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# Ichneumonid parasitoid wasps from the Early Eocene Green River Formation: five new species and a revision of the known fauna (Hymenoptera, Ichneumonidae)

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**Abstract** The parasitoid wasp family Ichneumonidae is one of the most species-rich groups of organisms, but its fossil record remains very poorly studied, which impedes inferences of the origin of its diversity. We here describe two new fossil genera and five new species of Ichneumonidae from the Eocene Green River Formation: *Carinibus molestus* gen. et sp. nov., *Ichninsum appendicrassum* gen. et sp. nov., *Mesoclistus?* *yamataroti* sp. nov., *Scambus?* *mandibularis* sp. nov., and *Scambus?* *parachuti* sp. nov. The newly described *Mesoclistus?* *yamataroti* represents the first record of the subfamily Acaenitinae from this fossil locality. In addition, we revise the ten previously described fossil ichneumonids from the Green River Formation, following a conservative approach when re-assessing their taxonomic positions: we keep the current placement of six revised fossils, but express the uncertainty in genus-assignment according to open nomenclature rules: *Eclytus?* *lutatus* Scudder, *Glypta?* *transversalis* Scudder, *Pimpla?* *eocenica* Cockerell, *Phygadeuon?* *petrifactellus* Cockerell, *Plectiscidea?* *lanhami* Cockerell and *Rhyssa?* *juvenis* Scudder. We exclude three

fossil genera from their current subfamilies and place them within Ichneumonidae *incertae subfamiliae*: *Eopimpla* Cockerell, *Lithotorus* Scudder and *Tilgidopsis* Cockerell. Furthermore, we move *Tryphon amasidis* Cockerell and LeVeque to the new genus *Trymectus* gen. nov. In the light of these revisions, we discuss the importance of careful taxonomic placement of fossils and difficulties in ichneumonid palaeontology caused by host-related homoplasies and a lack of knowledge about the age of the recent subfamilies.

**Keywords** Fossil Hymenoptera · Open taxonomy · New species · Ypresian · Colorado · USA

**Kurzfassung** Die parasitoide Wespenfamilie Ichneumonidae ist eine der artenreichsten Organismengruppen—ihr Fossilbericht ist jedoch kaum untersucht, was Rückschlüsse auf den Ursprung ihrer Diversität erschwert. Hier werden zwei neue fossile Gattungen und fünf neue Arten der Ichneumonidae aus der eozänen Green River-Formation beschrieben: *Carinibus molestus* gen. nov. et sp. nov., *Ichninsum appendicrassum* gen. nov. et sp. nov., *Mesoclistus?* *yamataroti* sp. nov., *Scambus?* *mandibularis* sp. nov. und *Scambus?* *parachuti* sp. nov. Die neu beschriebene Art *Mesoclistus?* *yamataroti* stellt den ersten Nachweis der Unterfamilie Acaenitinae aus dieser Fossilkundstelle dar. Zusätzlich revidieren wir die zehn bereits beschriebenen Ichneumoniden aus der Green River-Formation und unternehmen eine konservative Neubewertung ihrer taxonomischen Position: die gegenwärtige Anordnung sechs revidierter Fossilien wird beibehalten, die Unsicherheit in der Gattungszuordnung jedoch nach den Regeln der offenen Nomenklatur zum Ausdruck gebracht: *Eclytus?* *lutatus* Scudder, *Glypta?* *transversalis* Scudder, *Pimpla?* *eocenica* Cockerell, *Phygadeuon?*

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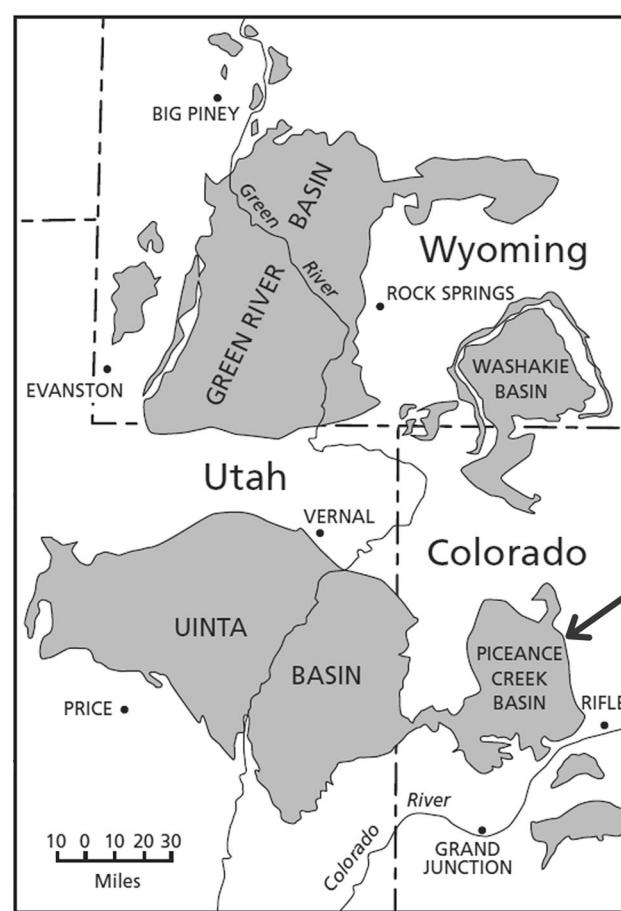
*petrifactellus* Cockerell, *Plectiscidea?* *lanhami* Cockerell und *Rhyssa?* *juvenis* Scudder. Drei fossile Gattungen werden aus den bisherigen Unterfamilien entnommen und nun innerhalb der Ichneumonidae *incertae subfamiliae* eingeordnet: *Eopimpla* Cockerell, *Lithotorus* Scudder und *Tilgidopsis* Cockerell. Außerdem wird *Tryphon amasidis* Cockerell und LeVeque in die neue Gattung *Trymectus* gen. nov. gestellt. In Hinblick auf diese Revisionen werden die Bedeutung einer sorgfältigen taxonomischen Einordnung von Fossilien sowie die Schwierigkeiten innerhalb der Ichneumoniden-Paläontologie in Bezug auf wirtsbezogene Homoplasien sowie der fehlenden Kenntnis über das Alter ichneumonider Unterfamilien diskutiert.

**Schlüsselwörter** Fossile Hymenoptera · Offene Nomenklatur · neue Arten · Ypresium · Colorado · USA

## Introduction

The Green River Formation consists of lacustrine deposits that extend over a considerable area in the three North American states, Wyoming, Utah, and Colorado. It formed during the early Paleogene as a consequence of the uplifting of the Rocky Mountains, which created three lakes, Fossil Lake, Gosiute Lake, and Uinta Lake (Grande 1984). Gosiute Lake covered the Great Green River Basin in Wyoming (divided into Green River Basin and Washakie Basin), while Uinta Lake covered the Uinta Basin in Utah and Piceance Basin in Colorado (Fig. 1). The age of the Green River Formation is in general estimated as 53.5–48.5 Ma (late Ypresian), but some layers in the western part of the Unita Basin have a minimum age of around 44.5 million years (Smith et al. 2003, 2008). All the newly described fossils in this paper were found in the Piceance Creek Basin within the Parachute Creek Member whose age is about 51.3–48.9 Ma (middle to late Ypresian, Smith et al. 2008) (Fig. 2).

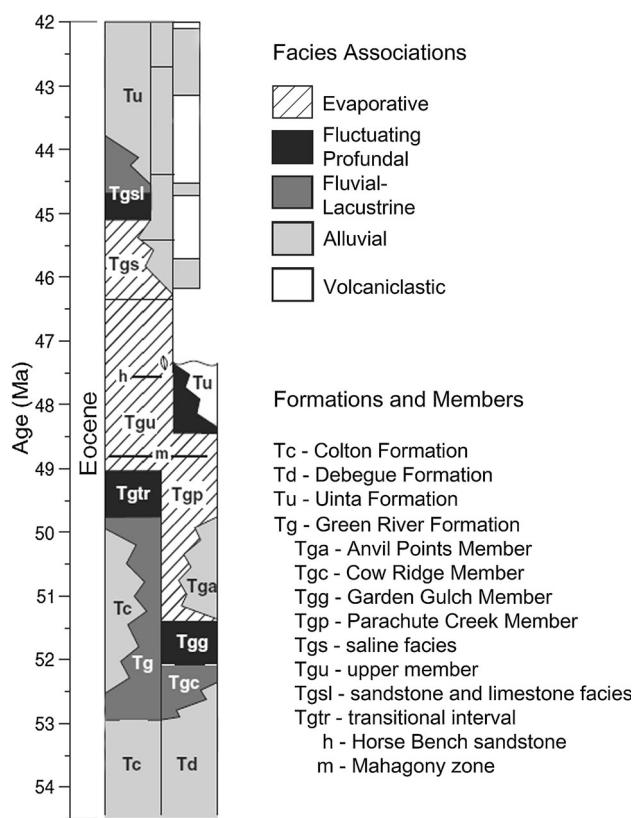
The Green River Formation is a very rich invertebrate fossil locality (fossil Lagerstätte) with more than 300 fossil insect species described to date (Scudder 1890; Cockerell 1920, 1921; Dlussky and Rasnitsyn 2002; Chaboo and Engel 2009; Antell and Kathirithamby 2016). Among them, Coleoptera and Diptera are the most common, while Hymenoptera are represented by 38 described species (Wilson 1978; PaleoBioDB 2016). Today, the parasitoid wasp family Ichneumonidae is among the most species-rich groups of organisms, with more than 24,000 described species (Yu et al. 2012). Its fossil record has been poorly studied, despite the fact that the family can be recognized rather easily from the venation of the fore wing, which is often well-preserved in fossils. There are more than 200 unidentified ichneumonid fossils from the



**Fig. 1** Location of the main basins of the Green River Formation. The black arrow indicates the collection locality of the newly described ichneumonid fossil species, Piceance Creek Basin (modified after Bartis et al. 2015; adapted from Smith 1980)

Green River localities registered in the major collections (Smithsonian National Museum of Natural History, University of Colorado Museum of Natural History). All previous work on representatives of Ichneumonidae in the Green River Formation was done in the first half of the twentieth century by Cockerell and Scudder, resulting in ten described species belonging to eight different subfamilies, Banchinae Wesmael, 1845, Cryptinae Kirby, 1837, Diplazontinae Viereck, 1918, Ophioninae Shuckard, 1840, Orthocentrinae Förster, 1869, Pimplinae Wesmael, 1845, Rhysinae Morley, 1913 and Tryphoninae Shuckard, 1840 (Scudder 1890; Cockerell 1919, 1920, 1921, 1941; Cockerell and LeVeque 1931).

Since these fossils were described, ichneumonid systematics has undergone major changes, with the number of recognised extant subfamilies increasing from five to 25 by the time of Townes's generic monographs (Townes 1969, 1970a, 1970b, 1971). Currently, there are 40 extant subfamilies recognised (Sharkey and Wahl 1992; Quicke et al. 1999, 2009; Bennett et al. 2013; Broad 2016; Li et al.



**Fig. 2** Graphic representation of stratigraphy and age estimates for the Uinta-Piceance Creek Basin, Green River Formation (modified after Smith et al. 2008)

2016) and five or six extinct ones, depending on whether Tanychorinae is included in Ichneumonidae (Kopylov 2009, 2010a) or not (Sharkey and Wahl 1992; Quicke et al. 1999). Considering that most of the ichneumonid Green River fossils were never studied again after their original description, their placement into subfamilies and genera should be treated with caution. In addition, higher-level classification in ichneumonids is especially challenging since many subfamilies look superficially alike due to host-related homoplasies (Gauld and Mound 1982). So, while ichneumonid specimens can easily be recognized as belonging to this family because of the very constant venation of the fore wing, subfamily placement can be difficult even for specimens of extant species. This could have caused erroneous fossil interpretations and placement.

In this paper, we describe five new Ichneumonidae fossils from the Parachute Creek Member of the Green River Formation in Colorado and discuss their placement in modern subfamilies. Furthermore, we revise and re-describe all previously described ichneumonids from the Green River Formation according to the current classification of the family, making use of open nomenclature to reflect uncertainty in their taxonomic affiliations.

## Materials and methods

### Specimens and morphological terminology

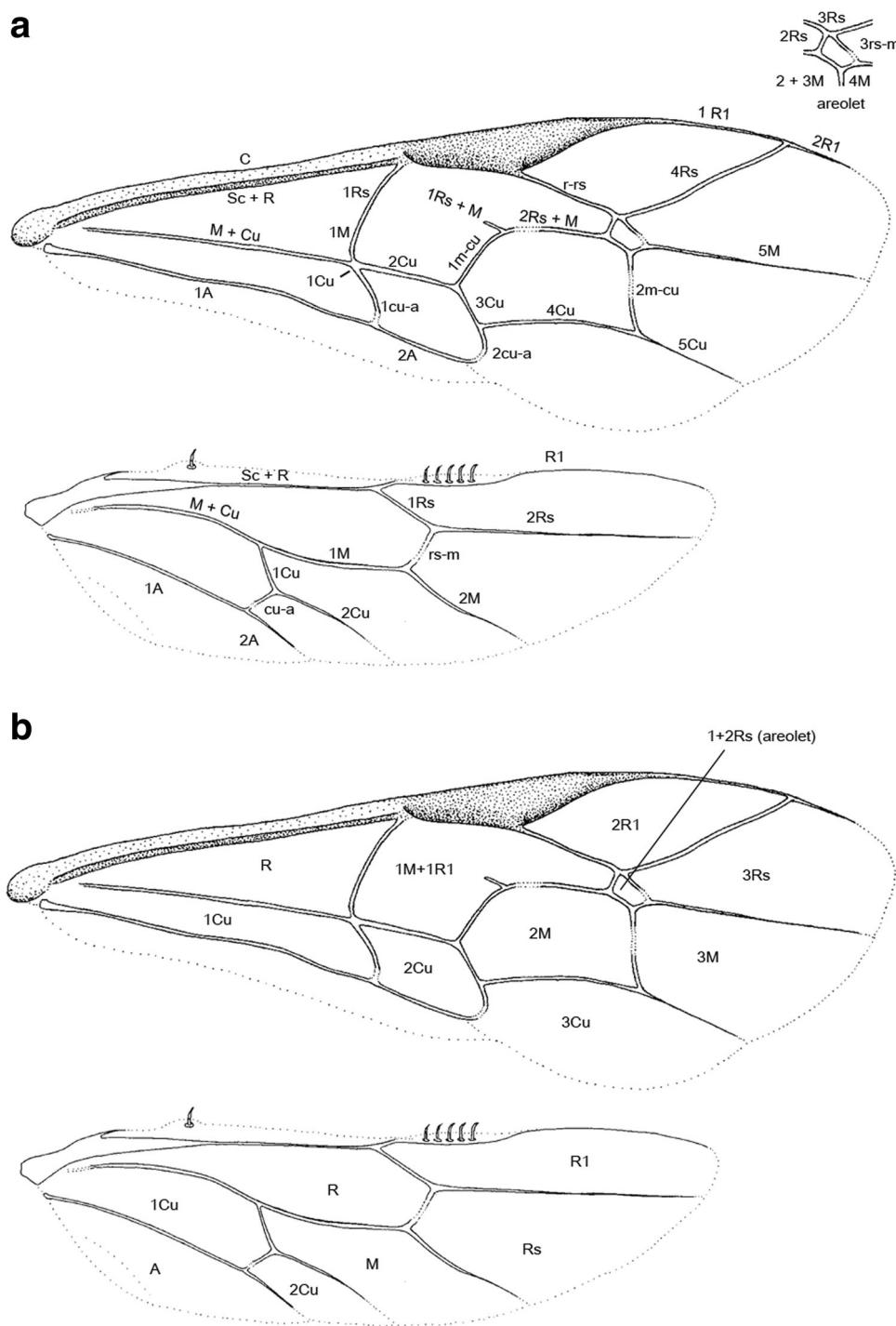
The fossil specimens newly described and revised below are deposited at the Paleobiology Department of the Smithsonian National Museum of Natural History (NMNH, specimen labels USNM), the Paleontology Section of the University of Colorado Museum of Natural History (UCM), and at the Museum of Comparative Zoology, Harvard University (MCZ, specimen labels PALE).

To describe general morphology, we used the terminology defined by Goulet and Huber (1993), while the wing venation terminology is mostly after Huber and Sharkey (Huber and Sharkey 1993) with a few modifications based on Kopylov (2009) (Fig. 3). Additional abbreviations and explanations: T = tergite, S = sternite, areolet = fore wing area surrounded by veins 2Rs, 2 + 3M, 4M, 3rs-m and, when the areolet is pentagonal, by 3Rs. The material was studied under a Leica WILD M8 stereomicroscope with no additional medium added to the stone surface. Photographs were taken with a Leica M205 C stereomicroscope linked to the ImageJ Client software. Line drawings were prepared by overlaying the original image in Adobe Photoshop CS4. Measurements were taken on the photographs using the software ImageJ. Body length was measured from the apex of the head to the tip of the metasoma (excluding the ovipositor). Unless stated otherwise, measurements represent lengths of the respective structures. The ovipositor/fore wing ratio was expressed as the relative length of the ovipositor sheaths (or the portion of the ovipositor projecting beyond the tip of the metasoma) compared to fore wing length. Given the preservation status of the fossils, we acknowledge a possibly larger measurement error than is common when studying extant species.

### Preservation and character interpretation in fossils

Wing venation represents one of the most reliable sources of information from compression fossils of Hymenoptera, as it is often very well-preserved. Accordingly, a considerable part of ichneumonid fossil taxonomy is based on wing venation characters (e.g., see Khalaim 2008; Kopylov 2009, 2010b). In most specimens, we managed to restore the complete fore wing venation, while hind wings were often incomplete or not preserved at all. There were major issues in recognising the position and size of the bullae in the fore wing, because breaks in a vein may also be a result of the fossilisation process. In contrast to the wings, most body parts regularly get distorted or detached during fossilisation, making character interpretation less

**Fig. 3** Ichneumonidae wing nomenclature based mostly on Huber and Sharkey (1993) with a few modifications after Kopylov (2009). **a** Wing veins and **b** wing cells



straightforward and less reliable. One of the most challenging steps was interpreting the position and view of the different body parts. For example, a ventral aspect of the metasoma could be misidentified as being dorsal, and in turn the sternites (only partially sclerotized in almost all Ichneumonoidea) can be mistaken for colour patterns on the tergites. Propodeal carinae could be interpreted differently depending on the angle of view onto the propodeum.

We thus took extra care interpreting these body parts by comparing different fossils. The fossils show colouration with different shades of brown and the colouration of body parts was recorded as observed. We assumed that the observed colour patterns in the fossils, even if not the colours themselves, reflect the state in live specimens since comparable colour patterns are present in recent taxa. Part and counterpart were defined based on the quality of the

fossil remains, with the part always better preserved than the counterpart. For the revised fossils, we followed the part and counterpart assignments in the original descriptions. In the taxonomic section, we noted when a certain character was visible only in the part [indicated by an “(a)’] or the counterpart [indicated by a “(b)’].

### Revision of described Green River ichneumonids

We tried to locate all the types of the previously described Ichneumonidae fossils from the Green River Formation by checking the online databases paleobiodb.org (PaleoBioDB 2016) and gbif.org (GBIF 2016) and by contacting institutions that are known to host Green River samples (NMNH, UCM, MCZ). We found holotypes of eight of the ten species and obtained high-resolution photographs for these. Two holotypes could not be located (*Rhyssa juvenis* Scudder, 1890 and *Glypta transversalis* Scudder, 1890). We re-described and revised all fossils based on the original descriptions and, when possible, on subsequent descriptions and photographs. Reassessment of their taxonomic placement followed the rules of open taxonomy.

### Open taxonomy to reflect taxonomic uncertainty

We follow a cautious approach when placing fossils into higher-level groups, making use of the nomenclature from open taxonomy (Matthews 1973). Accordingly, in cases where we were unable to place a fossil with some certainty in one of the extant subfamilies, it is placed within Ichneumonidae *incertae subfamiliae*. This applies both to taxa newly described and to revisions of previously described taxa. At the genus-level, we kept the previous classification when there was no clear evidence that a fossil does not belong to the assigned genus, but expressed insufficient evidence by adding a question mark (?) after the genus name. Differing from Matthews (1973), we kept the name of the original author without brackets when adding a question mark, as the brackets could be mistaken to indicate a change of the genus name.

### Systematic palaeontology

#### Description of new fossil species

Order Hymenoptera Linnaeus, 1758

Family Ichneumonidae Latreille, 1802

*Diagnosis.* Antennae long and filiform; fore wing veins C and Sc + R fused; cell 1M + 1R1 fused; vein 2m-cu present.

#### Ichneumonidae *incertae subfamiliae*

Genus *Carinibus* gen. nov.

*Etymology.* Named after the dorsal longitudinal carinae present on T1 and T2; gender masculine.

*Type species.* *Carinibus molestus* sp. nov.

*Diagnosis.* Strongly petiolate areolet with vein 4M absent. T1 and T2 with strong dorsal longitudinal carinae. Notauli present until around half of mesoscutum length, more or less parallel. Propodeum with almost complete carination. 1cu-a at junction of M + Cu and 1M. 2R1 cell clearly longer than wide. T1 slightly longer than broad with more or less parallel sides.

*Systematic placement.* The propodeal carination together with the shape of the first tergite and most of the wing suggests the subfamily Tryphoninae, and more precisely, the tribe Oedemopsini Woldstedt, 1877 due to the overall body shape. But the fossil differs from most of the representatives of this tribe by having the areolet closed (3rs-m present) and from all Tryphoninae by having two dorsal longitudinal carinae on T2. Such carinae are known to occur only in some species of the subfamilies Agriotypinae Haliday, 1838 (Bennett 2001), Metopiinae Förster, 1869 (several genera) (Townes 1971), Diplazontinae (*Enizemum* Förster, 1869; see Klopstein 2014), and Orthocentrinae (*Orthocentrus* Gravenhorst, 1829; see Veijalainen et al. 2014). However, the wing venation in this fossil differs clearly from that of Metopiinae, where the areolet is mostly longer than high, almost never without vein 4M and never as strongly petiolate, 1m-cu is not strongly bent at the base, and cell 2R1 is shorter. Furthermore, T2 and T3 are not fused into a syntergite as in Agriotypinae, and Diplazontinae and Orthocentrinae never have the areolet so strongly petiolate. Diplazontinae also have a reduced propodeal carination. The wing venation, especially the petiolate areolet, together with the propodeal carination could also point to Ctenopelmatinae Förster, 1869, but the fossil cannot be matched to any extant genus (Townes, 1970b). Considering that the combination of characters present in this genus is not seen in any of the extant genera and subfamilies, we here define the new genus *Carinibus* and place it in Ichneumonidae *incertae subfamiliae*.

*Carinibus molestus* sp. nov.

Figure 4

*Etymology.* Derived from the Latin “molestus”, meaning troublesome, which expresses the trouble we had placing the fossil.

*Holotype.* USNM 580881, part (a) and counterpart (b), female or male. Dorsolateral aspect of body with antennae,

fore wings, incomplete hind wings, and indication of hind legs; without ovipositor.

**Locality and horizon.** Anvil Point, Colorado, USA; Site No: 40193. Parachute Creek Member, Green River Formation, Eocene.

**Diagnosis.** As for the genus by monotypy.

**Description.** Head, mesosoma and T1 dark brown with lighter areas; anterior halves of T2–T4 brown while posterior halves lighter. Wing veins brown; pterostigma similar colour with small light area basally. Head in dorsal aspect. Antennae complete (b),  $1.32 \times$  as long as fore wing, with at least 27 flagellomeres. Scape  $1.57\text{--}1.76 \times$  as long as wide, truncated at angle of around  $50^\circ$ . Pedicel not conspicuously narrower but shorter than scape. Distinct but distorted impression of eyes, which might be a bit enlarged. Notauli present at least until 0.5 of mesosoma and on this part more or less parallel (a). Mesopleuron not completely preserved. Propodeum not obviously elongate and with several carinae visible (b): one lateral longitudinal carina, two medial longitudinal carinae, posterior transverse carina (at least middle and lateral portions), and anterior transverse carina (at least lateral portion). Fore wing areolet triangular petiolate, 2Rs around  $0.7 \times 2 + 3M$  and  $0.8 \times 3rs-m$ , 4M absent. 4Rs slightly sinusoidal to straight. Pterostigma  $4 \times$  as long as deep,  $0.81 \times 1R1$ . 2Cu  $1.19 \times 1M\&1Rs$ ,  $1.22 \times r-rs$ . 1cu-a at junction of M + Cu and 1M. 2m-cu probably with one large bulla in upper half of vein. Fore wing between  $0.31 \times$  and  $0.36 \times$  as deep as long. T1 in dorsal aspect around  $2.0 \times$  as long as wide, with two dorsal longitudinal carinae extending over entire length, parallel; T2  $0.71 \times$  as long as wide, with dorsal longitudinal carinae extending to at least 0.5 of length; remaining tergites transverse. Measurements: antennae = 6.6 mm; fore wing length = 5 mm, depth = 1.4 mm; body = 6.5 mm; metasoma = 3.8 mm; T1 = 0.8 mm; T2 = 0.5 mm.

### Ichneumonidae incertae subfamiliae

#### Genus *Ichninsum* gen. nov.

**Etymology.** From the root of the family name and latin “insum,” which means “belong” or “be in”; gender neuter.

**Type species.** *Ichninsum appendicrassum* sp. nov.

**Diagnosis.** Arolet quadrate with uneven sides. Hind wing 1Cu longer than cu-a. Femora thickened. Mesoscutum with long parallel notauli. Cell 2R1 clearly longer than deep. 2m-cu with two bullae. 1cu-a at junction of M + Cu and 1M. T1 elongate, around  $2 \times$  as long as broad.

**Systematic placement.** Based on the areolet shape, the two bullae in 2m-cu, the ratio 1Cu/cu-a in the hind wing and the

shape of T1, the fossil could belong to Pimplinae Tryphoninae or Ctenopelmatinae. These character states are probably homoplastic, which makes it difficult to place the fossil. The bicoloured hind tibia and thick femora and antennae match Pimplinae more closely than the other two subfamilies; within Pimplinae, the fossil resembles the genus *Theronia* Holmgren, 1859 in general appearance, but differs in the ratio of 1Cu and cu-a in the hind wing, shape of 2M cell and curved 1M&1Rs. The thick femora and antennae could point to Metopiinae, since these characters do not occur or are very rare in the other mentioned subfamilies. However, the wing venation is clearly different from Metopiinae that have 2m-cu with one bulla and very straight and the shape of cells 1M + 1R1 and 2R1 clearly different. The specimen also resembles *Brachycyrtus* Krichbaumer, 1880 (Brachycyrtinae Viereck, 1919) or *Labium* Brullé, 1846 (Labinae Ashmead, 1900) in general appearance, as they also have almost clavate antennae and a short mesosoma (very short in *Brachycyrtus*). However, it differs from all extant species of either genus by the shape of the areolet (vein 3rs-m absent in *Brachycyrtus* and areolet pentagonal in *Labium*), shorter T1 and the spiracle around the middle of T1 (Townes 1969). Overall, we cannot place the fossil into a single recent genus and thus describe a new genus and place it within Ichneumonidae incertae subfamiliae.

#### *Ichninsum appendicrassum* sp. nov.

##### Figure 5

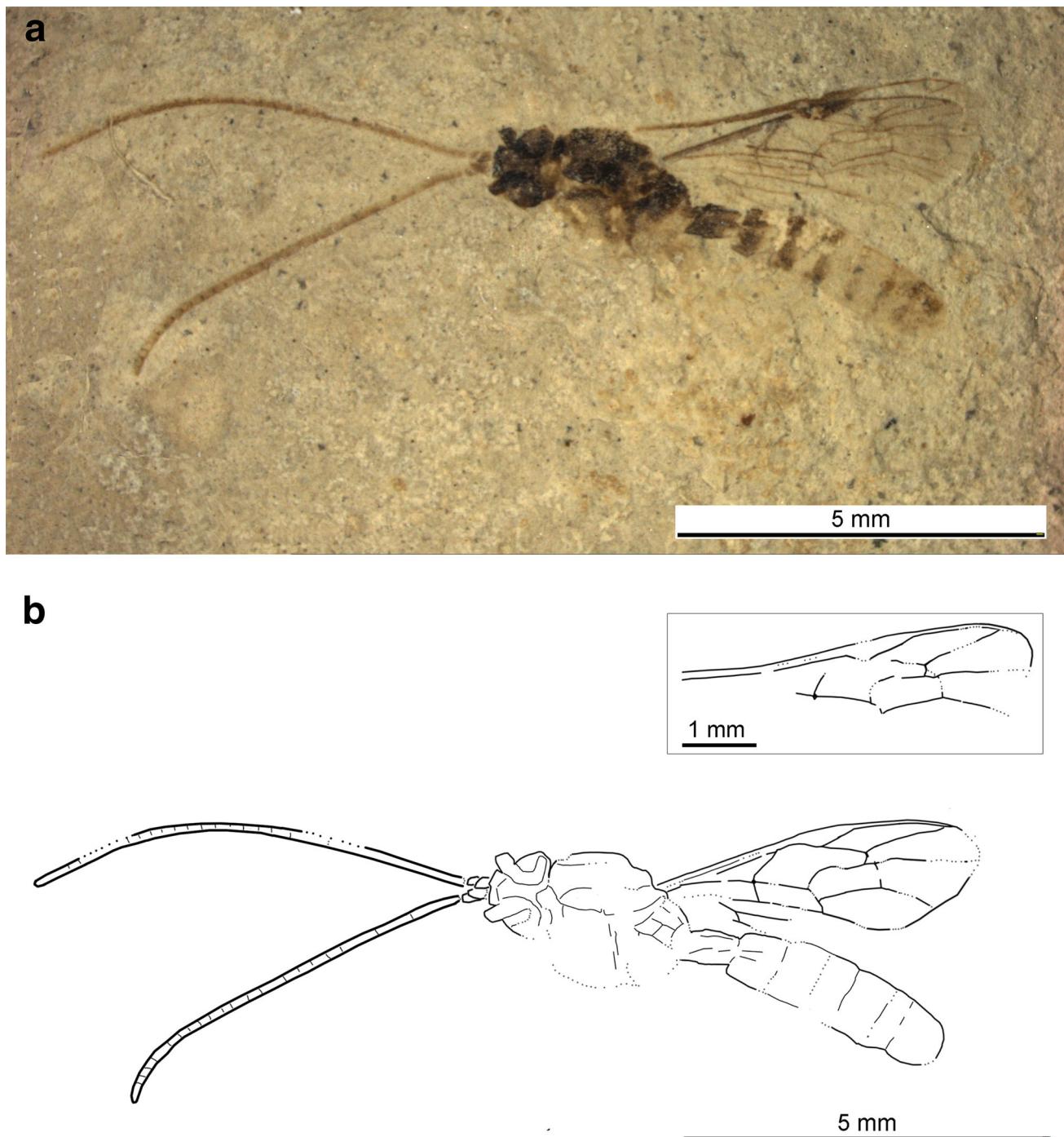
**Etymology.** From the Latin “appendix” meaning appendages and “crassus” meaning thick; it refers to the thick antennae of the fossil.

**Holotype.** UCM 39378, part (a) and counterpart (b), female or male. Lateroventral aspect of body with fore wings, hind wings and antennae; hind legs preserved as weak impressions; without ovipositor.

**Locality and horizon.** Denson, Garfield, Colorado, USA; UCM Locality: 2007238. Parachute Creek Member, Green River Formation, Eocene.

**Diagnosis.** As for the genus by monotypy.

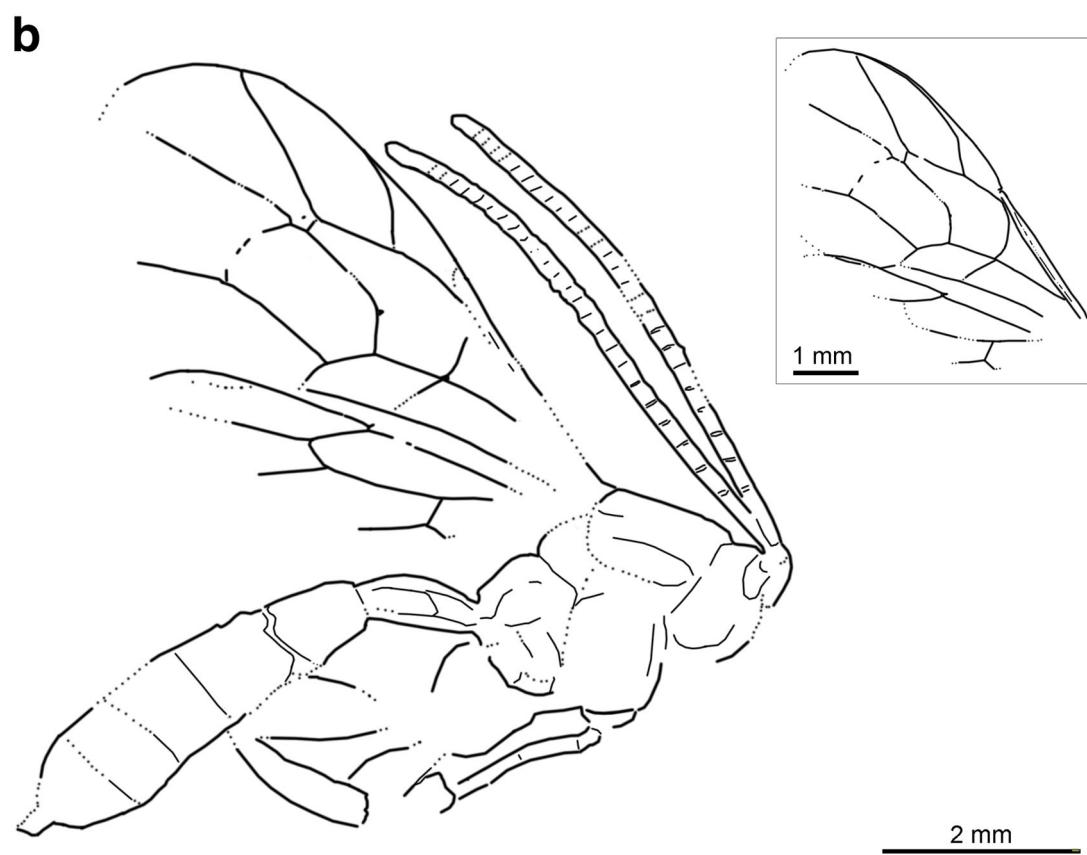
**Description.** Head and mesosoma dark brown, possibly with some lighter patches. T1 dark brown; remaining tergites with lighter colour in posterior halves. Antennae light brown. Wing veins brown; pterostigma darker brown with small light patch basally. Hind tibia bicoloured with subbasal area and apex brown and lighter band in between. Antennae complete, thick, about 27–28 flagellomeres, around  $0.9 \times$  as long as fore wing; central flagellomeres quadrate, distal ones transverse. Notauli present and



**Fig. 4** *Carinibus molestus* gen. et sp. nov., holotype USNM 580881. **a** Photograph and **b** drawing; dorsolateral aspect. Dashed lines indicate uncertain interpretations. Left and right fore wings were separated in the drawing

extending over entire mesoscutum, converging but never meeting. Epicnemial carina present at least laterally. Propodeum in lateral aspect with ventral portion partly visible and with pleural carina and probably lateral longitudinal carina (a). Fore wing areolet quadrate with uneven sides, 2Rs  $0.62 \times 2 + 3M$  and  $0.58 \times 3rs-m$ ,  $2 + 3M 3.4 \times 4M$ , 3Rs as long as width of surrounding veins. 4Rs straight.

Pterostigma  $2.9 \times$  as long as deep,  $0.57 \times 1R1$ . 2Cu  $0.98 \times 1M & 1Rs$ ,  $0.74 \times r-rs$ . 1m-cu & 2Rs + M angled to slightly arched; 1Rs + M as long as width of surrounding veins. 1cu-a at junction of M + Cu and 1M. 2m-cu probably with two bullae. 3Cu  $1.47 \times 2cu-a$ . Fore wing  $0.43 \times$  as depth as long. Hind wing 1Cu longer than cu-a, at most  $1.6 \times$ . Legs thickened, hind femur  $3 \times$  to  $3.5 \times$  as long as wide. Hind



◀Fig. 5 *Ichninsum appendicrassum* gen. et sp. nov., holotype UCM 39378. **a** Photograph and **b** drawing; lateroventral aspect. Dashed lines indicate uncertain interpretations. Left and right fore and hind wings were separated in the drawing

tibia slightly more than  $4.1 \times$  as long as wide. T1 and probably rest of metasoma mostly in ventral aspect. Sclerotized part of S1 reaching 0.42 length of T1; spiracle may be located at 0.47 of T1. T2 slightly elongate,  $1.22 \times$  as long as wide. T2–T3 with clear sculpture, rugulo-punctate; distance between punctures less than their diameter (b). Remaining tergites subquadrate to transverse. Measurements: antennae = 6.1 mm; fore wing length = 6.2 mm, depth = 2.9 mm; body = 7.9 mm; metasoma = 6.1 mm; T1 = 1.2 mm; T2 = 0.9 mm; hind femur length  $\approx$  1.5 mm, width  $\approx$  0.6 mm; hind tibia length  $\approx$  1.8 mm, width = 0.4 mm.

#### Subfamily Acaenitinae Förster, 1869

##### Genus *Mesoclistus* Förster, 1869

###### *Mesoclistus?* *yamataroti* sp. nov.

Figure 6

**Etymology.** Named after the superficial resemblance to the recent genus *Yamatarotes* Uchida, 1929 in general appearance, especially in terms of colour pattern and shape of T1.

**Holotype.** UCM 62725, part, female or male. Laterodorsal aspect of body with complete fore wings, indication of hind legs and incomplete antennae, hind wings and metasoma; without ovipositor.

**Locality and horizon.** Labandeira, Anvil Point, Garfield, Colorado, USA; UCM Locality: 2005026. Parachute Creek Member, Green River Formation, Eocene.

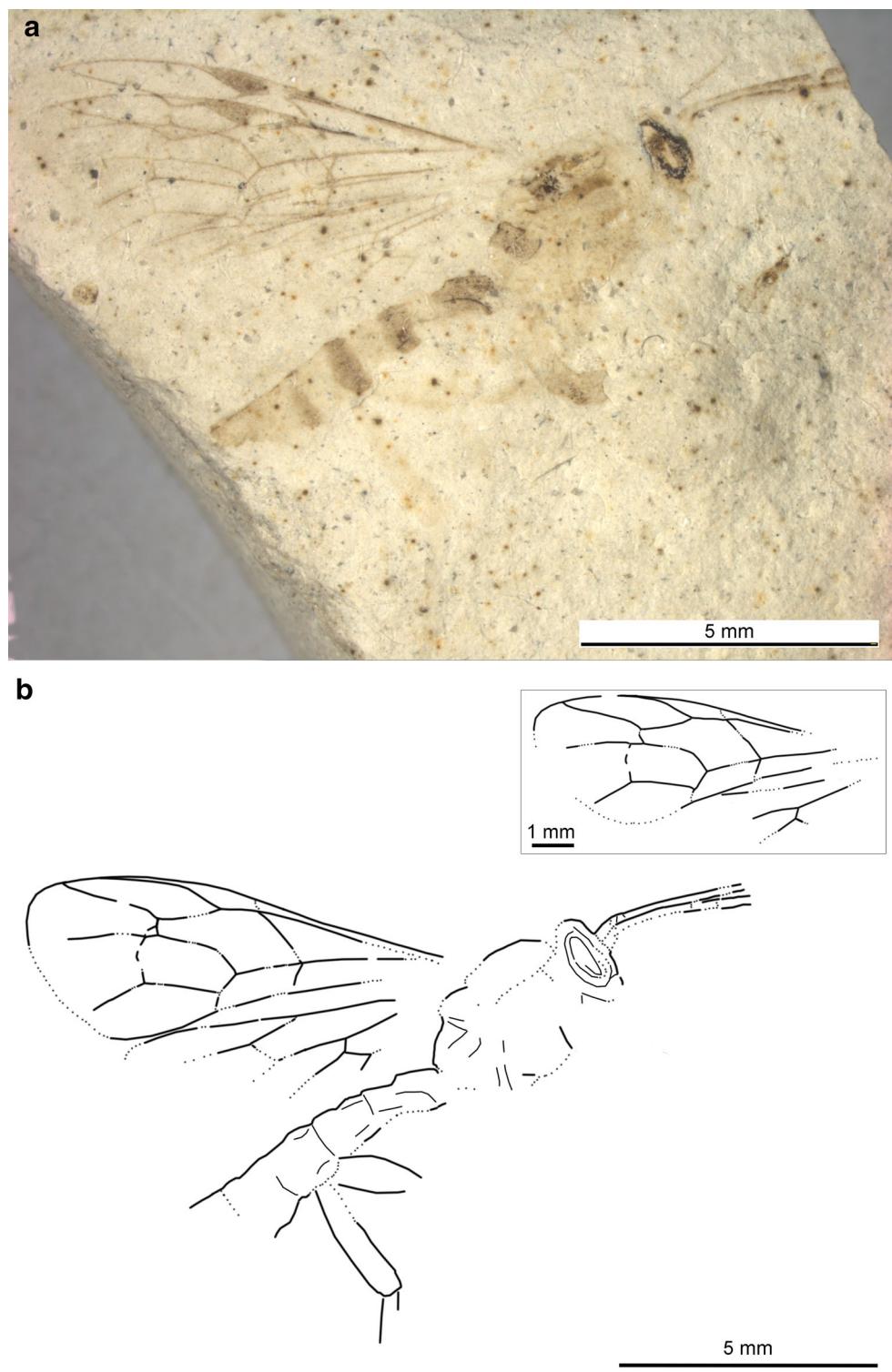
**Diagnosis.** Areolet triangular and strongly petiolate, 4Rs long and proximally curved, 2m-cu with two bullae; hind wing 1Cu around  $0.5 \times$  cu-a. Longitudinal impressions on lateral sides of T2 and T3. Femora thickened. Anterior halves of T1–T4 brown, distinctly lighter posterior.

**Comparison.** *Mesoclistus?* *yamataroti* sp. nov. differs from all the congeneric species by the light ground colouration of body and bicoloured metasomal segments T1–T4.

**Systematic placement.** The specimen is placed in the subfamily Acaenitinae based on the general appearance, petiolate areolet, proximally curved and long 4Rs, two bullae in 2m-cu, length of 1Cu compared to cu-a in the

hind wing, length and shape of T1, and the longitudinal impressions on T2 and T3 (Townes 1971). A petiolate areolet, proximally curved and long 4Rs, and longitudinal impressions on T2 and T3 all occur in the subfamily Banchinae, but not within a single genus. Furthermore, paired longitudinal impressions on the tergites, if present in Banchinae, are closer to each other than to the lateral margins of the tergites, 1cu-a is usually posterior to the junction of M + Cu and 1M, and 2m-cu is straight and often with one bulla. Within the subfamily Acaenitinae, a reasonable position is within the *Coleocentrus* genus-group because of the closed areolet, which is open in all extant members of the *Acaenitus* genus-group (there is no presumption of monophyly of the *Coleocentrus* genus-group; Wahl and Gauld 1998). The specimen fits well in the genus *Mesoclistus* considering fore wing length and 1Cu being  $0.57 \times$  cu-a; in almost all other coleocentrine genera, 1Cu is around  $0.3 \times$  or less the length of cu-a. It differs from *Mesoclistus* in the thicker femora and the conspicuous colour pattern. Such colouration is found more often within representatives of the *Acaenitus* genus-group—it bears a very strong resemblance to species of the extant genus *Yamatarotes*. In addition, *Yamatarotes* is characterized by elevations in the first half of T1 which strongly resembles the situation in the fossil, hence the species name.

**Description.** Head dark brown, possibly with lighter patches. Mesosoma light brown with darker brown patches; propodeum anteriorly dark brown. Anterior halves of T1–T4 brown, distinctly lighter posteriorly. Scape, pedicel, and about seven flagellomeres preserved; border of scape and pedicel not clear, pedicel distinctly smaller than scape. Head rather short and high. Mesosoma poorly preserved. Propodeum not elongate, with pleural carina and probably lateral longitudinal carina. Fore wing areolet triangular and strongly petiolate, 2Rs  $0.65 \times 2 + 3M$  and  $0.62 \times 3rs-m$ , 4M absent. 4Rs curved proximally and slightly distally. Pterostigma  $3.7 \times$  as long as deep,  $0.67 \times 1R1$ . 2Cu  $1.03 \times 1M & 1Rs$  and  $1.04 \times r-rs$ . 1m-cu at junction of M + Cu and 1M. 3Cu  $1.68 \times 2cu-a$ . 1m-cu & 2Rs + M arched to slightly curved. 2m-cu with two bullae occupying 20 and 20–30% of the vein, respectively (smaller bridge in between). Fore wing  $0.36 \times$  as deep as long. Hind wing incomplete, 1Cu  $0.57 \times$  cu-a. Large part of hind femur visible, whole hind tibia and part of first metatarsus. Hind tibia around  $4.6 \times$  as long as wide. Metasoma in dorsal aspect. T1 with long dorsal carina extending more than  $0.5 \times$  of T1. T2 and T3 slightly elongate to subquadrate. Longitudinal or slightly diagonal impressions on lateral sides of T2 and T3. Measurements: fore wing length = 8.6 mm, depth = 3 mm;



**Fig. 6** *Mesoclistus?* *yamataroti* sp. nov., holotype UCM 62725. **a** Photograph and **b** drawing; laterodorsal aspect. *Dashed lines* indicate uncertain interpretations. Left and right fore and hind wings were separated in the drawing

body  $\geq 9.5$  mm; mesosoma  $\approx 3.1$  mm; T1 = 1.5 mm; T2 = 1.1 mm; hind femur length  $\approx 1.9$  mm, width  $\approx 0.6$  mm; hind tibia length = 2.6 mm, width = 0.6 mm.

#### Subfamily Pimplinae Wesmael, 1845

##### Genus *Scambus* Hartig, 1838

###### *Scambus?* *mandibularis* sp. nov.

Figure 7

**Etymology.** Named after the well-preserved mandibles of the fossil.

**Holotype.** USNM 501474, part, female. Ventrolateral aspect of body with ovipositor, incomplete fore wings, hind coxa and weak indications of some other parts of hind legs; without hind wings, antennae and rest of legs.

**Locality and horizon.** Forked Gulch, Old Mountain, Colorado, USA; Site No. 40189. Parachute Creek Member, Green River Formation, Eocene.

**Diagnosis.** Arolet quadrate with uneven sides. 1cu-a at junction of M + Cu and 1M. 2m-cu curved and with two separate bullae. Ovipositor around  $0.5 \times$  fore wing and  $0.7 \times$  metasoma length. Head, mesosoma, hind coxae and T1 dark brown; remaining metasomal segments distinctly lighter. Pterostigma brown with lighter base.

**Comparison.** The species clearly differs from “*Scambus*” *fossilis* Khalaim (Antropov et al. 2014) in size (fore wing length 3.8 cm in “*Scambus*” *fossilis*), narrower 2R1 cell and shorter T1. *Scambus?* *mandibularis* differs from most of the extant congeneric species by the combination of (1) entirely dark brown mesosoma, (2) dark brown hind coxa (3) metasomal T2–T6 distinctly lighter than T1, which is concolorous with the mesosoma, (4) pterostigma more or less uniformly brown with base lighter and (5) ovipositor shorter than metasoma (Fitton et al. 1988; Kolarov 1997; Gomez and Yabar-Landa 2015). However, complete comparison with all the extent *Scambus* species is difficult considering the genus heterogeneity, high species number, and incompleteness of the fossil.

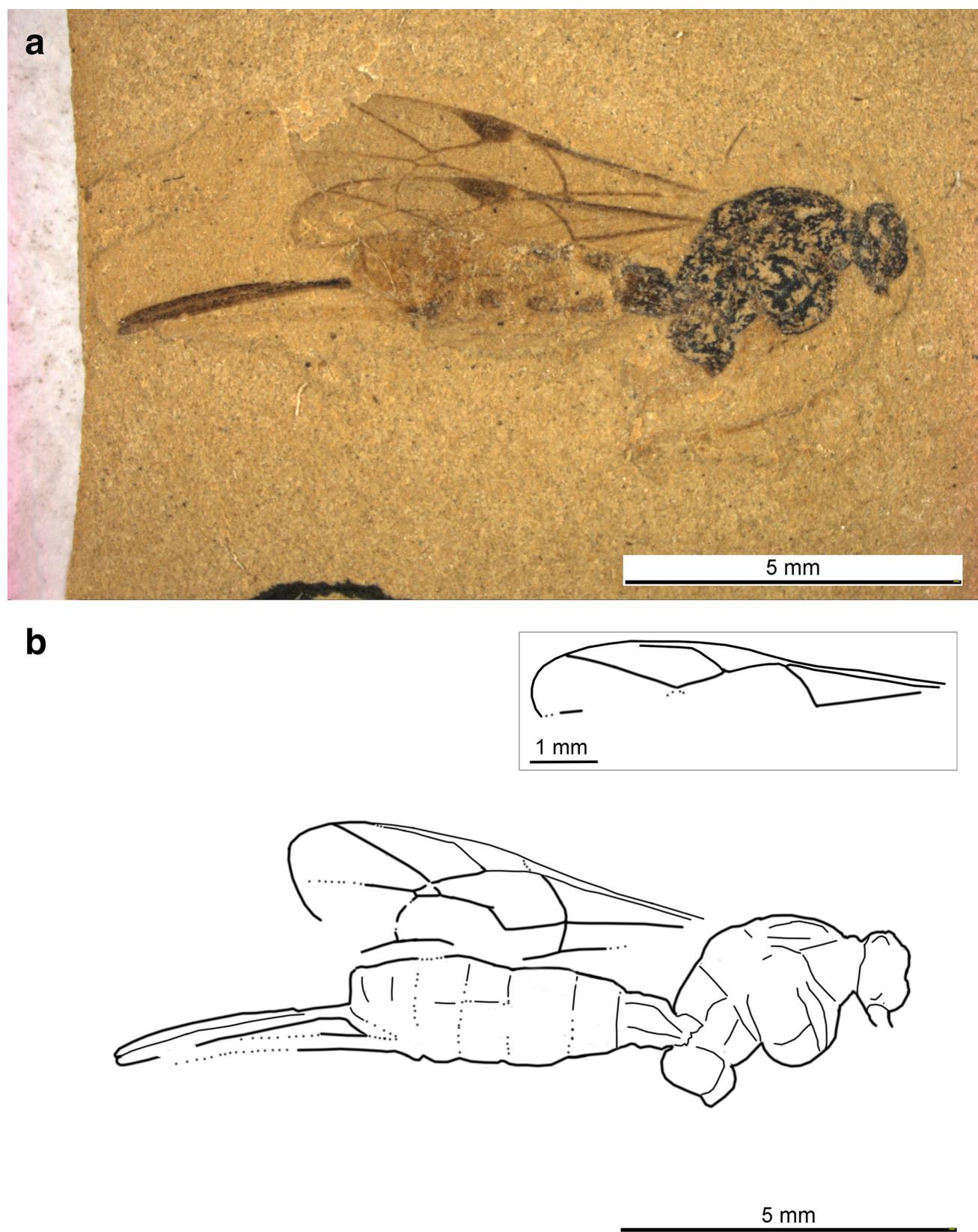
**Systematic placement.** The wing venation, especially the shape of the areolet, the shape of the first tergite, and ovipositor length and width are frequently seen in species of the subfamily Pimplinae. Similar venation and a short and parallel-sided tergite 1 also occur in certain representatives of the subfamilies Tryphoninae, Ctenopelmatinae, and Banchinae; the former two mostly have a much shorter ovipositor, while it is usually either very short or longer than the metasoma in Banchinae. Within

the subfamily Pimplinae, tribal placement is difficult since diagnostic characters are not visible (e.g. angled mesopleural sulcus, lobed claws, ratio of 1Cu and cu-a in the hind wing). We tentatively place the species in the genus *Scambus* because it fits in general appearance, wing venation, sclerotization pattern of the sternites and ovipositor length.

**Description.** Head, mesosoma, hind coxa and T1 dark brown; coloration of remaining tergites distinctly lighter than T1; dark patches on metasomal segments two to four probably representing sternites. Wing veins brown; pterostigma slightly darker than veins, with light spot basally. Ovipositor sheaths dark brown; ovipositor light brown. Antennae only weakly indicated, filiform; pedicel and scape not clearly outlined. Head rather short, in lateral aspect. One mandible clearly visible, probably with two teeth and around  $0.8 \times$  as broad as long; malar space moderately short, around  $0.3 \times$  mandibular base. Mesosoma in ventrolateral aspect, but crushed, with mesoscutum partly visible. Some irregularities present on mesoscutum, but no clear evidence of notaui. Mesosternum with epicnemical carina present at least until mid-height of pronotum. Mesosternum with deep mesosternal furrow. Propodeum not elongate, higher than long, presence or absence of carinae unclear. Fore wing areolet quadrate with uneven sides, 2Rs  $0.4 \times 2 + 3M$ ,  $2 + 3M 5 \times 4M$ , 3Rs as long as width of surrounding veins. 4Rs straight. Pterostigma  $3.25 \times$  as long as deep,  $0.71 \times$  as long as 1R1. 2Cu  $0.96 \times 1M & 1Rs$  and  $0.98 \times r\text{-}rs$ . 1m-cu&2Rs + M angled. 1Rs + M (ramulus) probably present and as long as width of surrounding veins. 1cu-a at junction of M + Cu and 1M. 2m-cu curved and with two separate bullae. Metasoma in ventrolateral aspect. T1 around  $1.35 \times$  as long as wide and probably humped in basal half. T2 and T3 not visible because dorsal aspect not preserved; T2  $0.83 \times$  as long as wide. Metasomal segments two to four with lateral dark patches which correspond to sclerotized parts of sternites (as is common in Pimplinae) rather than to laterotergites (those usually being same colour as tergites). Metasomal segment four to eight partly in lateral aspect, sclerotized plates complete only in lower part of metasomal segments four and five; border between tergites/sternites discernible where tergites partially cover sclerotized plates. T6 and T7 of similar lengths. Ovipositor sheaths well-preserved, stout and robust, around  $0.5 \times$  fore wing length. Ovipositor present as weak indication with base below T5 or T6. Measurements: fore wing length = 6.6 mm, depth  $\approx 2.2$  mm; body = 8.3 mm; metasoma = 4.9 mm; T1 = 0.9 mm; T2 = 0.7 mm; ovipositor sheaths = 3.5 mm.

###### *Scambus?* *parachuti* sp. nov.

Figure 8



**Fig. 7** *Scambus?* *mandibularis* sp. nov., holotype USNM 501474. **a** Photograph and **b** drawing; ventrolateral aspect. Dashed lines indicate uncertain interpretations. Left and right fore wings were separated in the drawing

**Etymology.** Named after the stratigraphic unit of Green River Formation where the fossil was found, the Parachute Creek Member.

**Holotype.** USNM 565885, part, female. Lateral aspect of body with antennae, fore wings, ovipositor and parts of hind legs; without hind wings.

**Locality and horizon.** Labandeira Site, Anvil Point, Colorado, USA; Site No. 41088. Parachute Creek Member, Green River Formation, Eocene.

**Diagnosis.** Areolet quadrate with uneven sides. 1cu-a at junction of M + Cu and 1M. 2m-cu with two separated bullae. Notauli present, more or less parallel and extending more than half of mesoscutum length. Ovipositor sheaths around 0.3× fore wing and 0.5× metasoma length. Antennae shorter than fore wing. Head, mesosoma and T1 dark brown; remaining tergites and hind legs conspicuously lighter; T2 with anterior half darker. Pterostigma brown with light base.

**Comparison.** The species clearly differs from “*Scambus*” *fossilis* Khalaim (Antropov et al. 2014) in size (fore wing length 3.8 cm in “*Scambus*” *fossilis*), narrower cell 2R1 and higher 3Cu/2cu-a ratio. In comparison with *S. mandibularis* sp. nov., *S. parachuti* sp. nov. has smaller ovipositor/fore wing and 2Cu/1M&1Rs ratios. The differentiation of *S. parachuti* sp. nov. from the recent congeneric taxa is based on the same combination of characters as for *S. mandibularis* sp. nov. with the exception that the hind coxae are probably light coloured in *S. parachuti* sp. nov.

**Systematic placement.** The specimen is placed in the subfamily Pimplinae based on the areolet shape, two bullae in 2m-cu, shape of T1 and remaining metasoma, and ovipositor length and width. Within the subfamily, the angled mesopleural sulcus rather points to the tribe Ephialtini Hellén, 1915 (although it can be similar in Delomeristini Hellén, 1915 and the *Theronia* genus-group of Pimplini Wesmael, 1845). The specimen shows a strong fit with some species of *Scambus* in wing venation, general body form and colouration, propodeum shape and carination and ovipositor length. However, we would need the ratio of 1Cu and cu-a in the hind wing to place this fossil unquestionably within *Scambus*.

**Description.** Head, mesosoma and T1 dark brown; remaining tergites conspicuously lighter; T2 with anterior half darker. Antennae brown, lighter ventrally in proximal half. Wing veins brownish; pterostigma slightly darker than veins, with light spot basally. Hind legs same colour as

most of metasoma. Ovipositor sheaths dark brown. Antennae complete, 0.81× as long as fore wing. Scape conspicuously longer than pedicel, 21 flagellomeres. Occipital carina present at least laterally. Pronotum as long as deep or slightly longer than deep. Notauli present at least on anterior 0.6× of mesoscutum, more or less parallel-sided to slightly converging. Scutellum evenly convex. Epicnemical carina present, curved around mid-height of pronotum towards anterior margin of mesopleuron. Mesopleural sulcus angled opposite mesepisternal scrobe. Propodeum not elongate with lateral longitudinal carina and lateral longitudinal bumps. Propodeal spiracle oval, about 2× as long as wide. Fore wing areolet quadrate with uneven sides, 2Rs 0.48× 2 + 3M, 2Rs 0.39× 3rs-m, 2 + 3M 7.12× 4M, 3Rs as long as width of surrounding veins; 3rs-m probably with two bullae. 4Rs straight. Pterostigma 3.18× as long as deep, 0.83× 1R1. 2Cu 0.8× 1M&1Rs, 1.05× r-rs. 1m-cu&2Rs + M angled. 1Rs + M absent. 1cu-a at junction of M + Cu and 1M. 2m-cu with two separated bullae. 3Cu approximately as long as 2cu-a. Fore wing 0.41× as deep as long. Ventrolateral aspect of first metasomal segment. S1 shorter than 0.5× T1. Rest of metasoma in lateral aspect, becoming higher from fifth metasomal segment. Ovipositor sheaths well preserved, stout, 0.3× fore wing length. Ovipositor base visible, below T5. Measurements: antennae = 6 mm; fore wing length = 7.4 mm, depth = 3.1 mm; body = 8.6 mm; metasoma = 5 mm; T1 = 1.3 mm; T2 = 1 mm; ovipositor sheaths = 2.3 mm.

## Revision of described Green River ichneumonids

Subfamily *Tryphoninae* Shuckard, 1840

Genus *Eclytus* Holmgren, 1857

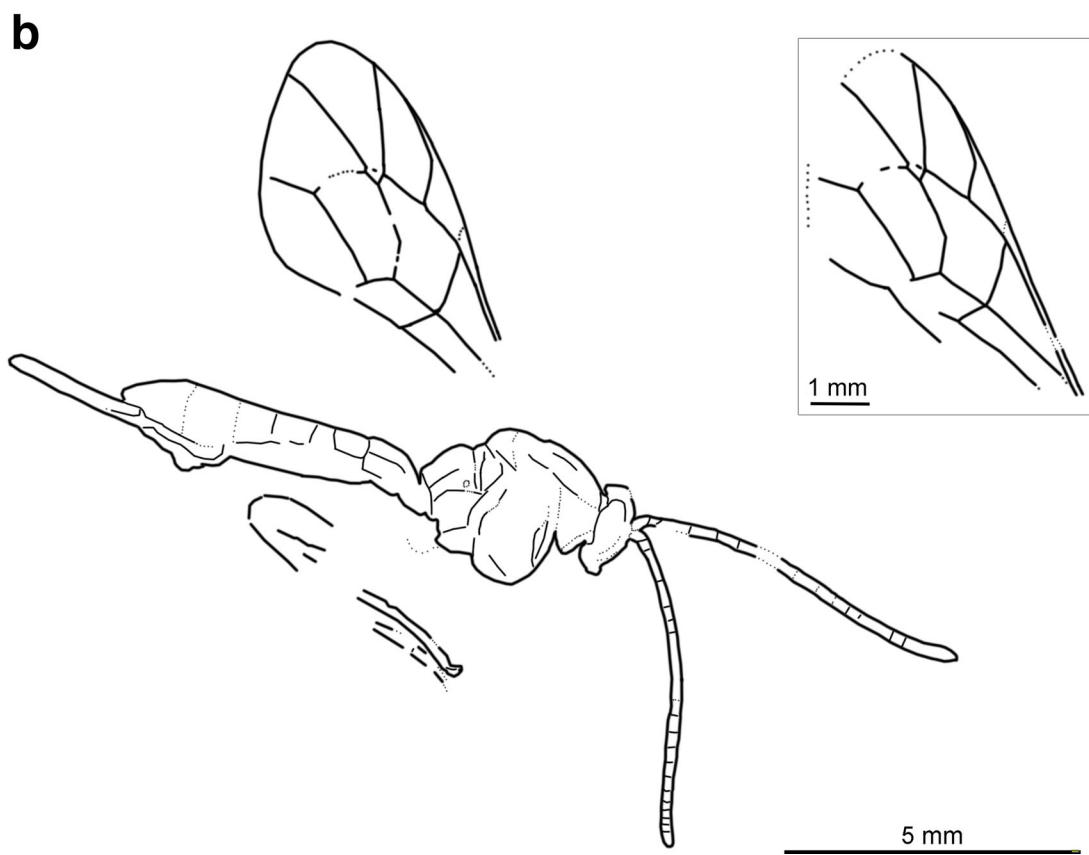
*Eclytus?* *lutatus* Scudder, 1890

Figure 9a

\*1890 *Eclytus lutatus* Scudder: p. 614, pl. X, Fig. 24

**Type material.** PALE-1481, part, female. Green River, Wyoming. Lateral aspect of body with incomplete fore wing, parts of antennae and possibly ovipositor; without legs; hind wings not visible on photograph, but might be present.

**Studied material.** We have examined the original description and drawing together with a photograph of the fossil and studied the interpretation of the drawing by Bennett (2015). The body parts are quite well preserved, but most of the wing venation is lacking. We find most of the characters difficult to interpret and thus only give a brief re-description.



◀Fig. 8 *Scambus?* *parachuti* sp. nov., holotype USNM 565885. a Photograph and b drawing; lateral aspect. Dashed lines indicate uncertain interpretations. Left and right fore wings were separated in the drawing

**Diagnosis (emended).** Pterostigma triangular and around 2× as long as deep; 1cu-a at the junction of 1M and M + Cu. Antennae approximately as long as fore wing, which is around 2.5 mm. T1 short to slightly elongated, around 2× as long as T2; T3–T7 transverse.

**Remarks.** The hind wing could not be discerned in the high-resolution photograph, neither was it represented in the drawing in the original description, even though Scudder used it to support the placement of the specimen in the genus *Eclytus* (Scudder 1890). Scudder also noted a short ovipositor (0.65 mm long) which was not visible in the photograph.

**Systematic placement.** The afore-mentioned combination of characters occurs in a few subfamilies, including Tryphoninae, Ctenopelmatinae, Cryptinae, and Orthocentrinae. The specimen differs from *Eclytus* in the deeper pterostigma and 1M&1Rs being shorter. However, we agree with Bennett (2015) that we do not have enough interpretable characters to confirm or change the placement of the fossil and thus leave it as questionable within *Eclytus*.

**Description.** Head, antennae and anterior part of mesoscutum dark red-brown; colouration of rest of mesoscutum and of mesopleuron poorly preserved. Propodeum and metasomal segments slightly lighter red-brown. Wing veins and pterostigma brown. Only distal half of antennae preserved with flagellomeres longer than wide; antennae around as long as fore wing. Considerable part of mesosoma missing and remainder hardly interpretable. Fore wing area around areolet indistinct, vein 3rs-m might or might not be present. Pterostigma triangular, around 2× as long as deep. 1cu-a at the junction of 1M and M + Cu. Remaining vein characters not preserved. T1 short to slightly elongate, around 1.94× as long as T2; T2 might be subquadrate, remaining tergites transverse. Most sternites visible as well, strongly coloured and/or sclerotized. Measurements: fore wing ≈2.5 mm; body ≈3.6 mm; metasoma ≈2.2 mm.

#### Ichneumonidae incertae subfamiliae

##### Genus *Eopimpla* Cockerell, 1920

**Type species.** *Eopimpla grandis* Cockerell, 1920

**Diagnosis (emended).** Head rather short. Mesoscutum with long notaui extending over half of its length. Epicnemical carina present. Fore wing cell 1M + 1R1 elongate. Hind wing 1Cu as long as or slightly shorter than cu-a. T1 longer than

broad, with spiracle in anterior half; sclerotized part of S1 short, less than half of T1 length. Fore wing around 11 mm.

**Remarks.** Cockerell used characters of the posterior part of the fore wing, such as the shape of cell 2Cu (“first brachial cell”, page 257 in Cockerell 1920) and the ratio 3Cu/2cu-a (“emitting the subdiscoideus almost at the lower (apical) corner”, page 257 in Cockerell 1920) to describe the new genus. However, the fore wing is clearly deformed which makes these characters doubtful. The areolet might be closed or open with either the outer vein 3rs-m or the inner vein 2Rs absent (as in Ophioninae and some Anomaloninae Viereck, 1918). However, an evenly wide T1, short S1 and spiracle on T1 around the middle excludes these two subfamilies. A similarly elongate wing with a long cell 1M + 1R1 occurs also in some Pimplinae (especially in the tribe Ephialtini), in Rhyssinae, and in Poemeniinae Narayanan and Lal, 1953; the presence of the epicnemical carina would exclude most Poemeniinae, although the carina is present in the tribe Pseudorhyssini Wahl and Gauld, 1998 and some Rodrigamini Wahl and Gauld, 1998. *Eopimpla* was originally placed in Pimplinae by Cockerell (1920) and this was supported by Carpenter (1992). However, Yu and Horstmann (1997) considered that the genus belongs to Ichneumonidae with uncertain placement. The reasons for excluding the fossil from Pimplinae are not discussed in the catalogue but probably derive from the uncertainty in placement expressed by the original author and the poor preservation of the fossil. Considering the wing length and the shape of the first tergite, we agree that the fossil might belong in Pimplinae or related subfamilies, but since we cannot place it in a single subfamily, we concur with Yu et al. (2012) that *Eopimpla* should be placed *incertae subfamiliae* within Ichneumonidae.

##### *Eopimpla grandis* Cockerell, 1920

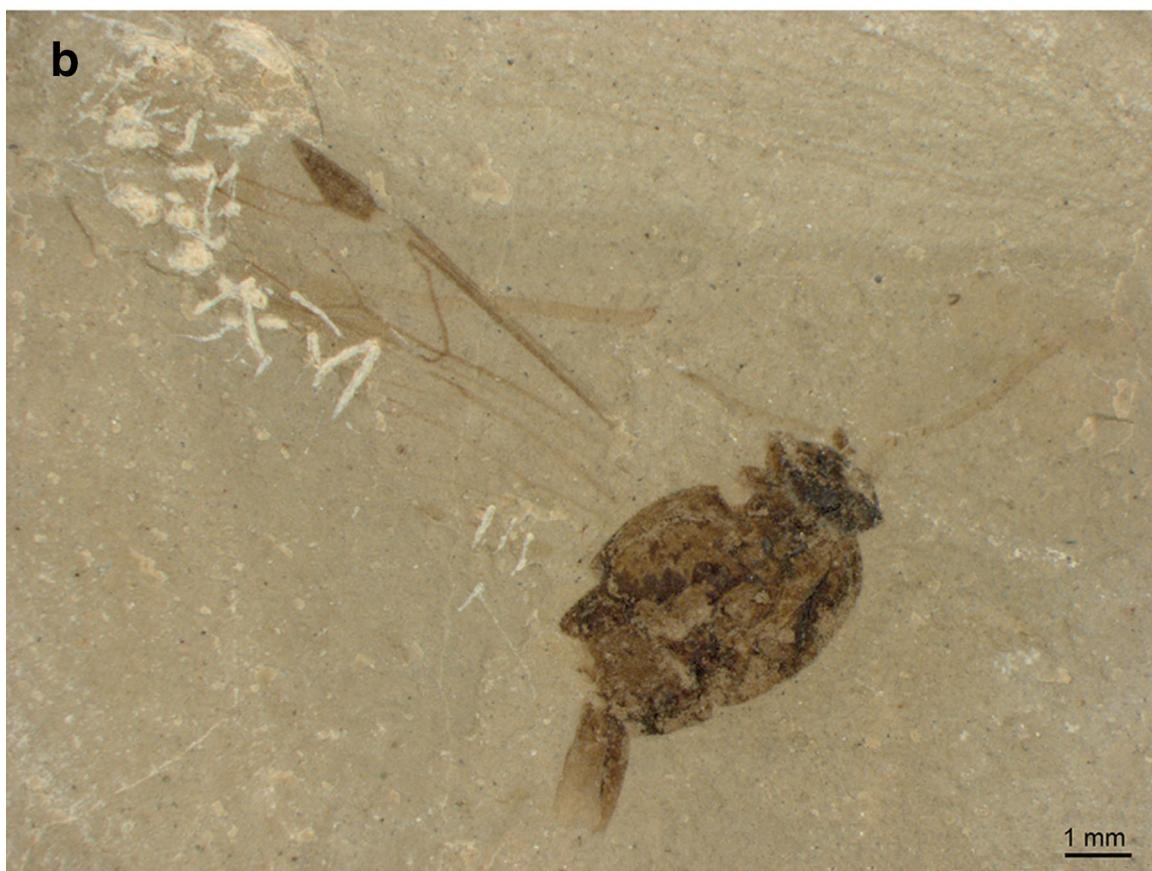
Figure 9b

\*1920 *Eopimpla grandis* Cockerell: p. 258, pl. 36, Fig. 7

**Type material.** USNM 66581, part, female or male. Cathedral Bluffs, Rio Blanco Country, Colorado, United States. Lateroventral aspect of body with incomplete antennae, fore and hind wings; only first metasomal segment present, rest missing.

**Studied material.** We have examined the original description including a drawing plus a high-resolution photograph of the fossil. The state of the fossil is rather poor, especially regarding the distorted fore wing venation and absence of most of the metasoma.

**Diagnosis.** As for the genus by monotypy.



◀Fig. 9 a *Ecytus?* *lutatus* Scudder, 1890, holotype PALE-1418; lateral aspect; ©President and Fellows of Harvard College. b *Eopimpla grandis* Cockerell, 1921, holotype USNM 66581; lateroventral aspect; ©Smithsonian Institute

**Description.** Head dark brown; mesosoma and T1 similar colouration with lighter patches. Wing veins light brown; pterostigma similar colour with light base. All visible antennal segments elongate to subquadrate. Head rather short. Strong, probably parallel, notauli present on almost entire length of mesoscutum. Some indication of epicnemical carina present, but not clear. Propodeum not elongate, deeper than long. Some longitudinal carinae visible which might correspond to pleural and/or lateral longitudinal carinae. Fore wing incomplete distally and deformed in its posterior half. Area around areolet unclear, covered by chisel marks which obscure the veins—the areolet might be open and inverted (2Rs missing) or, more probably, quadrate and closed. r-rs sinusoidal. Pterostigma around  $3.7 \times$  as long as deep. Cell 1M + 1R1 elongate, but clearly slightly deformed; 2Cu around  $0.8 \times$  1M&1Rs and r-rs. 1cu-a at junction of M + Cu and 1M or slightly posterior. 1m-cu&2Rs + M bent around middle but their shape likely artefactual. Hind wing 1Cu as long as or slightly shorter than cu-a. T1 longer than broad; spiracle at 0.48 or less of T1; sclerotized part of S1 short, probably extending only  $0.28 \times$  length of T1, but posterior border unclear. Measurements: fore wing  $\approx 11$  mm; mesosoma  $\approx 4.3$  mm; T1 at least 1.8 mm.

Subfamily **Banchinae** Wesmael, 1845

Genus **Glypta** Gravenhorst, 1829

**Glypta?** *transversalis* Scudder, 1890

\*1890 *Glypta transversalis* Scudder: p. 613, pl. X, Fig. 25

**Type material.** Holotype number unknown, part, female or male. Green River, Wyoming. Dorsal aspect of body with fore wings and incomplete hind wings; without legs or ovipositor.

**Studied material.** We have not been able to locate the holotype of this species and thus the re-description is based on the original description and drawing.

**Diagnosis (emended).** Areolet open. Hind wing 1Rs  $1.07 \times$  rs-m; M + Cu distally curved. Median part of head dark with lighter area along eyes; antero-median part and lateral parts of mesoscutum dark, light colour present along notauli; metasoma with paired dark marks laterally on T2–T4. Metasomal segments transverse.

**Remarks.** The wing venation is clearly depicted in the drawing, but with some disagreement between the two wing pairs. We based most of our interpretation on the wings on the right side of the body since the venation appears more natural and not deformed as on the left side. **Systematic placement.** Overall, the fossil might fit in the genus *Glypta*, especially considering the fore wing venation. On the other hand, the main diagnostic character for the tribe *Glyptini* Cushman and Rohwer, 1920, the oblique grooves on T2–T4, is not visible in the fossil. The ratio of rs-m to 1M in the hind wing is very characteristic and rather fits *Lycoriniae* Cushman and Rohwer, 1920 or *Scolobatini* Schmiedeknecht, 1911 (Ctenopelmatinae), although in the former, the hind wing vein 1Rs is clearly shorter than rs-m. *Physotarsus* Townes, 1966 (Scolobatini) could be a good candidate considering both fore and hind wing venation and the colour pattern. However, we did not find enough clear characters to change the placement of the fossil. A detailed examination of the type specimen would be necessary.

**Description.** Extensive dark and light colour pattern on head and mesoscutum: median part of head dark with lighter area along eyes; antero-median part and lateral parts of mesoscutum dark, light colour present along notauli; metasoma with paired dark marks laterally on T2–T4. Head rather broad compared to mesosoma. Fore wing areolet open with 2Rs as long as  $2 + 3M$  or longer. 4Rs straight. Pterostigma around  $3.6 \times$  as long as deep,  $0.96 \times$  1R1; 2Cu  $0.8 \times$  1M&1Rs,  $1.2 \times$  r-rs; 1cu-a at junction of M + Cu and 1M or slightly posterior; 3Cu longer than 2cu-a; 2m-cu straight with one or two bullae; 1m-cu&2Rs + M curved. Hind wing 1Rs  $1.07 \times$  rs-m, 1M  $1.6 \times$  rs-m; M + Cu distally curved. Metasomal segments transverse. No ovipositor visible.

**Ichneumonidae incertae subfamiliae** stat. rev. (formerly *Diplazontinae*)

Genus **Lithotorus** Scudder, 1890

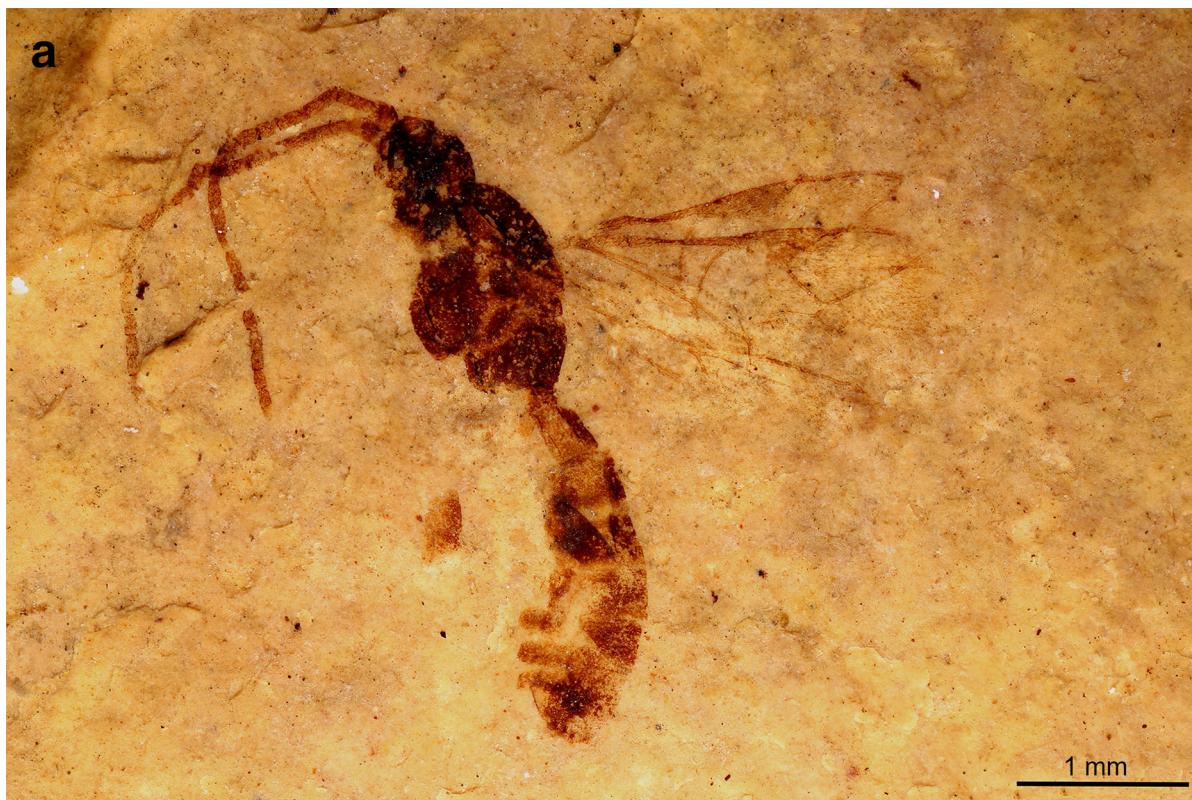
**Lithotorus cressoni** Scudder, 1890

Figure 10a

\* 1890 *Lithotorus cressoni* Scudder: p. 609, pl. X, Fig. 21

**Type material.** PALE-4652, part, female or male. Green River, Wyoming. Ventrolateral aspect of body with more or less complete antennae and fore wings and incomplete hind wings; without legs and ovipositor.

**Studied material.** We have examined the original description, including a drawing, and a high-resolution photograph of the fossil. Additionally, we have studied Townes' (1966) re-assessment of the fossil including his drawing.



◀Fig. 10 a *Lithotorus cressoni* Scudder, 1890, holotype PALE-4652; ventrolateral aspect; ©President and Fellows of Harvard College. b *Pimpla? eocenica* Cockerell, 1919, holotype USNM 66582; dorsolateral aspect; ©Smithsonian Institute

**Diagnosis.** Small species with fore wing around 2.8 mm long. Antennae approximately as long as fore wing, with 19 flagellomeres. Scape and pedicel rather stout and shortened. Areolet open or quadrate if closed. 1cu-a at junction of M + Cu and 1M. Hind wing 1Cu longer than cu-a. T1 slightly elongate, quite parallel-sided, with spiracle at anterior half of T1.

**Remarks.** Scudder (1890) described the genus *Lithotorus* and pointed out its similarity with the recent genus *Exyston* Schiødte, 1839 (Tryphoninae). He further writes about a character that supposedly distinguishes the fossil from all other members of the family Ichneumonidae: “(...) the separation of the first from the second cubital cell by a weak nervure, not shown in the plate, which extends entirely across the space usually left open in this family, though almost always closed in the Braconidae” (page 609 in Scudder 1890). He here refers to vein 1Rs + M. Townes (1966) later re-examined the fossil; he did not note the presence of this vein and also expressed uncertainty about the absence of fore wing vein 3rs-m (which would render the areolet closed). Vein 1Rs + M was not observable on the photograph of the type that we examined either, so we assume that this was an erroneous interpretation. According to Townes (1966), the fossil belongs to the subfamily Diplazontinae or is related to Orthocentrinae genera such as *Hemiphanes* Förster, 1869 or *Hyperacmus* Holmgren, 1858.

**Systematic placement.** Based on our examination, the specimen could be placed in Diplazontinae based on the box-like shape of T1 and its strong lateral longitudinal carinae (Klopfstein 2014); some diplazontine genera also show similar wing venation, except that the fore wing appears rather short and broad. This latter character state and the small size of the specimen would rather suggest that it belongs to the subfamily Orthocentrinae, and within the subfamily, the stout and short scape suggest the *Helictes* genus-group. Given that we cannot exclude either of these two subfamilies, we choose to exclude the fossil from Diplazontinae and place it in Ichneumonidae *incertae subfamiliae*.

**Description.** Antennae brownish. Head, mesosoma and T1 brown; remaining tergites similar colouration with possibly lighter patches at posterior ends. Pterostigma and wing veins light brown. Scape and pedicel seem rather stout and shortened; antennae with 19 visible flagellomeres; first

three flagellomeres around 3× as long as wide, remaining ones elongate but shorter; central flagellomeres clearly narrower proximally than distally. Other head characters indistinguishable. Propodeum not elongate, shorter than deep. Areolet probably open (or quadrate if closed), 2Rs 0.54× 2 + 3M; 4M distinguishable from 5M by angle, 2 + 3M 2.5× 4M. Pterostigma around 2.5× as long as deep, 0.8× 1R1 length. 1m-cu&2Rs + M bent; 1Rs + M absent. 1cu-a at junction of M + Cu and 1M. 2Cu 0.96× 1M&1Rs, 1.14× r-rs. 2m-cu with one or two bullae. Hind wing 1Cu longer than cu-a; 1Rs around 1.6× as long as rs-m. T1 slightly elongate, quite parallel-sided, possibly humped in basal half and with strong lateral carinae on T1; spiracle present at around 0.4 of T1. T2 subquadrate, around 0.86× as long as T1. Remaining segments more or less transverse. Measurements: antennae = 2.8 mm; fore wing = 2.8 mm; body = 4 mm; metasoma = 2.2 mm; T1 = 0.5 mm.

Subfamily **Pimplinae** Wesmael, 1845

Genus **Pimpla** Fabricius, 1804

**Pimpla? eocenica** Cockerell, 1919

Figure 10b

\*1919 *Pimpla eocenica* Cockerell: p. 122

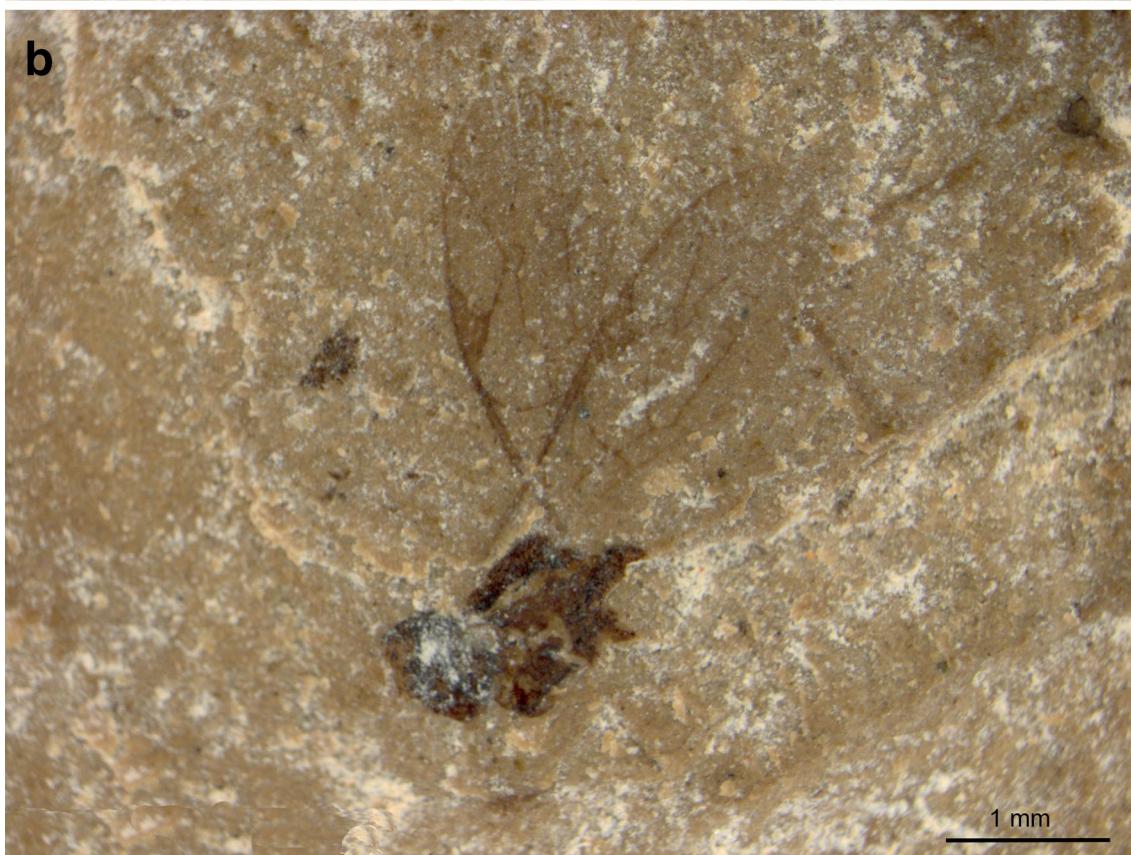
**Type material.** USNM 66582, part, female. Spring at head of Little Duck Creek, Colorado, United States. Dorsolateral aspect of body with one complete fore wing, an incomplete second fore wing, parts of hind wing and ovipositor; without antennae or legs.

**Studied material.** We have examined the original description including a drawing, and a high-resolution photograph of the fossil. Additionally, we have studied the re-description by Cockerell (1920).

**Diagnosis.** Mesoscutum with notauli present, strongly converging and extending at least over anterior 0.6. Areolet quadrate with uneven sides. 1Rs + M present, around 4× as long as width of surrounding veins. T1 subquadrate, with two dorsal longitudinal carinae. Ovipositor at least 0.2× as long as fore wing.

**Remarks.** Cockerell (1919) placed the fossil in *Pimpla*, but considered the genus in the broad sense, while also pointing out similarities with *Theronia* and related genera.

**Systematic placement.** We agree that the fossil most likely belongs to Pimplinae given the typical wing venation, shape of T1 and the rather stout ovipositor. However, many genera of the subfamily could fit these characters. As there



◀Fig. 11 *Phygadeuon? petrifactellus* Cockerell, 1920, holotype USNM 66580 **a** part and **b** counterpart (image flipped horizontally); dorsolateral aspect; ©Smithsonian Institute

are no clear disagreements with *Pimpla*, we decided to leave the species as questionable in this genus.

**Description.** Head, mesosoma and T1 brown, possibly with some light patches. Wing veins brown; pterostigma similar coloration with light area at base. T2 and remaining metasomal segments light brown. Ovipositor dark brown. Head crushed and not many details visible from photo. One mandible present, evenly and strongly tapered from base to tip. Notauli present, extending at least over anterior 0.6× mesoscutum, strongly converging. Details of mesopleuron not discernible. Propodeum not elongate, higher than long. Areolet closed, quadrate with uneven sides; not clear where 3rs-m is touching 5M; 2Rs 0.69× 2 + 3M and around 0.6× 3rs-m, 2 + 3M around 3.7× 4M. 4Rs straight. Pterostigma 3.46× as long as deep, 0.67× 1R1 length. 2Cu 0.97× 1M&1Rs, 1.04× r-rs. 1m-cu&2Rs + M curved; 1Rs + M present, around 4.3× as long as width of 1m-cu. 1cu-a at junction of M + Cu and 1M. T1 around 0.8× as long as broad or longer, evenly tapering from base to apex; with two dorsal longitudinal carinae. Ovipositor at least 0.2× as long as fore wing, but incomplete. Measurements: fore wing = 6.3 mm; body ≈ 8 mm; metasoma = 4.5 mm; T1 ≈ 1 mm; ovipositor >1.3 mm.

#### Subfamily *Cryptinae* Kirby, 1837

##### Genus *Phygadeuon* Gravenhorst, 1829

##### *Phygadeuon?* *petrifactellus* Cockerell, 1920

Figure 11

\*1920 *Phygadeuon petrifactellus* Cockerell: p. 257, pl. 36, Fig. 4

**Type material.** USNM 66580, part (a) and counterpart (b), female. White River, Colorado, United States. Dorsolateral aspect of body with fore wings and ovipositor; without antennae, legs or hind wings.

**Studied material.** We have examined the original description, including a drawing, and a high resolution photograph.

**Diagnosis.** Small species, fore wing around 3 mm. Areolet pentagonal with uneven sides. 1cu-a slightly posterior to junction of M + Cu and 1M. T1 elongate, slender and humped in anterior part. Metasoma oval shaped with tergites transverse. Ovipositor short, around 0.1× fore wing.

**Systematic placement.** It is very likely that the fossil belongs to Cryptinae, based on the overall body shape, shape of T1 and the clearly pentagonal areolet. There are no preserved characters, which would disagree with a placement in the genus *Phygadeuon*, thus we keep the current placement of the fossil, but recognize uncertainty given the numerous other possibilities among Cryptinae genera.

**Description.** Head, mesosoma and T1 reddish-brown. Wing veins and pterostigma brown. Metasoma from second metasomal segment on light brown. Ovipositor brown. No interpretable characters on head; rather broad apically. A line extending over entire mesoscutum might represent strong notauli or an artefact (a). Mesopleuron incomplete. Propodeum rather short, with some indications of at least posterior transverse carina (a). Areolet closed, pentagonal with uneven sides, 2Rs 0.53× 2 + 3M, 0.9× 3rs-m, 2 + 3M 1.8× 4M, 3Rs 1.01× 2Rs and around 2.7× r-rs width. Pterostigma 2.65× as long as deep and 0.88× 1R1 length. 4Rs slightly up-curved. 1m-cu&2Rs + M angled or curved, 1Rs + M absent. 2m-cu slightly curved in lower half with one or two bullae. 1cu-a posterior to junction of M + Cu and 1M; 1Cu about 2× as long as 1M width. T1 elongate, slender and humped in anterior part; remaining metasomal segments transverse, together forming an oval shaped metasoma (a). Ovipositor present and rather short, around 0.13× as long as fore wing, with apex pointed (a). Measurements: fore wing length = 3.2 mm, depth = 1.1 mm; body ≈ 3.7 mm; ovipositor ≈ 0.4 mm.

#### Subfamily *Orthocentrinae* Förster, 1869

##### Genus *Plectiscidea* Viereck, 1914

##### *Plectiscidea?* *lanhami* Cockerell, 1941

Figure 12a

\*1941 *Plectiscidea lanhami* Cockerell: p. 354, pl. I, Fig. 1

**Type material.** UCM 19167, part, female. Brush Creek A, Garfield, Colorado, United States. Laterodorsal aspect of body with incomplete antennae, fore wing; without hind wings or legs; some traces of hind coxa/tibia and ovipositor might be present.

**Studied material.** We have examined the original description and a high-resolution photograph of the fossil.

**Diagnosis.** Fore wing around 3.6 mm long. Areolet narrowly pentagonal. 1cu-a at junction of M + Cu and 1M. T1 longer than wide, humped in anterior half. Ground colouration brown; T2–T4 with lighter bands distally.



◀Fig. 12 a *Plectiscidea? lanhami* Cockerell, 1941, holotype UCM 19167; laterodorsal aspect; ©University of Colorado Museum of Natural History. B *Tilgidopsis haesitans* Cockerell, 1921, holotype USNM 66931; lateral aspect; ©Smithsonian Institute

**Remarks.** Cockerell (1941) placed the fossil in *Plectiscidea* (Orthocentrinae) based on the general appearance, which reminded him of *Plectiscus* Gravenhorst 1829, but with a closed areolet.

**Systematic placement.** We agree that the specimen likely belongs to Orthocentrinae based on body size, shape of T1 and proportions of the other tergites, propodeum shape, and most of the wing venation. However, within the subfamily, the pentagonal areolet is atypical (although not unknown) for members of the *Helictes* genus group, but more often present in the *Orthocentrus* genus group. However, typical characters of the *Orthocentrus* genus-group, such as the strongly protruding head at the level of the toruli, elongate scape and stout antennae, are not present in the fossil. Since the only disagreement with *Plectiscidea* would be the areolet shape and since some genera within the *Helictes* group show a tendency towards a narrowly pentagonal areolet, we keep the current taxonomic position of the fossil.

**Description.** Head dark brown; antennae light brown. Most of mesosoma and T1 brown; remaining tergites slightly lighter; T2–T4 with lighter bands distally. Wing veins and ovipositor brown. First six to seven flagellomeres visible; scape and pedicel not distinguishable. Remaining head characters not interpretable. Large part of mesosoma missing. Propodeum not elongate, probably deeper than long. Fore wing areolet closed, narrowly pentagonal, 3Rs at most as long as width of surrounding veins. 4Rs straight to slightly distally arched. Pterostigma  $2.8 \times$  as long as deep and around  $0.8 \times$  1R1 length. 1m-cu&2Rs + M curved. 2Cu  $0.64 \times$  1M&1Rs,  $1.2 \times$  r-rs. 1cu-a at junction of M + Cu and 1M. T1 longer than wide, humped in anterior half, sclerotized part of S1 probably reaching to about half length of T1; T2 subquadrate, around  $0.68 \times$  as long as T1; remaining tergites more or less transverse. Ovipositor may be present (elongate, narrow impression to right of fossil may be part of ovipositor of this specimen, but is not joined to metasoma). Measurements: fore wing length  $\approx 3.6$  mm; mesosoma  $\approx 1.5$  mm; metasoma 3.0 to 3.3 mm; T1 = 0.8 mm.

#### Subfamily *Rhyssinae* Morley, 1913

Genus *Rhyssa* Gravenhorst, 1829

*Rhyssa?* *juvenis* Scudder, 1890

\*1890 *Rhyssa juvenis* Scudder: p. 609, pl. X, Fig. 19

**Type material.** USNM 276640, part, female. Green River, Wyoming. Lateral aspect of body with incomplete antennae, fore wings and ovipositor, and traces of hind wings; without legs.

**Studied material.** We have not been able to locate the holotype and thus only examined the original description including a drawing. The fossil is poorly preserved with body parts of different insects overlapping. Considering that most of the characters are not interpretable, we here only give remarks without re-describing the fossil.

**Remarks.** From the drawing, two different fore wings are discernible, of which only one belongs to an ichneumonid. Antennae, head and mesosoma probably belong to the same animal. The very short metasoma (compared to the mesosomal length) most probably belongs to another insect or it represents a preservation artefact, as such short metasomas do not occur in Rhyssinae nor in any other ichneumonids. We are also not certain whether the ovipositor is from the same specimen. The areolet in the fore wing seems real and would fit Rhyssinae or related subfamilies. However, the other fore wing characters are mostly uninterpretable, and the shape of the most distal cells indicate strong distortion. Additional characters in favour of a placement in Rhyssinae are the transverse rugae on the mesoscutum (but which could as well be an artefact, which is difficult to judge from a drawing alone) and the ovipositor length. Based on the few unambiguous characters, placement of the fossil is probably not possible, and we cannot say whether it belongs to *Rhyssa* or even Rhyssinae, but since we have no evidence to place it elsewhere, we tentatively leave the fossil in its current placement until a more detailed examination is possible.

**Ichneumonidae incertae subfamiliae** stat. rev. (formerly Ophioninae)

Genus *Tilgidopsis* Cockerell, 1921

*Tilgidopsis haesitans* Cockerell, 1921

Figure 12b

\*1921 *Tilgidopsis haesitans* Cockerell: p. 37, Fig. 8

**Type material.** USNM 66931, part, female. White River, Colorado, United States. Lateral aspect of body with parts of antennae, one complete fore wing, part of second fore wing, partial hind legs and ovipositor.

**Studied material.** We have examined the original description and a high-resolution photograph of the fossil.



◀Fig. 13 *Trymectus amasidis* gen. nov. et comb. nov. (Cockerell and LeVeque 1931), holotype UCM 15690, **a** part and **b** counterpart (image flipped horizontally); dorsal aspect; ©University of Colorado Museum of Natural History

**Diagnosis.** Mesoscutum with strongly converging notaui. Arolet open. Pterostigma very narrow, around  $6.6 \times$  as long as deep. 3Cu shorter than 2cu-a. 1cu-a at or posterior of junction M + Cu and 1M. T1 elongate and rather slender; T2 around as long as T1. Ovipositor at least  $0.14 \times$  as long as fore wing. Prevailing colouration light brown; T1–T3 light anteriorly and brown posteriorly.

**Remarks.** Even though Cockerell (1921) placed the fossil in Ophioninae, he pointed out its similarity to the genus *Tilgida* Cameron, 1900 (today *Eugalta* Cameron, 1899) of the subfamily Poemeniinae.

**Systematic placement.** From the wing venation, especially the presence of 2Rs, *Tilgidopsis* clearly does not fit the current definition of Ophioninae. Based on the ratio of 2Rs and  $2 + 3M$ , the shape of T1 and the elongate propodeum and possibly hind coxae, the fossil could indeed fit with extant Poemeniinae. However, the mesosoma does not seem elongate and cylindrical enough for this subfamily. The fossil looks rather like some species of the genus *Megastylus* Schiødte, 1838 (Orthocentrinae) with the propodeum distinctly below the dorsal margin of the mesoscutum, slender legs and similar wing venation. Furthermore, it also resembles the genus *Diradops* Townes, 1946 (Banchinae) in the shape and coloration of the metasoma and with respect to the wing venation. Considering the state of the fossil and unclear interpretation of the mesosoma and propodeum shape, we cannot place it in any recent subfamily. We thus remove it from Ophioninae and place it within Ichneumonidae with uncertain subfamily placement.

**Description.** Head and mesosoma dark to light brown with light patches. T1–T3 light anteriorly and brown posteriorly. Antennae poorly preserved; scape and pedicel not distinguishable; only first few flagellomeres visible. Head appears roundish, rather large compared to body. Strongly converging notaui present at least on anterior third of mesoscutum. Propodeum slightly elongate, evenly declivous in profile; seems to be attached distinctly below dorsal margin of mesoscutum, but this might be an artefact. Arolet open (3rs-m absent), 2Rs  $2.2 \times 2 + 3M$ . 4Rs slightly sinusoidal. Pterostigma very narrow, around  $6.6 \times$  as long as deep,  $0.8 \times 1R1$ . 2Cu  $0.6–0.7 \times 1M & 1Rs$ ,  $0.5–0.6 \times r\text{-}rs$ . 3Cu shorter than 2cu-a. 1cu-a at or posterior of junction M + Cu and 1M. Fore wing around  $0.35 \times$  as wide as long. Only parts of hind legs preserved; probably

coxae discernible and elongate, around  $2 \times$  as long as high. T1 elongate and rather slender; T2 around as long as T1. Ovipositor at least  $0.14 \times$  as long as fore wing but might be incomplete. Measurements: fore wing  $\approx 5.3$  mm; body  $\approx 7.4$  mm; metasoma = 4.7 mm; T1 0.8–1.1 mm long; ovipositor  $\geq 0.9$  mm.

**Ichneumonidae incertae subfamiliae** stat. rev. (formerly Tryphoninae)

Genus *Trymectus* gen. nov.

**Etymology.** From the first three (Tryphoninae) and the first two (Metopiinae and Ctenopelmatinae) initial letters of names of three ichneumonid subfamilies to which this species could belong; gender masculine.

**Type species.** *Trymectus amasidis* (Cockerell and LeVeque, 1931) comb. nov.

**Diagnosis.** Body robust with thick antennae and hind femora. Arolet quadrate with uneven sides; 1Cu more than  $0.5 \times$  1cu-a. Propodeum with almost complete set of carinae. T1 subquadrate with two dorsal longitudinal carinae extending to about half length of tergite.

**Remarks.** Cockerell and LeVeque (1931) expressed their uncertainty in placing this fossil by putting it in the genus *Tryphon* Fallén, 1813 sensu lato (the definition of *Tryphon* at that time was much broader).

**Systematic placement.** The fossil clearly differs from the recent definition of *Tryphon* in the much longer fore wing 1Cu, longer 1R1, straight 2m-cu, wider T1 and thicker antennae and femur. It still might belong to the subfamily Tryphoninae if we consider arolet shape, 1m-cu being posterior to the junction of M + Cu and 1M, and propodeal carination. A very good fit was also observed with *Panteles* Förster 1869 (Stilbopinae Townes and Townes, 1949), especially with 1cu-a being so strongly posterior to 1M; the propodeal carination fits as well, as do the shape and carination of T1 and the straight and long 4Rs; however, the arolet shape is different and the thickened antennae and femora do not match well. Some Metopiinae are similar with fore wing vein 1cu-a being strongly posterior to the M + Cu and 1M junction, similar propodeal carinae, thick antennae and legs; however, the rest of the wing venation is clearly different, especially the arolet shape and shape of cell 1M + 1R1. Additionally, we cannot exclude that the fossil belongs to the tribe Pionini Smith and Shenefelt, 1955 (Ctenopelmatinae) whose representatives can have the same shape and carination of T1, same propodeal carination and very similar wing venation. Considering that the fossil does not fit in the genus *Tryphon* nor in any other recent genus and that placement in a single subfamily is not

possible, considering the combination of characters such as well-developed carinae on the propodeum, quadrate areolet and thickened hind femora and antennae, we describe a new genus within Ichneumonidae with unclear subfamily placement.

**Trymectus amasidis** (Cockerell and LeVeque, 1931) comb. nov.

Figure 13

\*1931 *Tryphon amasidis* Cockerell and LeVeque: p. 356, p. 355 photographs 3, p. 358 drawings 3

**Type material.** UCM 15690, part (a) and counterpart (b), female or male. Green River PB no data [Station 26, Roan Plateau, 1923 (Henderson and Byram)]. Dorsal aspect of body with fore wings, incomplete antennae and parts of hind wings; without ovipositor (?) or legs, except one hind coxa, hind femora, and part of hind tibia.

**Studied material.** We have examined the original description and high-resolution photographs of the fossil.

**Diagnosis.** As for the genus by monotypy.

**Description.** Head and mesosoma dark brown to light reddish-brown. Antennae light brown. Wing veins brown; pterostigma similar colour with lighter patch basally. T1 dark to light brown, T2–T4 light brown with darker bands on distal 0.17–0.27 of their length. Antennae thick with at least 22 flagellomeres; shorter than fore wing. Head crushed, with some indication of eyes which might be slightly enlarged (a). Some indications of notauli on mesoscutum (b). Propodeum not elongate, with distinct carinae: lateral portions of posterior transverse carina, complete anterior transverse carina, medial portion of medial longitudinal carinae, at least medial and posterior portions of lateral longitudinal carinae, and probably complete pleural carina (b). Fore wing areolet quadrate with uneven sides, 2Rs  $0.52 \times 2 + 3M$ , 2Rs  $1.03 \times 3rs-m$ , 2 + 3M  $7.61 \times 4M$ , 4M and 3Rs as long as width of surrounding veins; 3rs-m with one bulla that occupies 0.2 of vein. 4Rs straight. Pterostigma around  $3.2 \times$  as long as deep and  $0.64 \times$  R1. 2Cu  $0.78 \times$  1M & 1Rs,  $0.93 \times$  r-rs. 1m-cu & 2Rs + M arched. 1cu-a strongly posterior to junction 1M and M + Cu, 1Cu  $0.61 \times$  1cu-a. 3Cu  $1.72 \times$  2cu-a. Fore wing 0.35–0.38× as deep as long. Hind wing with only Sc + R, R1 and 1Rs visible. Hind femur enlarged, around  $2.4 \times$  as wide as long. T1 short and broad with a slight constriction in anterior half and two dorsal longitudinal carinae extending  $0.7 \times$  length of tergite;  $1.07 \times$  as long as wide. T2–T5 transverse; T2  $0.59 \times$  as long as wide and  $0.8 \times$  T1 length. Measurements: antennae  $\geq 2.9$  mm; fore wing length = 5.1 mm, depth  $\approx 1.8$  mm; body = 6 mm; metasoma = 3.7 mm;

T1 = 1.2 mm; T2 = 0.8 mm; hind femur length  $\approx 1.2$  mm, width  $\approx 0.5$  mm.

## Discussion

The timing of the evolution of the parasitoid wasp family Ichneumonidae and its constituent subfamilies is largely unknown due to an insufficiently studied fossil record and lack of molecular dating studies. The oldest fossils that can be associated with this family belong to the extinct subfamily Palaeoichneumoninae Kopylov, 2009, from the Early Cretaceous with two further subfamilies, Labenopimplinae Kopylov, 2010b and Novichneumoninae Li et al. 2016, described from Late Cretaceous fossils. Representatives of extant subfamilies have been described from the Cretaceous (Labeninae, McKellar et al. 2013) and Eocene (see checklist, Menier et al. 2004), but interpretation of many of these is hampered by considerable uncertainty with respect to their subfamily placement, given that many species were described in the first half of the last century and have never been revised in the light of a modern classification.

We here revised all known fossil ichneumonids from the Eocene Green River Formation and described five additional species. Considering the subfamily associations of these fossil species, we can anticipate how diverse this group is at the Green River locality in particular and in the fossil record in general. Representatives of Pimplinae have already been described from Green River deposits, while *Mesoclitus?* *yamataroti*, described here, represents the first record of the subfamily Acaenitinae from this locality (Menier et al. 2004). Both of these subfamilies have been reported from the Late Eocene fauna of other localities, such as the Isle of Wight, Bouldnor Formation (Antropov et al. 2014) and Florissant, Colorado, Florissant Formation (Brues 1906). Considering older fossil records, one species of the subfamily Pimplinae, *Pimpla stigmatica* Henriksen, 1922, has been described from the Early Eocene Fur Formation. *Mesoclistus?* *yamataroti* might even be the oldest representative of the subfamily Acaenitinae if we omit the doubtfully placed *Phaenolobus arvernus* Piton, 1940 from the Late Paleocene locality of Menat, Puy-de-Dôme (France) (Piton 1940).

The taxonomic placement of ichneumonid fossils in the correct subfamily is usually very difficult. One reason for this is a high rate of homoplasy observed in ichneumonids (Gauld and Mound 1982). Both body shape characters, which are often associated with host ecology, and wing venation regularly show this phenomenon. For instance, very similar (and possibly plesiomorphic) venation can be found in some Pimplinae, Banchinae, Tryphoninae, and

Ctenopelmatinae, all of which also have a similar shape of the first tergite. This has, for example, been an issue when placing the newly described *Ichninsum appendicrassum*. Another example for a problematic subfamily association is the Cretaceous *Tryphopimpla xoridoptera* Kopylov (2010b), a specimen showing characteristics of three different subfamilies, but which does not fit into a single one completely; this is expressed in the etymology of the genus and species name, which combines parts of the names of the recent subfamilies Tryphoninae, Pimplinae, and Xoridinae Shuckard, 1840. In such cases, it becomes challenging to resolve whether a specimen belongs to an extant subfamily, to a stem lineage, or to an extinct subfamily, especially since it is unclear if these subfamilies were already in existence at the time. Having more precise age estimates for the ichneumonid subfamilies would certainly facilitate such decisions. An additional aggravating factor in palaeontology is certainly imperfect preservation that leads to important synapomorphies being invisible or not interpretable. Together with difficulties in character interpretation, this can lead to significant taxonomic errors. It is important to note that identification of many extant ichneumonids relies on viewing morphological characters from various parts of the body, many of which are often absent from fossils. Ichneumonid subfamilies tend to be polythetic, although often readily recognisable on the sum of their morphological parts. Machine learning algorithms, when trained on enough genera of extant Ichneumonidae, could prove better than human eyes at suggesting potential placements for compression fossils of wings.

When revising the previously described fossils and determining the placement of the newly described ones, we applied a rather conservative approach, which resulted in eight fossils, including two newly described ones, placed within Ichneumonidae without definite subfamily associations. This approach appeared more useful to us than placing the fossils in an extant subfamily with considerable uncertainty, as it will reduce mistakes related to an erroneous fossil placement in later studies. We followed the open-taxonomy approach (Matthews 1973) to denote uncertainty in generic and subfamily placements, which proved very convenient. The importance of an accurate placement of fossils becomes evident in the context of palaeoecological and molecular dating studies, where the results rely heavily on the correct taxonomic position of fossils. It has been shown that incorrectly placed fossils can strongly bias divergence time estimation (Donoghue and Benton 2007; Ronquist et al. 2012; Kimura et al. 2015). One should thus bear in mind the afore-mentioned problems in Ichneumonidae palaeontology, which apply to many other taxa as well. Molecular phylogeneticists should favour a thorough examination of each fossil prior to analysis when there is any doubt that the fossil descriptions

are in full accord with the current standards and taxonomic knowledge.

One possibility to increase the accuracy and objectivity of fossil placement as well as to maximise the use of the preserved information would be to include them in a morphological matrix for phylogenetic analysis. Considering that only a very small portion of the ichneumonid fossils found to date have been formally described (Menier et al. 2004), and that the known fossils have mostly been described in the early twentieth century and thus urgently require revision, such an approach would greatly improve the state of modern Ichneumonidae palaeontology.

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