

FIVE NEW GENERA AND SPECIES OF DARWIN WASPS (HYMENOPTERA:
ICHNEUMONIDAE) FROM THE LOWER OLIGOCENE RENOVA FORMATION OF
MONTANA

BY

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THESIS

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ABSTRACT

Fossils provide a unique glimpse into the evolutionary history and ancient diversity of life on Earth. The study of fossil insects—paleoentomology—has only scratched the surface of exploring and documenting the rich hexapod fossil record. Vast numbers of taxa, even entire faunas, still await formal description. Therefore, documenting and describing the diversity of ancient insects through taxonomic treatments is essential to elucidate the evolutionary history of this highly speciose group of arthropods.

The Renova Formation (Lower Bozeman Group) is a thick suite of Cenozoic rocks that outcrops across much of western Montana. The deposits comprising the formation range in age from Lower Eocene (36 MYA) to Lower Miocene (10 MYA) and rest unconformably atop Proterozoic basement rocks in numerous post-Laramide extensional basins throughout the region. The highly fossiliferous lacustrine shales of the Lower Oligocene Climbing Arrow Member outcrop extensively in the Upper Ruby Basin and have yielded thousands of well-preserved fossil insects and plants. Among insects, Hymenoptera are particularly abundant and diverse. Here, I describe five new genera and species of Darwin wasps (Hymenoptera: Ichneumonidae): *Magna labyrinthia* gen. et sp. nov., *Aperta emiliae* gen. et sp. nov., *Archaeomortus setifera* gen. et sp. nov., *Oligoextenterus excavata* gen. et sp. nov., and *Triorthocentrus renovensis* gen. et sp. nov. The new taxa are compared to other fossil and extant Ichneumonidae and their paleoenvironmental, paleoecological, and paleoclimatological implications discussed.

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TABLE OF CONTENTS

INTRODUCTION	1
GEOLOGICAL SETTING	4
MATERIALS AND METHODS.....	6
SYSTEMATIC PALEONTOLOGY	8
DISCUSSION.....	28
FIGURES	30
REFERENCES	39

INTRODUCTION

Insects have a long and rich fossil record. First appearing in the Early Devonian (Grimaldi & Engel 2005), they have since come to dominate terrestrial ecosystems both in terms of species diversity and ecological impact. Among the insects, the Hymenoptera (primarily ants, bees, and wasps) stand out as one of four hyperdiverse orders (Fernández et al. 2021), a list that includes the Coleoptera (beetles), Diptera (flies), and Lepidoptera (moths and butterflies). Hymenopterans first appeared in the Triassic (Ronquist et al. 2012), and their subsequent radiation was likely a result of the appearance of angiosperms in the Early Cretaceous (Bateman 2019). Since their origin, Hymenoptera have diversified into a wide array of ecological niches and have become one of the largest extant insect orders. The order Hymenoptera is divided into two suborders: Symphyta (sawflies) and Aculeata (bees, ants, and wasps). The Darwin wasps (family Ichneumonidae), the focus of this study, belong to the latter.

Fossil evidence of ichneumonids did not appear in the fossil record until the Early Cretaceous (Kopylov 2010), but a molecular dating study by Spasojevic et al. (2021) indicated an origin as early as the Jurassic Period. Cretaceous ichneumonids have been preserved in amber (Kopylov 2010) and as compression fossils (Kopylov 2018), though the majority of fossils described are from the Paleogene Period which contains extant subfamilies. Eocene deposits have yielded the greatest number of ichneumonids (Kopylov et al. 2018; Spasojevic et al. 2019; Manukyan 2019; Klopstein 2022), yet no ichneumonids have been found within the Oligocene. The Renova Formation provides paleontologists with the unique chance to view the fossil Darwin wasp assemblage from a relatively under studied time period. A revision of previously described ichneumonid fossils found tentative placements into new subfamilies and genera (Spasojevic et al. 2022). Spasojevic et al. primarily moved the taxa from Pimplinae into more

suitable subfamilies (Orthocentrinae, Tryphoninae, Phygadeuontinae, Ctenopelmatinae, Cremastinae, and Metopiinae) as well as assigning different genera to already correct subfamily placements. The deposit that is perhaps the most relevant to this study is the Green River Formation (GRF) of the Eocene. This formation is critical to understanding the Renova Formation's ichneumonids due to their temporal and positional proximity to one another. Despite the abundance of fossil insects described from this formation, only several were ichneumonids (Spasojevic et al. 2018).

The family Ichneumonidae is a member of the superfamily Ichneumonoidea (parasitic wasps) and currently has 1,547 described genera, composed of 23,765 species (Yu et al. 2024). Ichneumonidae has been robustly recovered as a monophyletic group (Quicke et al. 2020; Bennett et al. 2019) through molecular and morphological analyses, though the nature of the specific relationships within this family remains ambiguous. Original work on the ichneumonids suggested the existence of 25 subfamilies (Townes 1969), but further morphological analyses (Wahl 1990, 1993; Gauld 1991; Porter 1998; Gauld et al. 2002) increased this number to 37. Early molecular work utilizing an analysis of 28S rDNA (Belshaw et al. 1998; Laurene et al. 2006; Quicke et al. 2005; Quicke et al. 2009) would eventually conclude a total of 39 subfamilies exist. Quicke et al. (2009) were the first to use morphological characters to supplement molecular work on this family. More recent studies have significantly increased the resolution of the ichneumonid phylogeny (Broad 2016; Santos 2017; Klopstein et al. 2019) with Bennet et al. (2019) publishing the most up-to-date and comprehensive taxonomic revision finding the present number of 41 extant subfamilies within Ichneumonidae. This classification does not include the extinct family Lambenopimplinae.

In this thesis, I describe five new genera and species of Ichneumonidae from the lowermost Oligocene Climbing Arrow Member of the Renova Formation, a sequence of highly fossiliferous lacustrine paper shales, fluvial sandstones, and tuffaceous deposits that outcrop in the Upper Ruby Basin of southwest Montana. These new taxa represent the first Hymenoptera to be formally described from this important and practically unstudied Oligocene deposit.

GEOLOGICAL SETTING

The Renova Formation (part of the lower Bozeman Group) is a heterolithic sequence of argillaceous, siliciclastic, and tuffaceous rocks that outcrop across much of western Montana (Vuke 2021). Deposits that comprise the formation range in age from Lower Eocene to Lower Miocene and rest unconformably atop Proterozoic basement rocks in the numerous post-Laramide extensional basins scattered throughout the region. The highly fossiliferous Lower Oligocene (Rupelian, 33.9–27.8 Ma) Climbing Arrow Member outcrops extensively in the Upper Ruby Basin and is composed of extremely fissile millimetrically-laminated lacustrine shales (“paper shales”) intercalated with ash horizons and sandstones of fluvial origin. These shales sit unconformably on top of the various schists and gneisses of the highly metamorphosed Paleozoic basement (Hanneman et al. 2003). Stratigraphically, the paper shales of the Climbing Arrow Member are the lowermost beds of the sedimentary sequence in the Upper Ruby Basin and are overlain conformably by medium to coarse-grained sandstones of the Dunbar Creek Member, which in a few places appear themselves overlain by more shales that may belong to the primarily lacustrine deltaic Passamari Member (S.W. Heads, pers. comm. 2024). Current understanding of the stratigraphy of the Upper Ruby Basin is shown in Figure 1.

The paper shales of the Climbing Arrow Member represent ancient lake sediments deposited in still water with anoxic bottom conditions and have yielded thousands of beautifully preserved fossil insects and plants of lowermost Oligocene (Rupelian) age. The most extensive, albeit deeply weathered, outcrops of paper shales are found in a sub-basin of the Upper Ruby Basin to the immediate west of the Ruby Dam, appropriately called Fossil Basin. These deposits present a unique opportunity to study the paleobiota of Western North America during the Oligocene. Many North American deposits yield fossils from the Eocene and later Miocene

epochs, but the intervening Oligocene fossil record of the region has remained shrouded in mystery due to an apparent lack of fossiliferous deposits of this age. Thus, the fossils of the Climbing Arrow Member have the potential to record how the paleobiota adapted to the dramatic climatic and environmental shifts that occurred during the Eocene–Oligocene transition. Such insights are extremely valuable to our understanding of the evolution of North American terrestrial ecosystems throughout the Cenozoic. The flora of the Renova Formation shows a succession of subtropical forests by temperate deciduous forests (Lielke et al. 2012). The vegetation of the basin is derived from areas of high and low elevation (Lielke et al. 2012). Such a diverse array of plant life allowed a rich ecosystem to thrive in and around the ancient lake, making it one of the most valuable Oligocene deposits in North America.

While the Renova Formation has yielded an extensive collection of fossil insects, very little taxonomic work has been published to date and the task of describing the diverse insect assemblage remains daunting. Becker published a series of works documenting the paleoflora of the basin (Becker 1959; 1960; 1961; 1966) and collected many insect fossils that now reside in the collections of the Yale Peabody Museum and the University of Michigan Museum of Paleontology. These insects remain unstudied and unpublished. The few insects that have been published from this locality were done so by Lewis (1971a,b; 1972a,b,c; 1973a,b,c,d; 1975a,b; 1977; 1978) though the descriptions are rarely over a page long, contain numerous taxonomic errors, and do little to provide the in-depth analysis necessary for each specimen. Extensive excavations over the past decade by the Fossil Insect Research Group at the Prairie Research Institute's (PRI) Center for Paleontology, University of Illinois Urbana-Champaign, has produced an extensive collection of fossil insects from this locality which is now allowing detailed taxonomic work on this important deposit to proceed.

MATERIALS AND METHODS

Specimens studied herein are deposited in the Illinois Natural History Survey Paleontology Collection (INHS-P) at the PRI Center for Paleontology, University of Illinois Urbana-Champaign, and at the University of Michigan Museum of Paleontology (UMMP). The fossils are preserved on extremely thin pieces of paper shale and were glued to appropriately sized Makrolon polycarbonate plates with acryloid to prevent breaking and other damage.

Specimens were imaged using a 100mm lens on a Canon EOS Mark IV with lighting provided by LED panels. For highlighting smaller diagnostic characters, a Keyence VHX-7000 digital microscope was used. Z-stacking of images was performed in Helicon Focus 6 (v. 6.8.0). Postproduction including adding scale bars, minor color correction, and contrast/exposure adjustments were made using Adobe Photoshop ©2023 and ©2024. Drawings were made using Adobe Illustrator ©2023 and ©2024. Measurements were made using ImageJ (1.54g; Java 1.8.0_345 [64-bit]).

Darwin wasp characters used for initial sorting included (1) a narrow waist with (2) long antennae, typically exceeding 16 segments, (3) the ‘horse head’ shape the discosubmarginal cell presents as, and (4) in most cases the presence of the first radial sector cell known as the areolet (Broad et al. 2018). Whether the areolet is closed and its size can often be important characters when identifying an ichneumonid to species. Due to the diversity of ichneumonids, synapomorphic characters and morphological traits commonly confounded subfamily keys and presented a challenge when assigning these wasps to their correct taxon. Thus, the best taxonomic treatments are provided for specimens with the most complete fore- and hind wing venation. The ichneumonid subfamily key of Broad et al. (2018) was used subfamily assignment as far as a specimen allowed given its degree of completeness. Wing nomenclature also follows

Broad et al. (2018) and is shown in Figures 3–4. Further taxonomic treatment was completed through comparative morphology of extant relatives.

SYSTEMATIC PALEONTOLOGY

Class INSECTA Linnaeus, 1758

Order HYMENOPTERA Linnaeus, 1758

Suborder APOCRITA Gerstaecker, 1867

Superfamily ICHNEUMONOIDEA Latreille, 1802

Family ICHNEUMONIDAE Latreille, 1802

Subfamily TRYPHONINAE Shuckard, 1840

Tribe EXENTERINI Förster, 1869

Genus *Oligoexenterus* gen. nov.

Diagnosis: 1 bulla present on 2m-cu with a closed rectangular areolet on the forewing.

Type species: *Oligoextenterus excavata* sp nov.

Etymology: A combination of Oligocene and the suffix *-exenterus*, meaning “coming from”.

Named for the specimen found in a deposit from the Oligocene.

Oligoextenterus excavata sp. nov.

(see Figure 5)

Diagnosis: As for the genus by monotypy.

Holotype: INHS-P21720.

Type locality and horizon: USA, Montana, Madison County, Upper Ruby Basin; Renova Formation, Climbing Arrow Member (Lower Oligocene: Rupelian).

Description

Coloration: Head, mesoscutum, and scutellum preserved black. Proximally posterior to notaulus presents as brown with ivory matrix mixed in, either a record of the insect's color or an artifact of mineralization. Propodeum and anterior T1 preserved black with remaining tergites being brown. All wing venation is preserved brown with the stigma being more darkly preserved.

Head/Antennae: Antennae completely absent from the specimen, but antennal sockets clearly present. Antennal sockets are 0.20 mm across giving an indication of the size of the scape. Unfortunately, posterior region of the head is missing, giving no record of the occipital carina or vertex. One of the few specimens from this formation with mouthparts intact, very prominent mandibles are protruding from the head. Discerning mandible type is difficult given indistinct preservation but appears bidentate. Clypeus is not visible or poorly preserved. Malar space difficult to measure given orientation of preservation.

Mesosoma: Mesoscutum prominently outlined, with the axillae sitting much lower in the shale matrix than the mesoscutum. Right tegula is preserved with the left being missing. Left side of the metanotum is preserved with the right being hidden in the darker mineralization. Propodeum

appears large with anterior carinae present around area supermedia but is ventrally interrupted on both sides. Posterior and lateromedian longitudinal carinae make the propodeum largely flat.

Metasoma: Tergites 1-3 preserved with the remaining tergites missing. T1 long (1.64mm) and apically thin, gradually widening posteriorly. T1 0.76mm wide where it meets T2. Latero-median carinae of first metasomal segment faintly preserved, appearing proximally to propodeum and running parallel to each other almost entire length of tergite. Dorsal muscle deeply grooved into T1. T2 pinched anteriorly at connection to T1 with both T2 and T3 widening posteriorly. T2 and T3 both x1.5 wide than long. Spiracles and thyridium both not preserved.

Legs: Legs are heavily disarticulated, making identification of character locations difficult. These characters required the most interpretation. Two coxae are preserved along with three other indeterminate segments as well, most likely being femurs or tibiae. No spurs can be found on the specimen but does not mean they were not once there. The nature of the disarticulation makes it challenging to definitively say which leg segments went to which coxae.

Forewing: Right forewing of the specimen is almost entirely preserved, but sections of the apical wing margin are lost making it difficult to accurately measure its length. The left forewing is largely missing, complicating much of the right forewing interpretation. Forewing has a closed non-petiolate areolet, loosely resembling a triangle. The areolet shape is in part due to 2M being x2.89 longer than 3M. 2rs-m x1.2 1M and 3rs-m. RS absent from the areolet. Only one bulla is present and exists at the midpoint of 2m-cu. Separation of stigma and pterostigma is difficult to interpret, but a rough measurement shows it is 4.7x longer than it is wide. 2CU 1.4x 1M.

Ramulus short, evenly separating 1m-cu&M and M&RS is 1.36mm long. R x1.4 M+CU making for a weakly convex bend in M&RS. 1cu-a postfurcal to M&RS. Postnervellus x1.4 1cu-a and 2CU x1.6 2cu-a. AA absent from the forewing.

Hind wing: Both hind wings show incomplete preservation, with the left providing the most diagnostic characters. R almost completely straight as is M. M+CU weakly pointing posteriorly. RS/rs-m ratio is 1.9. 1CU potentially incomplete but cannot be compared to cu-a given it is not preserved. 1CU is 0.33 mm long.

General measurements: Mesosoma = 2.31 mm, Metasoma (T1-T3) = 3.58 mm, Head = 1.43 mm wide and 1.28 mm tall, Forewing = 7.68 mm long and 3.92 mm wide.

Etymology: Called *excavata* from the Latin root ‘excavat’, translating to mean “hollow out”. Named in honor of the hard work UIUC’s Center for Paleontology team has done excavating the Renova Formation.

Remarks: Specimen is placed in Tryphoninae. Tentative placement of the specimen was considered for Ichneumoninae, Orthocentrinae, Oxytorinae and Tryphoninae. Oxytorinae is unlikely given its lack of diversity and Orthocentrinae is also unlikely given the large nature of the mouthparts. Tryphoninae is the most likely diagnosis due to the presence of a single bulla on 2m-cu as well. This feature in combination with the 2M vein being almost nonexistent gives a striking resemblance to wing venation seen in the tribe Exenterini. Additional evidence in favor

of this diagnosis includes the fact that extant members of Exenterini are parasitoids of sawflies, which have also been found within the Renova Formation material.

Subfamily PIMPLINAE, Wesmael 1845

Genus *Archaeomortus* gen. nov.

Diagnosis: Enlarged stigma with no bulla present on 1m-cu&M. Heavily sclerotized mesosoma and thick setae found on the posterior of the head as well as the frons.

Type species: *Archaeomortus setifera* sp. nov.

Etymology: Derived from the Greek word *archaios* meaning “ancient” and the Latin word *mortus* meaning “death”. Named for its very disarticulated nature during fossilization.

Archaeomortus setifera sp. nov.

(see Figure 6)

Diagnosis: As for the genus by monotypy

Holotype: INHS-P25189

Type locality and horizon: USA, Montana, Madison County, Upper Ruby Basin; Renova Formation, Climbing Arrow Member (Lower Oligocene: Rupelian).

Description

Coloration: Specimen is almost entirely brown except for the head and setae which are almost black. Mesosoma structures darkly outlined, making for relatively easy morphological assignment.

Head/Antennae: Only four flagellomeres can be counted despite antennae being 2.2 mm long. Face of the insect appears to be covered in thick setae, although confirming this feature is difficult because of the lack of definitive head shape. Eyes are large vertically ovate being. Malar space cannot be measured because mouthparts, while appearing to be preserved, cannot be confidently outlined due to the head orientation. Clypeus either not discernable or not preserved.

Mesosoma: Mesoscutum outlined definitively with notaulus present. Scutellum shows heavy sclerotization and metanotum faintly preserved. Subtegular ridge is deeply grooved and is anteriorly notched. Sternaulus ventrally flat and almost seamlessly merges with mesepisternum. Propodeum present but anterior and posterior carinae are absent or not preserved, giving a flat appearance. Hind coxae preserved though not distinguishable from each other and are immediately posterior to the metapleuron. Juxtacoxal carina absent. Thick setae present on anterior mesoscutum or pronotum. Pronotum potentially preserved though outline is undefined. Proximal to mid coxa the metapleuron is darkly outlined.

Metasoma: No metasomal segments preserved.

Legs: Only three legs appear to be preserved and are very disarticulated. Four femurs are present and are 4.6x longer than wide. Counting tibiae is difficult given the positioning and undefined structure of the legs. The longest tibia is 2.7 mm long. No tibial spurs are present on this specimen and tarsal claws poorly preserved. Hind coxae very well preserved and are still attached posteriorly to the mesosoma.

Forewing: Left forewing is almost completely absent with the costa and AA being preserved. The right forewing is present but incomplete. The basal, discosubmarginal, subbasal, first subdiscal, and marginal cells are preserved with the second subdiscal and second discal cells being incomplete. All remaining cells are absent. The areolet is incomplete and cannot be described, making assigning an ID challenging. No bullae are present anywhere in the wing. The stigma is incomplete but best measurements show it is 4.9x longer than wide. 1m-cu&M is 1.5x longer than M&RS and 1.9x longer than 2r&RS.

Hind wing: No hind wings are present.

General measurements: Mesosoma = 4.2 mm, Metasoma = absent, Head = 1.2 mm tall, Forewing = 4.6 mm long and 2.0 mm wide.

Etymology: Named *setifera* for the prominent setae found on the body, giving it a distinct appearance.

Remarks: Lack of extensive preservation of the forewing or hind wing made identification difficult. The potential presentation of setae on the head and anterior mesoscutum make this wasp a strong candidate for Pimplinae. The setae may be an artifact of mineralization, and the absence of 2m-cu makes this subfamily placement within Pimplinae tentative.

Subfamily ORTHOCENTRINAE Förster, 1869

Genus *Triorthocentrus* gen. nov.

Diagnosis: Open and triangular areolet on the forewing. 2r&RS elongate with a smaller stigma, making for a longer ‘horse-head’ shape than the stouter ones seen in other genera. Three bullae present in the forewing.

Type species: *Triorthocentrus renovensis* sp. nov.

Etymology: *Triorthocentrus* comes from a combination of an existing genus within Orthocentrinae called *Orthocentrus* and the prefix *tri*. The specimen has very similar characters to wasps in *Orthocentrus* except the areolet has a pentagonal shape instead of the triangular shape seen in this wing venation.

Triorthocentrus renovensis sp. nov.

(see Figure 7)

Diagnosis: As for the genus by monotypy.

Holotype: UM33641

Type locality and horizon: USA, Montana, Madison County, Upper Ruby Basin; Renova Formation, Climbing Arrow Member (Lower Oligocene: Rupelian).

Description

Coloration: Specimen is largely preserved brown with large parts of the mesosoma being white or ivory. The white coloration is likely an artifact of the ash layers from active volcanism found throughout the deposit. Antennae largely preserved brown with darker spots in the center of each flagellomere until halfway through. Metasoma preserved dark brown anteriorly and abruptly becomes tan as it loses its preservation and shape. Ovipositor sheaths present as tan with a faint dark line (most likely the ovipositor) running down the bottom sheath. Legs preserved tan except the coxae, which are very dark. Wing venation preserved dark brown.

Head/Antennae: Head is pointed laterally, with well-preserved mouthparts. Mouthparts are most likely bidentate. Malar space to basal mandible width ratio is 2.9. Antennae are also very well preserved with only one break occurring in the right antenna. Within the antennae, thirteen flagellomeres can be distinguished. The antennae are 10.0 mm long though less than half of that length has clearly outlined flagellomeres. The scape is 0.7 mm tall and 0.3 mm wide while the pedicel is 0.1 mm tall and 0.2 mm wide. Potential tyloids present on both antennae. A single eye is preserved and is 1.0 mm tall and 0.7 mm wide. No clypeus or ocelli are present.

Mesosoma: Mesosoma presents with deeply grooved notaulus. Tegula seems to be intact. Epicnemial carina long and submetapleural carina complete. Propodeum present, but insect position makes distinguishing characters difficult. Only posterior propodeum seems to be separated from the metasoma with a carina. Both hind coxae still attached to mesosoma. Mesoscutum well defined and the pronotum largely pale in color. Pronotal collar well preserved. Juxtacoxal carina absent or poorly preserved due to metapleuron not showing many characters.

Metasoma: The metasoma presented a challenge to interpret given how it is preserved. The dorsal longitudinal carinae is strongly impressed on T1. S1 does not reach the middle of T1. Number of metasomal segments difficult to count due to undefined margins. T1 gradually widens posteriorly and is interrupted by rock matrix before T2 can be reached. Ovipositor is preserved well, though incomplete because it runs into the posterior margin of the shale. Ventral and dorsal valve clearly separated, but ovipositor tip most likely not preserved making total length difficult to measure thus making identification difficult. The ovipositor sheath is preserved and appears complete, being at 2.0 mm in length. The ovipositor could be used as a potential indicator for the total ovipositor length. Potential metasomal segments exist proximal to the ovipositor and its sheath. Spiracles and thyridium absent from the specimen.

Legs: Specimens legs are preserved, but in varying degrees of clarity. Hind legs are excellently preserved with mid and fore legs being layered on top of one another giving an indeterminate shape. Hind coxae are 1.7 mm long and 1.0 mm wide. Trochanter and trochantellus are well preserved. Femur and tibiae rather long being 3.5 mm and 5.4 mm long respectively. Individual tarsi are difficult to discern but a tarsal claw is very well preserved.

Forewing: The forewings are preserved proximally to one another and in some cases are layered on top of the hind wings, making discerning hind wing venation challenging. Both forewings are complete with the apical margin being almost entirely intact. The areolet is triangular and open. 1RS and 2M are very short, almost absent. 1M and 3rs&m are both 0.4 mm long, though 3rs-m is interrupted by a bulla. There are a total of 4 bullae present in these forewings, one in 1m-cu&M, one in 2m-cu, and one in 3rs-m. The ramulus is absent; instead 1m-cu&M gradually curves toward the 2rs-m junction. The stigma is 5.8x longer than wide. Wing flexion is excellently preserved and corresponds with bullae locations when it crosses wing venation. The postnervellus is 1.4x the length of 1cu-a. Postnervellus is unevenly split, its total length measuring 1.0 mm and the junction of 2CU occurring at 0.4 mm from the bottom. 2CU is 2.0x the length of 2m-cu. R is 1.3x the length of M+CU making M&RS weakly convex. 1cu-a is postfurcal to M&RS junction. AA and therefore anal cell are preserved in this specimen.

Hind wing: Both hind wings are almost complete, but their layering directly on top of one another as well as under the forewings makes interpretation a challenge. Hind wing nervellus intercepted (above the middle) by second abscissa of 1CU. Nervellus is 0.7 mm long with the junction of 2CU being at 0.3 mm from the bottom. 1RS is 2.3x the length of rs-m. C appears to not be preserved though RA is.

General measurements: Mesosoma = 4.5 mm, Metasoma = 14.5 mm, Head = 1.8 mm tall and 1.0 mm wide, Forewing = 11.0 mm long and 4.2 mm wide, Hind wing = 7.3 mm long and 1.6 mm wide.

Etymology: *Renovensis* is Latin for ‘from Renova’, named after the deposit from which these fossils were collected.

Remarks: Preliminary input and interpretation were given by Seraina Klopstein (Naturhistorisches Museum Basel), Tamara Spasojevic (Natural History Museum Vienna), Oleksandr Varga (Schmalhausen Institute of Zoology), and Filippo DiGiovanni (University of Pisa). The ovipositor is difficult to see given its attachment to the ovipositor sheath. However, this characterization of the ovipositor is nonspecific as it is seen in Orthocentrinae, Banchinae, and Ctenopelmatinae. Forewing venation has many bullae, and practically no 1RS vein with a strong resemblance to the genus *Gnathochorisis* or *Plectisicidea* within Orthocentrinae, although the ovipositor is much smaller in this specimen than in the latter.

Subfamily incertae sedis

Genus *Magna* gen. nov.

Diagnosis: Crisscross pattern on the lateral region of the propodeum, long tibial spurs, and a shorter and more rounded abdomen. Ovipositor is short and thick.

Type species: *Magna labrynthia* sp nov.

Etymology: *Magna* comes from the Latin word *Magnus* meaning large. This name was selected due to the specimen's abnormal size for other Darwin wasps of this deposit.

Magna labrynthia sp. nov.

(see Figure 8)

Diagnosis: As for the genus by monotypy

Holotype: INHS-P21149

Type locality and horizon: USA, Montana, Madison County, Upper Ruby Basin; Renova Formation, Climbing Arrow Member (Lower Oligocene: Rupelian).

Description

Coloration: Specimen is largely preserved tan in color. Black coloration is spread throughout the mesoscutum with three white patches near the apical margin. Whether this is preservation of structures or color pattern is unknown. Antennae posteriorly black and progressively turn to brown anteriorly before returning to black at the final flagellomere. Both tibiae preserved black with remaining leg segments brown. Metasoma a darker brown with patches of black on T2 and posterior of T1.

Head/Antennae: Head outline is clear though the structures preserved are few. The only head features present are the antennae. Right antennae appear to be complete with the final flagellum looking pointed. Antennae are 6.6 mm long and only twelve flagellomeres outlined, though more most likely exist. Right antenna has an elbowed shape possibly because of disarticulation rather than the actual character state.

Mesosoma: Mesosoma shows excellent preservation, with many informative characters present that are not seen in other specimens. The specimen is oriented in a way that shows a partial dorsal view as well as many lateral characters. The propodeum is well defined with anterior and posterior carinae present. A spiracle is present on the area spiracularis and in the area lateralis very angular rugae or excess carinae appear to be present. However, proximal to the spiracle is more strigose cuticular rugae. Epicnemial carina long and well preserved. Sternaulus complete and metapleuron well defined. Mesoscutum shows an anterior color pattern with three light-color circles on the anterior end that may be an artifact of preservation and should not be considered a diagnostic character. No coxae seem to be attached to the mesosoma.

Metasoma: Metasoma very round being only 6.6 mm long excluding the ovipositor and 3.3 mm tall at its tallest. T1 very narrow with dorsal longitudinal carinae partially preserved. T1 and S1 both reach T2 completely. Eight tergites are preserved with very little loss of shape between each one. Ovipositor attached and is 2.4 mm long. Ovipositor tip is indiscernible but is rather short and thick. The ovipositor weakly points dorsally, most likely remnant of the mode of preservation rather than an actual morphological character. T4-T8 5x taller than wide and T2-T3 2.5x taller than wide. This may be due to not all tergite outlines being preserved and instead shows a single large tergite. No spiracles or thyridium preserved on the specimen.

Legs: Preservation only seen in three legs, most likely all from a single side. No coxae are preserved, instead preservation begins at the trochanter and trochantellus. The hind femur is 2.3 mm long and 0.6 mm wide. Both tibiae seem to be very narrow in comparison being 0.4x the width of the femur. Tibial spurs are present on each leg but with inconsistent numbers. The front leg shows a single longer tibial spur while the mid leg shows two shorter spurs. The unattached leg segment is most likely a femur given its width of 0.7 mm. This leg segment is larger than the other tibiae, presenting 1.3x wider than the others. No other leg segments are attached or preserved across the specimen.

Forewing: The right forewing is fairly well preserved, only showing missing characters in the apical margin, anterior margin of the stigma. As well, 2m-cu is very faint. The left forewing is anteriorly missing, showing preservation just before M&RS and beyond. The stigma in this forewing is also interrupted due to a leg structure cutting across it. The posterior margin of this wing is also uneven and poorly defined making accurate length measurement difficult. The

areolet is a closed, non-petiolate, and pentagonal shape on its axis. Veins 1M and 3rs-m are the same length and are 1.6x the length of 2M. 2M and RS are both relatively short, making for an odd-looking shape. Two bullae are present in the forewing, one on the posterior side of 1m-cu&M and one on 2m-cu. These interpretations are difficult to confirm due to the faint preservation of the right forewing. The discosubmarginal cell is long as a result of 1m-cu&M being 1.9x the length of 1CU. 1cu-a postfurcal from M&RS junction, making it almost distad. The postnervellus is 1.7x longer than 1cu-a with the 2CU being 0.7 mm long and 2cu-a being 0.3 mm long. Ramulus is absent from 1m-cu&M, causing it to gradually bend convexly as opposed to being more angular. The stigma height and width ratio is not possible to measure given the nature of preservation. 2r&RS leaves the stigma at a sharp angle before bending abruptly back toward the areolet, making for a very prominent notch in the anterior margin of the discosubmarginal cell. M+CU 1.7x longer than M&RS. AA is present in the wing, but posterior margin of the wing poorly preserved. Wing flexion well preserved in the right forewing.

Hind wing: The hind wings of this specimen are almost entirely missing, showing only the anterior margin of a single hind wing. The only vein that can be measured is RS, being 1.0 mm long. All other veins are either incomplete or not preserved.

General measurements: Mesosoma = 5.3 mm, Metasoma = 6.6 mm, Head = 2.1 mm wide,
Forewing = incomplete, Hind wing = incomplete

Etymology: *Labyrinthia* is derived from the Greek word *Labyrinthos*, meaning “maze”. This name was given due to the intricate and bewildering pattern located on the propodeum.

Remarks: Specimen is placed in the subfamily incertae sedis due to its close association with three large subfamilies. The presence of tibial spurs makes Pimplinae a real possibility, but the disarticulation of the legs makes a conclusion difficult to draw. Ichneumoninae is also possible and cannot be ruled out due to the lack of complete hind wing preservation. The last possible subfamily is Cryptinae which could not be ruled out because of its diversity of characters within the subfamily.

Genus *Aperta* gen. nov.

Diagnosis: Open areolet with 1M being extended and 2M shortened. Three bullae present on the forewing; two on 2m-cu and one on 1m-cu&M.

Type species: *Aperta emiliae* sp nov.

Etymology: *Aperta* is Latin for “open” (fem.), given the open areolet found in the holotype.

Aperta emiliae sp. nov.

(see Figure 9)

Diagnosis: As for the genus by monotypy

Holotype: INHS-P20543

Type locality and horizon: USA, Montana, Madison County, Upper Ruby Basin; Renova Formation, Climbing Arrow Member (Lower Oligocene: Rupelian).

Description

Coloration: Head is preserved black with visible ventral side tan. Mesosoma mostly tan with carinae and internal structures being outlined in black. Propodeum and T1 are black with S1 being almost white. T2-T6 are tan while legs darkly colored. Antennae present as black as does the stigma of the forewing. The remaining wing venation is brown or tan.

Head/Antennae: Antennae show sufficient preservation in combination with each other. Right antennae present the scape (0.25 mm tall and 0.16 mm wide) and pedicel is obscured while the left antennae is missing structures. Maximum number of flagellomeres preserved are thirteen. Antennae most likely have more given their size, but the flagellomere outlines are indiscernible. Antennal length cannot be measured because of the disarticulation or lack of preservation. Occipital carina clearly preserved and is very weakly pointing posteriorly, most likely as a result of the head orientation. A single ocellus may be present though the correct identification of this structure cannot be confidently given. Ventrally between the head and mesosoma a structure is present, but its nature is unknown. For this description it is considered a leg fragment given the disarticulation present in all other leg structures.

Mesosoma: Mesoscutum clearly defined but lacks notaulus. Scutellum and metanotum preserved, though ventral to that characters are undefined due to ash remnants obscuring visibility. Juxtacoxal carina very prominent as are speculum and mesopleuron. Propodeum anteriorly

obscured, but posteriorly well-defined leaving out structures anterior of the anterior carinae.

Anterior and posterior carinae strongly raised. Posterior to propodeum poorly distinguished, but heavily sclerotized.

Metasoma: Metasoma is complete with little disarticulation. T1 and S1 the same length with T1 presenting as almost completely black and S1 being more ivory colored. This feature could be an indicator of T1 being heavily sclerotized. Only six metasomal segments can be counted and most are ventrally poorly preserved making heights just an estimate. T1 sharply narrowed anteriorly and is 0.72 mm long. T2-T6 are generally 2x tall than wide. Ovipositor short and narrow (1.29 mm long). Ovipositor sheaths not present and ovipositor tip is indeterminate.

Legs: Legs very poorly preserved and difficult to determine the proper leg order. One hind coxae is preserved and is attached to a partially preserved femur. The tibia is contorted but may have a tarsal claw at the end of it. Tarsal claw shape is ill-defined.

Forewing: All forewings and hind wings are preserved on top of one another, making the preservation less than ideal for interpretation. The top forewing has the costa and stigma intact, but is missing the discosubmarginal, basal, subbasal, first subdiscal, and anal cells. The second discosubmarginal, first subdiscal, and a partial subbasal cell are preserved in the other forewing. Combined, most of the forewing can be reconstructed. The areolet is open with 3rs-m missing. 1M is 3.4x longer than 2M and 1.64x longer than 1RS. Three total bullae are present, two being in 2m-cu and one being in the discosubmarginal cell. The stigma outline is poorly defined, but appears to be thick, making 2r&RS short (0.32 mm long). 1cu-a is interstitial to M&RS junction.

Postnervellus is incomplete. 2m-cu junction at the areolet is sharply angled basally before angling sharply apically. This gives the third discal cell a very pointed appearance. AA is absent.

Hind wing: A single hind wing is present in this specimen and is missing many important characters. With RA missing the length of 1RS is difficult to measure but is estimated to be 1.39x the length of rs-m. 1M is complete and is 1.84 mm long, but M+CU is incomplete.

General measurements: Mesosoma = 2.3 mm, Metasoma = 3.6 mm, Head = 0.6 mm wide and 1.0 mm tall, Forewing = 4.3 mm long and 1.4 mm wide.

Etymology: Named after my fiancée Emily for her unending support of my career as an entomologist.

Remarks: The subfamily key produced Brachycyrtinae as a result but was quickly ruled out because 1cu-a is not distad from the base of RS&M. Orthocentrinae and Cryptinae were both yielded from the key but were discarded due to the range of shared morphological characters between the two subfamilies. It is because of this uncertainty the specimen was placed within the subfamily incertae sedis

DISCUSSION

Due to the diverse nature of ichneumonids, confidently placing these new species as well as future ones into a subfamily is difficult. Adhering to the existing and widely used subfamily key (Broad et al. 2018) often produced ambiguous results that would make adding these data to phylogenies less than useful. One of the many pitfalls biologists can encounter when working on such a large group is incorrectly placing specimens into subfamilies and genera. For the purposes of this paper all wasps were given new genus and species names to make future work done on the holotypes easier to follow in the literature. Due to the nature of fossil work, much guesswork is needed when interpreting specimens and should therefore be more carefully scrutinized. While correctly identifying the Darwin wasps was labor-intensive and yielded unclear results, it at least paved the way for future work. Even today new techniques are employed to identify and describe new Darwin wasps such as using geomorphometrics (Viertler et al. 2022; Li et al. 2019). In combination with a trained eye, future descriptions will be more robust than traditional ones.

The Renova Formation has yielded many well-preserved fossils, providing a unique glance into an otherwise cryptic and tumultuous time in Earth's past. The ichneumonids found within this material highlights but a small area of hymenopteran diversity within the Eocene and Oligocene. Radiation events of parasitoids are challenging to pinpoint with only preliminary work being done on them (Peters et al. 2017). With new species of ichneumonids as well as other parasitoids within this deposit being described, it is hoped a more detailed analysis of radiation events within Hymenoptera, and better calibration of existing phylogenies can be provided. Within the material of the Renova Formation this work is paramount for establishing a working idea of the climate these insects were found in. As the fossils are placed into subfamilies with known climate preferences (i.e. tropical versus temperate) a more high-resolution understanding

of the Renova Formations own climate can be revealed. A better understanding of the insects in this deposit further adds to entomologists understanding of evolution within these groups as gaps in knowledge of the fauna of the Oligocene can help scientists make systematists make more informed placements of extant relatives.

FIGURES

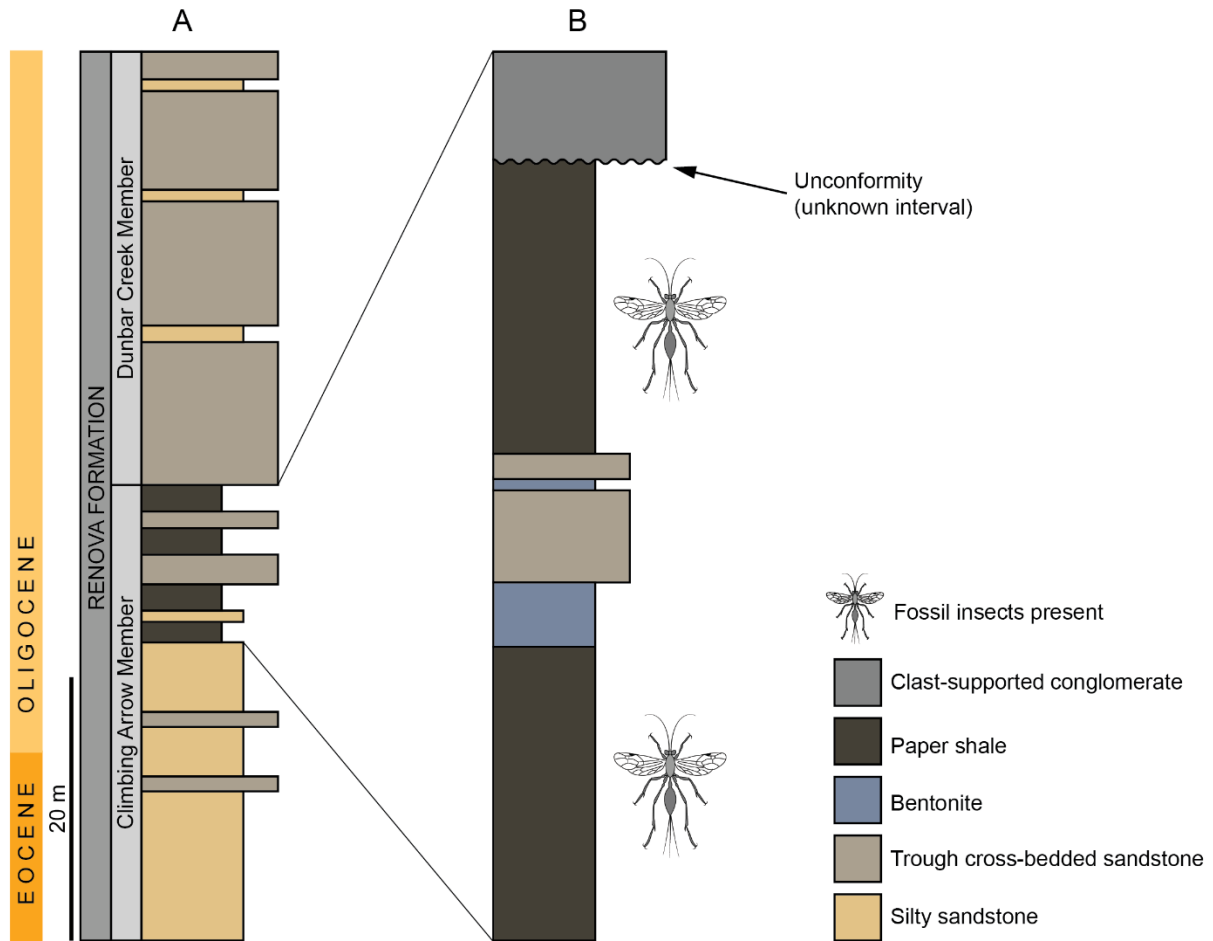


Figure 1: Stratigraphic relationships between geological units of the Upper Ruby Basin. **A**, stratigraphy of the Renova Formation within the Upper Ruby Basin; **B**, stratigraphy of the Renova Formation within the Fossil Basin sub-basin. Modified from Heads (unpublished).



Figure 2: Map of Montana with a focused window on the southwest portion of the state where the basin lies. Map by Danielle Ruffatto, used with permission.

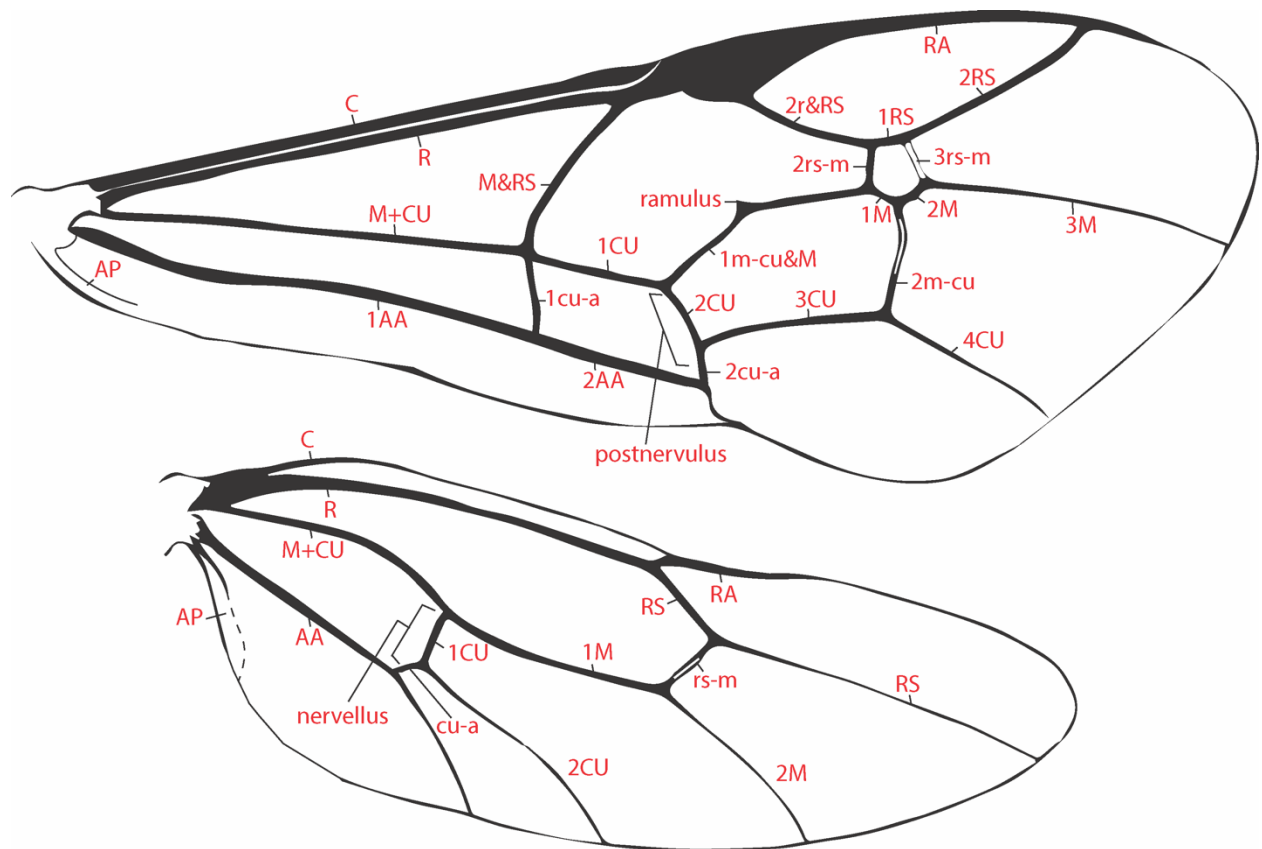


Figure 3: Naming scheme of fore- and hind-wing venation. Adapted from Broad et al. 2018.

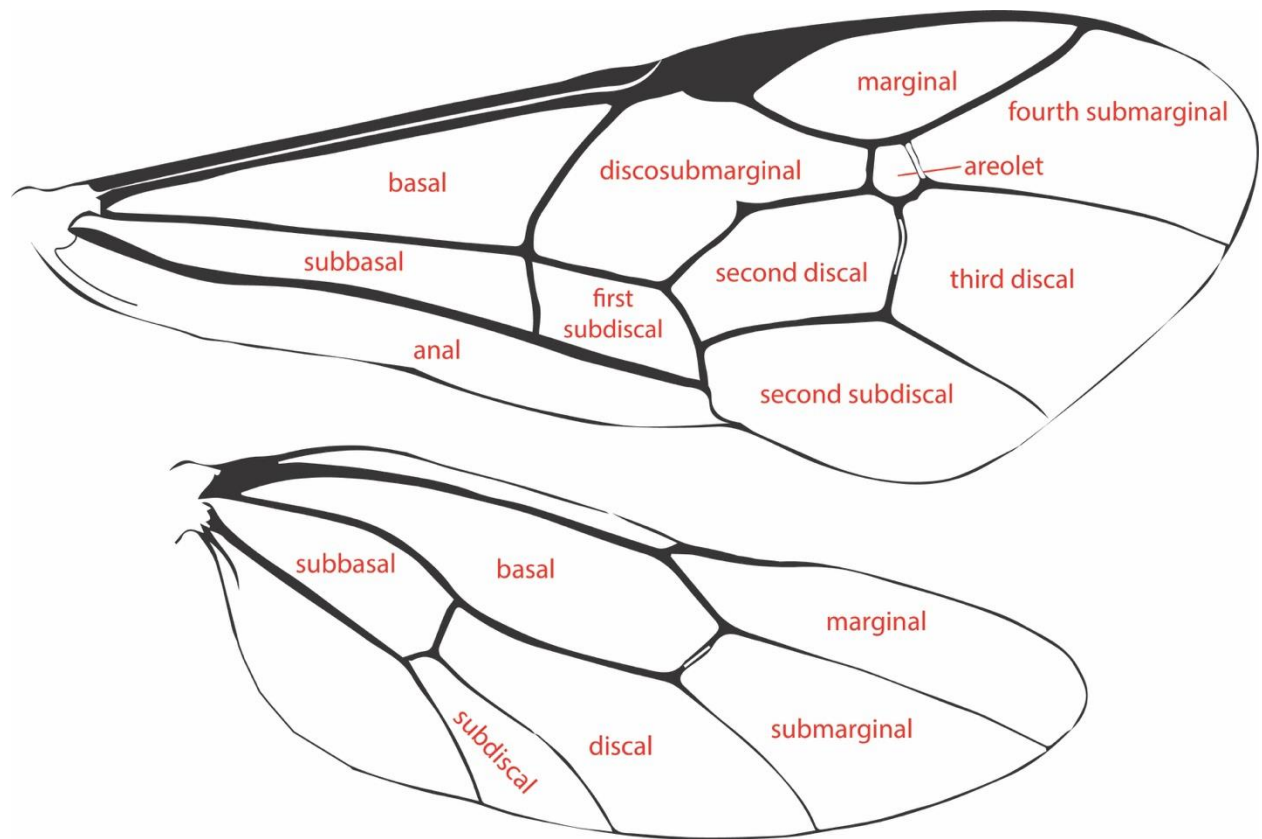


Figure 4: Naming scheme of fore- and hind wing cells. Adapted from Broad et al. 2018.

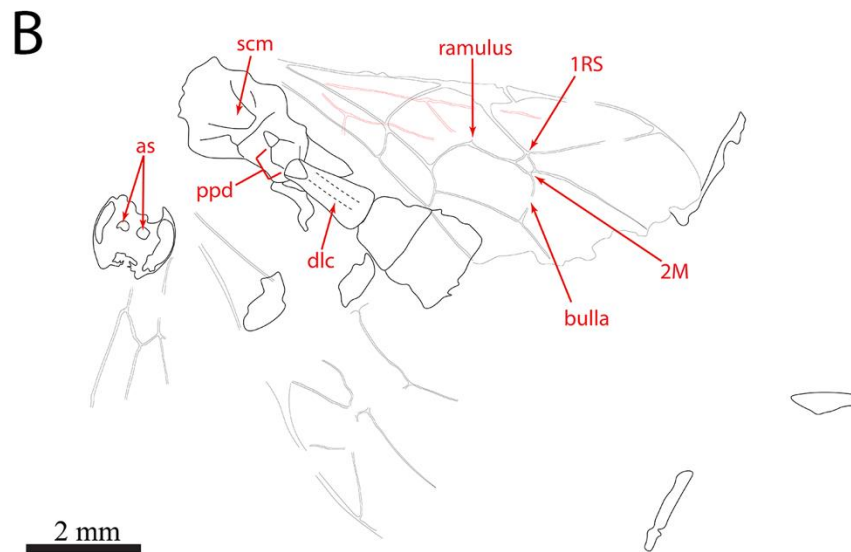


Figure 5: Specimen INHS-P21720 (A) with no interpretation and (B) with drawing interpretation and corresponding labels to key characters; as – antennal socket; dlc – dorsal longitudinal carina; ppd – propodeum; scm – scutellum.

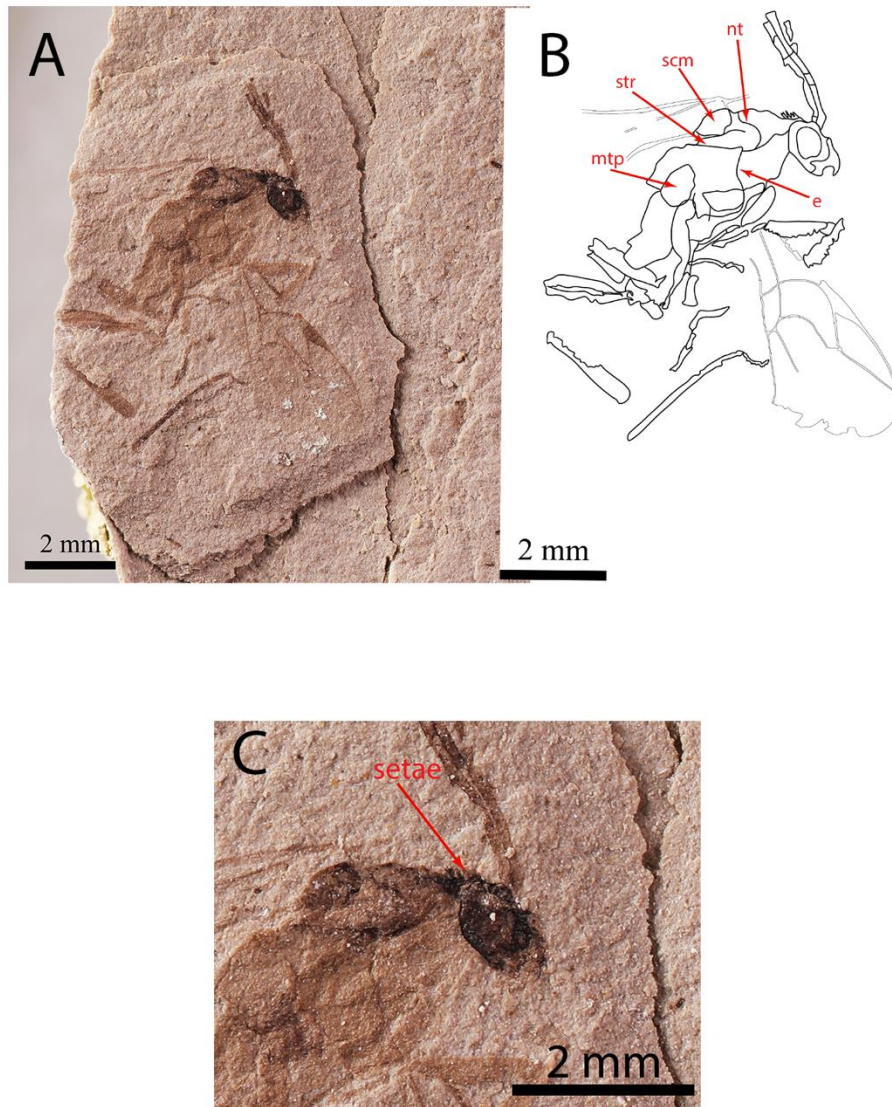


Figure 6: Specimen INHS-P25189 (A) with no interpretation, (B) with drawing interpretation and corresponding labels to key characters; e – epicnemium; mtp – metapleuron; n – notaulus; scm – scutellum; str – subtegal ridge; and (C) an enlarged look at the head with setae noted.

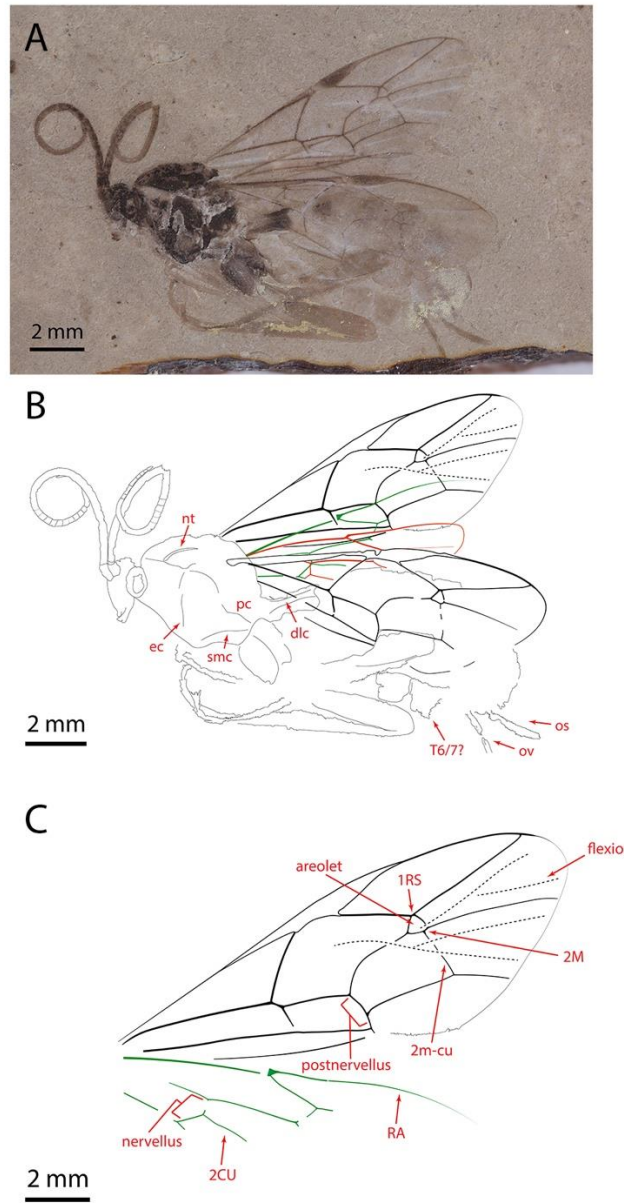


Figure 7: Specimen UM33641 (A) with no interpretation, (B) with drawing interpretation and corresponding labels to key characters; dlc – dorsal longitudinal carina; ec – epicnemial carina; nt – notaulus; os – ovipositor sheath; ov – ovipositor; pc – pleural carina; scm – scutellum; T6/7 – tergite 6/7; and (C) an enlarged view of the forewing and hind wing with appropriate labels.

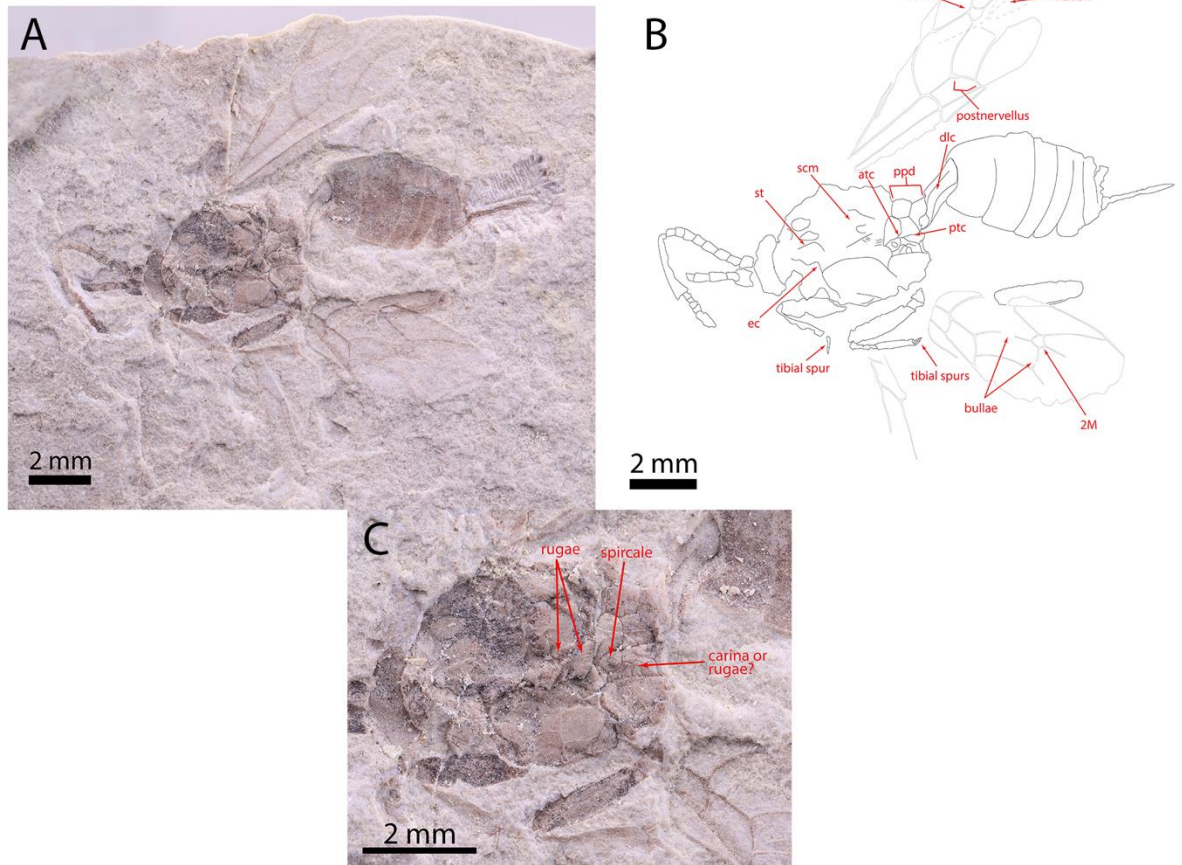


Figure 8: Specimen INHS-P21149 (A) with no interpretation, (B) with drawing interpretation and corresponding labels to key characters; atc – anterior transverse carina; dlc – dorsal longitudinal carina; ec – epicnemial carina; nt – notaulus; os – ovipositor sheath; ov – ovipositor; pc – pleural carina; ppd – propodeum; ptc – posterior transverse carina; scm – scutellum; st – sternaulus; and (C) an enlarged view of the mesosoma with diagnostic characters highlighted.

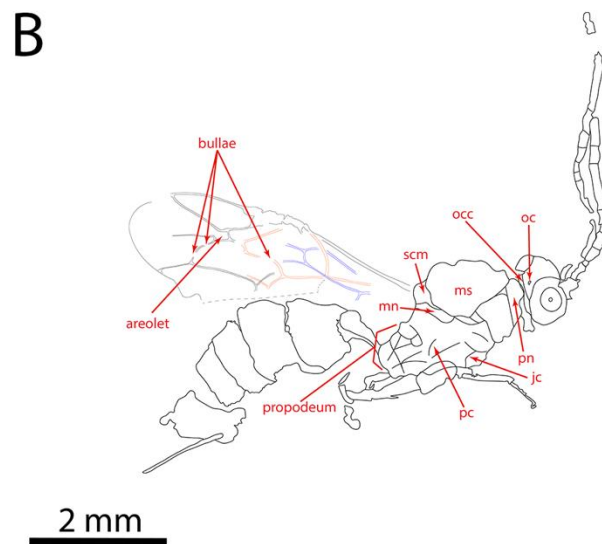
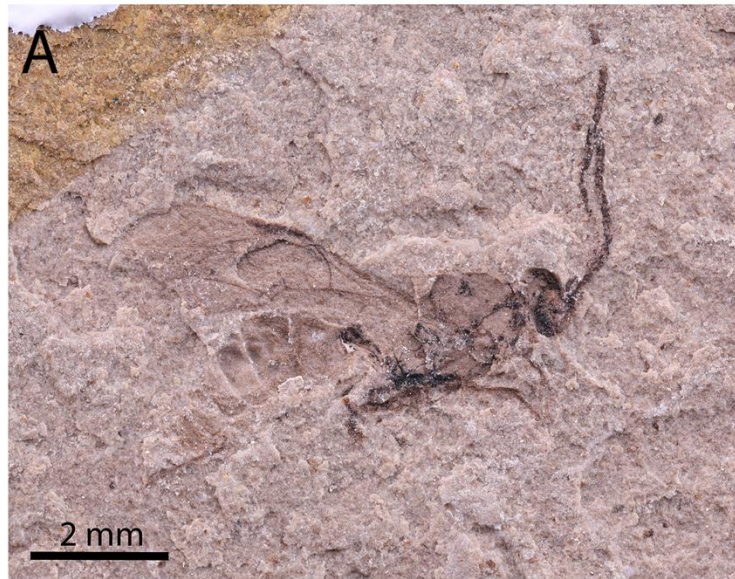


Figure 9: Specimen INHS-P20543 (A) with no interpretation and (B) with drawing interpretation and corresponding labels to key characters; jc – juxtacoxal carina; mn – metanotum; ms – mesoscutum; oc – ocellus; occ – occipital carina; pc – pleural carina; pn - pronotum; ptc – posterior transverse carina; scm – scutellum.

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