore wing** 5.35 mm, with areolet quadrate and slightly oblique, receiving 2m-cu a bit apical of its centre, 4M thus shorter than 3M; 1cu-a meeting 2Cu distinctly after 1M; 3Cu a little longer than 2cu-a; vein 1m-cu & 2Rs+M conspicuously bowed; cell 2R about 3.5 as long as wide. **Hind wing** with 1Cu a bit longer than 1cu-a and 1Rs about 1.6× longer than rs-m. **Legs** of normal dimensions, hind femur 3.6× longer than wide, hind tibia with two slender spurs. **Metasoma** with T1 clearly longer than wide, with strong lateral and laterodorsal carinae and probably deep glymma, with dorsal longitudinal carinae at least present on basal half and with some longitudinal carinulae; T2 a bit longer than wide, following tergites subquadrate, all with what look like rather deep punctures; hypopygium rather prominent, triangular. **Ovipositor** about 1.5 mm, 1.3× as long as hind tibia, parallel sided and down-curved; ovipositor sheaths evenly hairy and somewhat expanded around middle.

Interpretation. The deep glymma, bowed vein 1m-cu & 2Rs+M in the fore wing, and shape of the metasoma suggest membership in Tryphoninae, where the down-curved ovipositor and possibly medially expanded sheaths point to genera such as *Thymariscus* Förster, 1869 or *Neliopisthus* Thomson, 1883 in the tribe Oedemopsini. In addition, *Monoblastus* from Tryphonini also has a down-curved tip of the ovipositor and sheaths which are weakly medially expanded. As the extant *Thymariscus* have a more slender first tergite and *Neliopisthus* more strongly expanded ovipositor sheaths than what we see in the fossil, we place the fossil in *Monoblastus*, to which the fossil also closely resembles in the wing venation. However, we add a question mark behind the genus name as the laterally extended epicnemial carina and longitudinal sculpture on T1 correspond better to *Thymariscus*.

Tryphoninae Shuckard, 1840

Zagryphus Cushman, 1919

Zagryphus tilloyi (Theobald, 1937), comb. nov.

Fig. 17

**Promethes tilloyi* Theobald, 1937

Material. **Holotype** (part only, #Am_8 / MNHN.F.B24392) examined at MNHN.F. Photograph obtained from MNHN.F.

Stratum. Aix-en-Provence, Bouche-du-Rhône, France. Late Oligocene (Chattian), 28.4–23.0 Ma.

Description. Female. Holotype in lateral to ventro-lateral view with nearly complete antennae, head, mesosoma with details indistinct; fore wings darkened and on top of each other, venation in part difficult to discern, one hind wing; at least parts of all legs, and metasoma with ovipositor with sheaths. Body length 6.1 mm.

Dark brown, antennae reddish at base and with white bands around mid-length; with reddish colouration on head and mesosoma, wings strongly tinted, brown; legs dark brown; metasoma dark, but possibly with irregular lighter markings on T2, ovipositor orange, its sheaths dark brown.

Head quite round, with large eyes, with a nose-like protrusion where clypeus would be. **Antennae** 4.5 mm, with at least 28 (probably around 32) flagellomeres, basal ones elongate, those apically of white band quadrate to transverse. **Mesosoma** not well preserved, with mesosternal scrobe, indication of epicnemial carina and notauli reaching at least over first third of mesoscutum. Metapleuron as long as wide, with submetapleural carina complete; propodeum with pleural carina, lateral longitudinal and maybe other carinae complete, meeting point of lateral longitudinal and posterior transverse carina might be thickened (cf. propodeal apophyses). **Fore wing** 3.6 mm, rather stout; areolet open, 2Rs rather short; 1cu-a meeting M + Cu opposite of 1M; 1M & 1Rs bowed inwards; 3Cu more than 3× longer than 2cu-a, strongly inclivous; cell 2R1 2.9× lon-

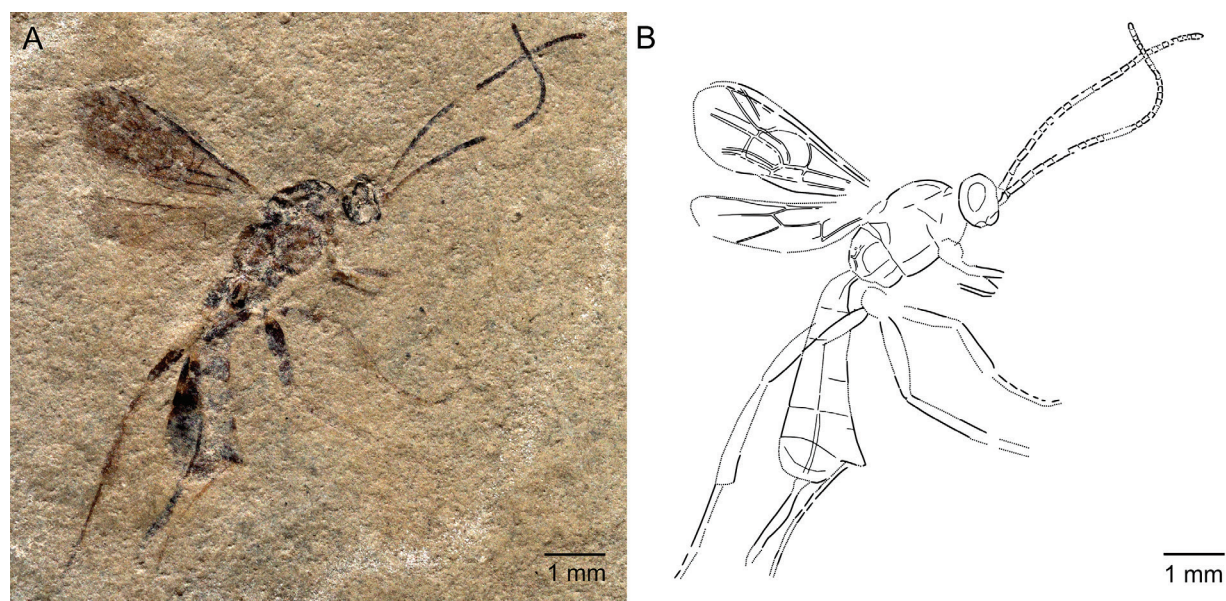


Figure 17. *Zagryphus tilloyi* (Theobald, 1937) comb. nov. **A.** Photograph of the holotype obtained from MNHN.F; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

ger than wide. **Hind wing** with 1Rs about as long as rs-m and 1Cu much longer than cu-a. **Legs** slender, hind femur 4.4×, hind tibia 7× longer than wide, dark dorsally light ventrally. **Metasoma** compressed from T4 or T5; T1 not well preserved, but slightly elongate and tapering towards base, following tergites transverse; sternites quite well sclerotized; hypopygium triangular in lateral view. Ovipositor 1.9 mm, about 1.3× as long as hind tibia, curved downwards; ovipositor sheaths widened around mid-length.

Interpretation. Even though many characters are not clearly visible, the medially expanded ovipositor sheaths firmly place this fossil in the Tryphoninae tribe Oedemopsini. Indeed, the specimen shows a remarkable similarity to the extant *Zagryphus nasutus* (Cresson, 1868): the nose-like expansion of the clypeus, inclivous 3Cu in the fore wing and short cu-a in the hind wing, triangular but not strongly elongate hypopygium, and down-curved ovipositor with medially expanded sheaths support a placement in this genus. Even the colouration is a good match, including the white band on the antenna and orange base, a pattern often observed in *Zagryphus* and related genera. *Zagryphus tilloyi* can be distinguished from the other members of the genus by its smaller size (at least 4.8 mm in extant species) and more strongly tinted wings.

Xoridinae Shuckard, 1840

Xorides Latreille, 1809

Xorides sejugatus (Brues, 1910)

Fig. 18

**Xylonomus sejugatus* Brues, 1910

Material. Photographs of the holotype (#PALE-2211) and of two paratypes (#PALE-2212 and #PALE-2213), obtained from the MCZ.

Stratum. Teller County, Florissant shales, Colorado, USA. Late Eocene (Chadronian), 37.2–33.9 Ma.

Description. Female. Holotype, paratypes with sex unknown. Holotype in lateral aspect showing head, few basal segments of antennae, rather well-preserved mesosoma, almost complete fore and hind wings, nearly complete legs, metasoma and ovipositor with partial sheaths. Paratypes less well preserved, #2212 showing lateral aspect of partial mesosoma, base of wings, T1–T5 and most of hind legs; #2213 with lateroventral aspect of head, partly discernible antennae, outlined but not well-preserved meso- and basal metasoma, wings and partial legs. Body length 17.25 mm.

Black or dark brown on head and mesosoma and hind coxae, brown wing veins and metasoma, legs lighter brown except for darkened hind femur. Ovipositor dark brown.

Head rather short and high, with long cheek, in #2213 with what looks like two chisel-shaped mandibles. **Antennae** incomplete, but rather slender and at least 1.3× as long as fore wing. **Mesosoma** cylindric, not very elongate, pronotum with epomia strong and reaching mesoscutum; mesoscutum with long notauli, mesopleuron with epicnemial carina reaching pronotum at about mid-height. Propodeum strongly areolated, with lateromedian and lateral longitudinal and pleural carinae, posterior transverse and at least partial anterior transverse carina. **Fore wing** 11 mm, with areolet open, vein 2Rs almost obliterate; 1cu-a meeting 2Cu slightly distally from 1M; cell 2R1 strongly elongate, 4.2× as long as wide. **Hind wing** with 1Cu a little longer than cu-a and 1Rs a little shorter than rs-m. **Legs** partly preserved, hind femur 3.0×, and hind tibia 5.8× as long as wide. **Metasoma** depressed, slightly enlarged apically; T1 about 2.3× as long as wide, slightly expanding apically, with strong ventrolateral, dorsolateral and median dorsal carinae, and with distinct diagonal grooves laterally which form

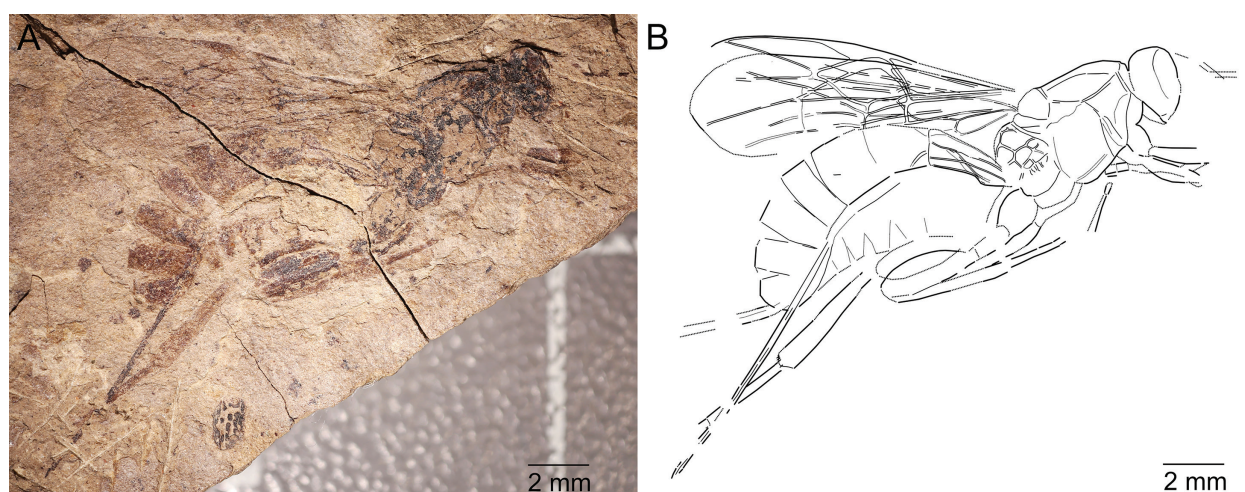


Figure 18. *Xorides sejugatus* (Brues, 1910) comb. nov. **A.** Photograph of the holotype obtained from the MCZ; **B.** Our interpretative drawing of the fossil (below). Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

part of a constriction around middle of tergite; T2 approximately quadrate, with oblique basal grooves cutting off basolateral corners; T3 a bit wider than long; T4–T6 transverse; T7 slightly longer than T6; S2–S5 visible as brown patches. **Ovipositor** 9.6 mm, 2.2× as long as hind tibia, rather narrow.

Interpretation. Several characters firmly place this fossil in *Xorides*, including the chisel-like mandibles, long epomia that seems to connect with the dorsal margin of the pronotum, fore wing venation including an open areolet with very short 3rs-m, grooves anteriorly on T2, and lateral diagonal impressions on T1. The only character not usually observed in recent species of the genus are the thickened hind femora.

Ctenopelmatinae Förster, 1869

Parapimpla Theobald, 1937

Parapimpla rhenana Theobald, 1937, stat. rev.

Fig. 19

Material. *Holotype* (part F1321/1 and counterpart F1321/2) examined at the NMBA.

Stratum. Kleinkembs, Pays de Bade, Haut-Rhin, France. Early Oligocene (Rupelian), 33.9–28.4 Ma.

Description. Sex unclear. Dorsal aspect of head, base and some fragments of antennae, dorsolateral view on mesosoma, partial fore wings (one of which is folded longitudinally), partial hind wing and legs, and first five

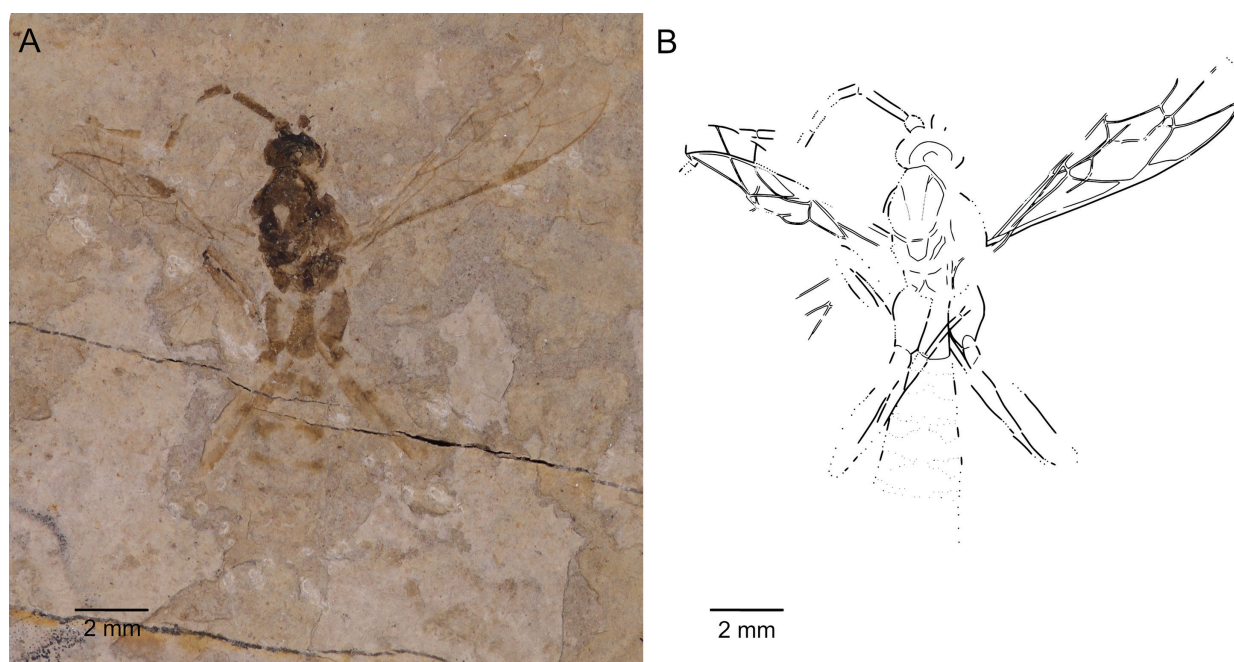


Figure 19. *Parapimpla rhenana* Theobald, 1937 stat. rev. **A.** Photograph of the holotype taken at NMBA; **B.** Our interpretative drawing of the fossil. Thicker lines indicate outlines of body structures, thinner lines show characters inside these outlines, and dotted lines represent uncertain interpretations.

tergites visible. Body length unclear as tip of metasoma is missing, but probably a bit more than 10 mm.

Dark brown on head and mesosoma, orange-brown legs, wing veins, T1, and basal spots on T2–T5, remainder very light brown or yellow.

Head short, with short gena, occipital carina well developed and evenly rounded above. **Antenna** only partly preserved, scape and pedicel of average dimensions; first flagellomere 6× as long as wide, the few other visible fragments showing rather elongate flagellomeres. **Mesosoma** partly crushed, with lighter parts and of normal dimensions; mesoscutum rather long, front margin truncated and prominent, with an indication of a long, converging notaulus, with a light mark in middle; propodeum with pleural, lateral longitudinal and at least partial lateromedian longitudinal carinae, transverse carinae probably present but a bit unclear. **Fore wings** well preserved, 8.3 mm, but left fore wing longitudinally folded on itself; pterostigma 4.6× as long as wide, brown with a light base; areolet large and quadrate, almost rhombic, with veins r-rs and 4Rs meeting at its anterior end in ~110° angle; 2m-cu very short and probably with a single bulla anteriorly; cell 2R1 very long (3.5×); 1M somewhat curved just before it meets M + Cu. **Hind wing** only partially preserved, cell R nearly complete; 1Rs almost 3× longer than rs-m. **Hind legs** partly preserved, elongate, femur more than 4.5×; tibia 9.5× longer than wide. **Metasoma** only partly preserved; T1 narrow anteriorly and evenly tapering posteriorly, almost twice as long as wide at apex, without distinct division into petiole and postpetiole; T2 subquadrate; T3 and T4 transverse, each with light colouration and brown paired marks near base.

Interpretation. This fossil has a very elongate and narrow T1, which does not occur in Pimplinae. The poor preservation, especially of the wing venation and tip of the metasoma, makes a clear attribution of this genus to any of the extant subfamilies challenging. If the shape of T1 is as preserved, then Ctenopelmatinae would be a good match, as they also often have similar wing venation. Similar T1 also occurs in some Banchinae, Cremastinae and Campopleginae. However, we can rule out Banchinae based on the presence of longitudinal carinae on the propodeum, and Cremastinae and Campopleginae can be discounted based on the wing venation. Thus, we move this monotypic genus to Ctenopelmatinae.

Discussion

We here revised 18 fossil ichneumonid species from the Palaeogene, all described before the major reclassification of ichneumonids by Henry Townes. We concluded that the original subfamily placement of 12 of them are unreliable and for 11 of them, we demonstrated a wrong subfamily placement and moved them mostly to extant genera in the better fitting subfamilies. As the main reasons for the initially erroneous taxonomic placement, we identified the shortcomings of the initial classification systems for ichneumonids, inaccurate interpretation of preserved characters and undue reliance on homoplastic characters.

Artefacts of the pre-Townes classification in the ichneumonid fossil record

The most common genus of ichneumonids in the fossil record is *Pimpla* with 22 described species, all from the Palaeogene. We here revised six of those species, none of which turned out to belong to *Pimpla* with certainty. *Pimpla* is a type genus of one of the five ichneumonid subfamilies recognized in the first half of the 20th century (Cryptinae, Ichneumoninae, Ophioninae, Pimplinae, Tryphoninae), each of which was split into several different subfamilies in the comprehensive taxonomic work of Henry Townes (Townes 1969a, 1969b, 1970, 1971). Therefore, many ichneumonid fossils were probably named based on superficial resemblance to the type genera of the five subfamilies. Moreover, these genera used to be very broadly defined and often included subgenera that today have genus status. Finally, the subfamily association of some ichneumonid genera and even tribes has changed multiple times, even after Townes' seminal work (Quicke et al. 2009; Santos 2017; Bennett et al. 2019; Klopstein et al. 2019). There are already indications that these artefacts of the pre-Townes classifications, as well as homoplasy (see below), also impact fossils placed in *Tryphon* (Bennett 2015; Spasojevic et al. 2018b), and we expect that the case is similar in fossils placed in the genera *Ichneumon* and *Cryptus*, which are all very common in the fossils record. This stresses the importance of the revision of more than 140 ichneumonid fossils described before Townes' work. As in the *Pimpla* species treated here, we can expect that only very few fossil species will retain their original placement after a thorough revision incorporating recent taxonomic and phylogenetic insights (Quicke et al. 2009; Broad et al. 2018; Klopstein et al. 2019).

High prevalence of homoplasy in ichneumonids

Homoplasy has been pointed out as one of the major problems in classifying extant (Gauld and Mound 1982) and, even more so, fossils ichneumonids (Spasojevic et al. 2018b). Our findings strongly support those observations, especially in the case of the revised *Pimpla* fossils, where we had sufficient character evidence for moving three of them to a different genus in a different subfamily: *P. morticiina* to the newly described genus *Armadilleon* in Phygadeuontinae, *P. revelata* to *Acerataspis* in Metopiinae, and *P. senilis* to *Monoblastus* in Tryphoninae. All three fossils do resemble *Pimpla* in the relatively stout body, broad and short T1, and fore wing with a closed areolet, but these are all highly homoplastic characters and thus not informative for classification. Therefore, it is important to avoid homoplastic and fast-evolving characters for identifying fossil taxa, acknowledging all possible placements of a fossil and express the uncertainty in the chosen placement.

Difficulties in character interpretation in ichneumonid fossils

Many crucial autapomorphies of different subfamilies and genera were not preserved in the revised fossils and this greatly impairs their original as well as revised placements. For instance, the association of *Hallocinetus? arvernus* with Acaenitinae could neither be confirmed nor refuted due to the poorly preserved apical part of the metasoma. However, the identification of a closed areolet in the holotype, which was overlooked by the original author (Piton 1940) renders the original generic placement untenable. The placement of two fossils in *Dimophora*, both of which were formerly placed in different subfamilies, was uncertain because the presence of the thyridium was unclear. In Pimplinae, many genera can be confirmed or ruled out by the state of their tarsal claws, which are very rarely preserved in fossils (but see Spasojevic et al. 2018b). As a result, for more than half of the fossils, we could not establish a firm generic placement. As missing data is inevitable when studying fossilized organisms, the correct interpretation of those characters that are preserved is even more crucial for their taxonomic placement.

The wrong interpretation of the aspect in which the fossil is preserved, such as dorsal versus ventral, contributed to erroneous placements of *Lycorina? indura* and *Acerataspis? revelata*. Indeed, because of the weakly sclerotized sternites in Ichneumonoidea, the metasoma of a fossil might appear to show a dorsal view, as certain aspects of the more strongly sclerotized tergites often show prominently even in ventral view (Spasojevic et al. 2018b). This can lead to darkened parts of sternites being mistaken for colour patterns on tergites, and careful interpretation is needed to avoid such pitfalls (Kopylov 2009). For a correct interpretation of the orientation of the body of a fossil, it is thus crucial to combine clues from all body parts, with the often strongly sclerotized mesosternal scrobe often acting as an important guide in Ichneumonoidea fossils.

Aside from the aspect of a fossil, several other characters were wrongly interpreted in the fossils studied here. For instance, head parts were mistaken for ocelli in *Lycorina? indura*, T1 was interpreted as pimpline-like (short and stout) instead of petiolate in *Dimophora? wickhami*, while the areolet was interpreted as open instead of closed and petiolate in *Hallocinetus? arvernus*. To better understand the preservation state of a fossil, it is important to study taphonomic processes which cause deformation of the preserved structures (Martínez-Delclòs et al. 2004). Although there are many studies concerning the taphonomy of insects in rock deposits (e.g., Henning et al. 2012; Smith 2012; Wang et al. 2013; Cunningham et al. 2014; Greenwalt et al. 2014; Karr and Clapham 2015; Osés et al. 2016), none addressed ichneumonids specifically. Therefore, the interpretation of the aspect in which an animal is preserved and of specific body parts, such as the propodeum and its carination and the sternites of the metasoma, remains difficult. Deposits where several

dozen ichneumonids have been preserved in various aspects, such as the Fur Formation in Denmark (Klopfstein 2021), Messel Pit in Germany (Spasojevic et al. 2018a), Green River and Kishenehn Formations in the USA (Spasojevic et al. 2018b, personal observations), can provide invaluable information on the taphonomy of ichneumonids. Furthermore, experiments with extant species can provide important insights into how the body of a particular taxon reacts to decay and pressure under different environmental conditions (Martínez-Delclòs et al. 2004; Briggs and McMahon 2016; Gäb et al. 2020; Slater et al. 2020), but such experiments still have to be performed on this group.

Implications of erroneous fossils placement

With the spread of phylogenetic dating studies, which rely on fossils to estimate the absolute divergence times of organisms, the correct interpretation of fossil classification became crucial to a broader scientific community. In particular, erroneous fossil placement affects the node dating approach, where the age of a fossil is directly used to calibrate the age of the node in the phylogeny of extant taxa that it is associated with (Parham et al. 2012). Several simulations and empirical studies support this notion, where wrong calibrations lead to wrong age estimates (Warnock et al. 2011; Parham et al. 2012). This mostly happens because molecular phylogeneticists often rely on the original placement of a fossil without reevaluating it or because they misinterpret the affiliation of the fossil with stem versus crown lineages and vice versa. The alternative approach, total-evidence dating (Pyron 2011; Ronquist et al. 2012), has the advantage of not a priori assuming the taxonomic position of a fossil, but instead it infers it by employing morphological data from both extant and fossil taxa. It has already been shown that the total-evidence analysis combined with RoguePlots, a graphical visualisation of placement probabilities of fossils in Bayesian phylogenetic inference (Klopfstein and Spasojevic 2019), can be a helpful tool for assessing placement of fossils. Although the total-evidence approach is immune to erroneous fossil placements, it is not immune to wrong character interpretations that lead to biased morphological data. Therefore, it is crucial that palaeontologists express uncertainty in both character interpretation and taxonomic placement of newly described fossils. The latter is easily done by applying open taxonomic nomenclature, such as adding a question mark behind an uncertain subfamily or genus placement.

Conclusions

Contributions to the fossil record of Darwin wasps, either through descriptions of new taxa or revisions of the described species, are needed for understanding the past diversity and evolutionary history of this group. We here contributed to this topic by revising 18 fossil

species from the Palaeogene, all described before the taxonomic work of Henry Townes. The placement of all but three fossils was unreliable, resulting in a new generic and, almost always, a new subfamily placement for most of the fossils. Underlying reasons for the initial erroneous taxonomic placement of the revised fossils are mostly due to the shortcomings of the initial classification systems for ichneumonids, erroneous interpretation of character evidence and reliance on homoplastic characters for placement of the fossils. Our revision highlights the need for further reinterpretation of the ichneumonid fossil record and for widely adopting the open taxonomic nomenclature, which will greatly allow for more adequate integration of fossils in phylogenetic dating studies.

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