

# At the dawn of megadiversity – Protoitidae, a new family of Chalcidoidea (Hymenoptera) from Lower Cretaceous Lebanese amber

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## Abstract

The earliest representatives of Chalcidoidea are described from Barremian age Early Cretaceous Lebanese amber and classified in Protoitidae Ulmer & Krogmann, **fam. nov.** (Hymenoptera: Chalcidoidea). Protoitidae exhibits a high morphological diversity of the terminal metasomal tergum which may indicate a broad spectrum of oviposition capabilities and the ability to occupy a diverse range of ecological niches. Protoitidae comprises two genera, *Protoita* Ulmer & Krogmann, **gen. nov.**, and *Cretaxenomerus* Nel & Azar, 2005 based on *C. jankotejai* Nel & Azar, 2005, which is transferred from Scelionidae (Hymenoptera: Platygastridae) to Protoitidae. Together, 10 new species, all by Ulmer and Krogmann, are described in the two included genera—*Protoita bidentata*, *P. istvani*, *P. noyesi*, *P. petersi*, *Cretaxenomerus brevis*, *C. curvus*, *C. deangelis*, *C. mirari*, *C. tenuipenna*, and *C. vitreus*. Keys to the genera and species of Protoitidae are provided. In addition, we examine the postulated plesiomorphies and apomorphies within Chalcidoidea with respect to the fossil record, and provide additional hypotheses on their biogeographic origins.

## Keywords

Barremian age, Palaeoentomology, plesiomorphic, taxonomy

## Introduction

Today, chalcid wasps (Hymenoptera: Chalcidoidea) are among the most diverse lineages of life, following a megaradiation event in the Late Cretaceous (Heraty and Darling 2009; Peters et al. 2018; Cruaud et al. 2023). This diversification however can obfuscate much of the early morphology and homology of the group's origins with rapid radiation often leading to high degrees of homoplasy in groups (Çıplak et al. 2021). Despite their current abundance, the described fossil record of chalcids is sparse. However, those known from prior to the radiation boundary are increasingly important for understanding of the group's evolutionary paths and phylogenetic dating.

Due to its extreme diversification, Chalcidoidea has been the subject of numerous phylogenetic studies since the end of the last century (e.g., Gibson 1986; Heraty et al. 2013; Peters et al. 2018; Cruaud et al. 2023). Chalcidoidea's diversity can be partly attributed to its occupation of nearly every niche and life history strategy for parasitoids, exhibiting thirteen of the fifteen feeding habits of insects (Grissel and Shauff 1990). The rapid diversification which has led to staggering morphological diversity, has also resulted in a high level of morphological convergences (Krogmann and Vilhelmsen 2006). Gibson (1986) began an era of morphologically based phylogenetic studies for the group, as the first to formally examine hypotheses of character evolution within a cladistic concept. He postulated autapomorphies of Chalcidoidea in several additional papers expanding on the understanding of both internal and external anatomy and sister-group relationships (Gibson 1985; Gibson et al. 1999). The three autapomorphies of Chalcidoidea proposed by Gibson (1986) were the presence of a specialized structure of multiporous plate sensillae (MPS) on the flagellar segments, a laterally exposed, free prepectus, and position of the mesothoracic spiracle at the lateral level of the mesoscutum. The loss of the posterior condyle leading to flexible mandibles was recently postulated as an additional autapomorphy (van de Kamp et al. 2022). All of these above-mentioned morphological studies were based heavily, and often solely, on extant crown-group taxa leaving the identity of extinct stem-group chalcids and the ancestral states of morphological characters speculative.

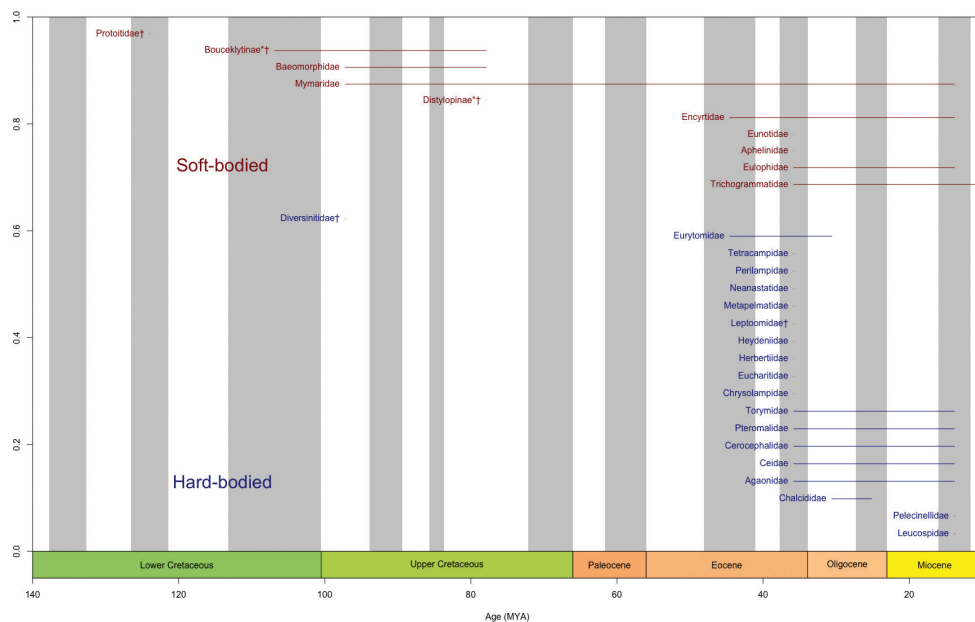
The early pattern of evolution of Chalcidoidea is still uncertain, in part because of the low number of fossils ( $n \approx 154$  species) (from paleobioDB; McClennen et al. 2017) relative to the sheer species abundance of extant taxa, more than 22,700 described (Huber 2017a), and an estimated true diversity of 500,000 (Heraty et al. 2013). Likewise, the megaradiation of crown-group Chalcidoidea is shrouded by the 'taxon gap' of the Early Paleocene, which can be clearly seen in the trends of the chalcid fossil record (Fig. 1) as well as from recent molecular studies (Cruaud et al. 2023). The advent of genomics and subsequent introduction of fossils into research of extant taxa, as a tool for calibration of phylogenies, has generated new found interest into the fossil record of Chalcidoidea. The known paleofauna of Chalcidoidea is mostly Eocene taxa that can be associated with extant groups (Fig. 1), however, the relative few described Cretaceous taxa ( $n = 27$  species) have been invaluable resources for understanding the timeline of early divergence.

Chalcidoidea is a notoriously difficult group to assess for statements of homology (Krogmann and Vilhelmsen 2006; Heraty et al. 2013). This is only more so the case when working with exclusively extinct lineages relative to extant ones, which can lead to “ambiguous ambiguity” in analysis and interpretation of phylogenies based on fragmentary records (Kearny and Clark 2003). Taphonomy of many fossils, often though not exclusively, those not preserved in amber can also lead to functional ambiguity with structures damaged or obscured leading to fragmentary information in a given fossil itself. All of these variables have made the introduction and interpretation of fossil chalcids into superfamily level studies a difficult task, with studies only in the past decade beginning to integrate early extinct lineages for calibrating phylogenies.

Peters et al. (2018) suggested a late Jurassic origin for Chalcidoidea, with the earliest distinct lineages emerging during early to mid-Cretaceous (129–81 MYA), and the extant crown groups not forming until the Early Paleogene (75–53 MYA). The earliest root node taxon, which was utilized to provide a minimum age for the superfamily, is here described as *Protoita petersi*, gen. et. sp. nov. It came from Lebanese amber and was initially associated with Chalcidoidea only by possession of the apomorphy of specialized MPS along the flagellomeres. An even earlier divergence of crown Chalcidoidea was established by Cruaud et al. (2023) at 162 MYA with the initial split from the hypothesized sister lineage of Chalcidoidea, Mymarommatoidea, occurring in the Early-Middle Jurassic boundary (174 MYA). Subsequent splitting of the major extant clades was determined during the late Jurassic to mid Cretaceous (153–80 MYA), aligning reasonably with the fossil record, in which Mymarommatoidea are often found in Lebanese deposits (Rasnitsyn et al. 2022).

While no Chalcidoidea have previously been described from Lebanese amber, several undoubtedly chalcid taxa have been uncovered from mid-Cretaceous amber deposits, which coincides with the diversification of the superfamily (Fig. 1). *Minutoma yathribi* Kaddumi, 2005, described as the oldest chalcid from Jordanian amber (115 MYA) was initially placed in Mymaridae, the sister family to all Chalcidoidea (Gibson et al. 1999; Munro et al. 2011; Peters et al. 2018; Cruaud et al. 2023). Later, Heraty et al. (2013) suggested this might be a member of the subfamily Bouceklytinae Yoshimoto 1975, a fossil subfamily of Tetracampidae known already from Campanian Cretaceous Canadian amber (83.5–70.6 MYA) (Yoshimoto 1975). Kaddumi (2005) also mentioned a eupelmid (Chalcidoidea: Euplemidae) wasps in the same amber (lower Cretaceous amber deposits of the Zarqa river basin), but based on wing venation and a dorsoventrally compressed metasoma it is very likely Scelionidae (Platygasteroidea).

This uncertainty of fossil placement is further seen in the description of the putative pteromalid, *Parviformosus wohlraabeae* Barling et al. (2013), which was described from a compression fossil from a late Aptian Crato deposit in Brazil (110 MYA). Due to the nature of compression fossils, many of the necessary diagnostic characters of Chalcidoidea are not visible and its placement was based purely on a comparable gestalt to the subfamily Sycophaginae (Agaonidae). The species was subsequently moved to Proctotrupomorpha *incertae sedis* by Haas et al. (2020).



**Figure 1.** Graph of identified Chalcidoidea families along the fossil record. Points are singleton taxa known only within the fossil record from one time period, whereas those with a fossil record extending multiple ages are shown as a line through the ages in which they are represented. Alternating gray and white bands represent geological eras. Extinct families are denoted by †. Boucekytinae and Distylopinae are noted with an asterisk (\*) because their familial placement is uncertain. Taxa in red correspond to the “soft-bodied” clade (Soft-bodied), while taxa in blue correspond to the “hard-bodied” (Hard-bodied) lineages based on Cruaud et al. (2023). Data sourced from PaleoDB. Family names adopted from Burks et al. (2022) and Gibson and Fusu (2023).

Fossil “true” Chalcidoidea are more prevalent within the Upper Cretaceous (Burmese) deposits, although the sister group Mymarommatoidea is known already from Lebanese amber (Rasnitsyn et al. 2022). The earliest confirmed chalcids are *Myanmymar aresconoides* Poinar & Huber, 2011 (Mymaridae) and *Baeomorpha liorum* Huber, Shih & Ren, 2019 (Baemorphidae), both from Burmese amber (99 MYA) (Poinar and Huber 2011; Huber et al. 2019). These taxa are consistent with the current calibrated superfamily phylogeny (Cruaud et al. 2023) as Mymaridae and Baemorphidae are the oldest known extant lineages of Chalcidoidea. *Baeomorpha* Yoshimoto, 1975 was originally described from Campanian Canadian Cretaceous amber (83.5–70.6 MYA) and classified within Tetracampidae, but was later transferred to the small extant, relictual family Baemorphidae by Gumovsky et al. (2018). Baemorphidae was previously known as Rotoitidae, which contained two extant genera prior to being synonymized under Baemorphidae due to priority in subfamilial names (Burks et al. 2022). Gumovsky et al. (2018) subsequently described 10 additional species of *Baeomorpha* as well as a new fossil genus, *Tai-*



*myromorpha*, within Baeomorphidae, all from Upper-Santonian Yantardakh amber (85.8–83.5 MYA). This makes Mymaridae and Baeomorphidae, the two basalmost lineages (Cruaud et al. 2023), one of the most prevalent chalcids within the fossil record from Lower Cenomanian through the Miocene (paleoDB 2022; Fig. 1). Unlike Mymaridae, no Baeomorphidae are known between the Cretaceous fauna and the two extant genera.

Excluding Bouceklytinae (uncertain subfamily), Diversitinidae was the only valid extinct family of Chalcidoidea described from Cretaceous (Burmese) amber (Haas et al. 2018). The family consists of three monotypic genera, *Diversinitus attenboroughi*, *Burminata caputaeria*, and *Glabiala barbata* Haas, Burks & Krogmann. Its placement as a chalcid is well supported by the presence of multiporous plate sensillae (MPS) on the flagellum as well as a laterally distinct prepectus, though its phylogenetic placement within Chalcidoidea is uncertain. Despite its age, it shares few symplesiomorphic characters with Mymaridae and Baeomorphidae such as an exposed labrum and MPS on the flagellomere 1 (fl1) in males and some females. While it retains many putative plesiomorphies of the superfamily (well-developed fl1, presence of a frenum, and peg-like cerci), this could indicate a ‘gap’ in the fossil record of potentially transitional taxa between the early lineages of Chalcidoidea from the Cretaceous and their descendants (Gibson 2003; Krogmann and Vilhelmsen 2006; Heraty et al. 2013; Haas et al. 2018).

The Chalcidoidea fossil record prior to this work consists of approximately 154 described species (Suppl. material 1). Of that, only 27 species have been described from the Cretaceous, with the vast majority (n=127) being from the Eocene onward (Fig. 1). Hong (2002) also described two new chalcid families from Ypresian Xilutian amber from China (56–47 MYA), but all the species names, and hence the two new families are considered as unavailable because the author provided no explicit statement of the depository of the primary type material (see ICZN 1999, Article 16.4.2; Noyes 2021).

Lebanese amber is one of the oldest fossil sources, dating to the Barremian age of the Lower Cretaceous (~130 MYA) (Azar et al. 2010; Granier et al. 2016; Maksoud and Azar 2020; Maksoud et al. 2017, 2022). Due to its age, Lebanese amber includes some of the earliest representatives of the extant lineages of insects, as well as extinct families which are likely ancestors of known groups. Lebanese amber likewise provides one of the only examinations of the earliest radiations of major insect lineages over northeastern Gondwana (Poinar and Milki 2001). The study of the different Lebanese amber inclusions has allowed for the reconstruction of the palaeoenvironment. The information provided by well-preserved inclusions including palynology data corroborate the palaeoenvironment of the resin deposits as a tropical dense, warm, and humid forest with a very complex fluvial system, altogether close to the sea (Poinar and Milki 2001). In addition, most of the fauna entombed in Lebanese amber was living on the lower to mid-parts of trees. This could be explained by the fact that this type of fauna has more chance to be trapped because normally all resin-drops falling

from a tree pass inevitably and more frequently through these zones (Azar et al. 2010; Maksoud and Azar 2020; Maksoud et al. 2022). The environment of the Barremian age is comparable to the younger and more commonly studied Burmese amber of Eastern Gondwana.

Because the most recent paleobiogeographic models suggest a Southern Gondwana origin for chalcids (Cruaud et al. 2022), with multiple northward dispersals between 150 and 100 MYA, the examination of older northeastern Gondwanan fauna can provide novel insights into the earliest range expansions of a fledgling group. Herein, we provide the description of a new family of Chalcidoidea from Lebanese amber, the earliest currently known, based on 15 fossils. The new family is classified as two genera (one described as a new) and 11 species, of which ten are newly described. Postulated plesiomorphies and hypotheses about the early diversification of Chalcidoidea pre-radiation are discussed.

## Methods

### Specimens

Among the 450 different outcrops of amber-bearing sediment from the Lower Cretaceous in Lebanon, 29 outcrops provide biological inclusions. In the present study we examined 15 specimens from two outcrops:

1. Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian (Granier et al. 2016; Maksoud et al. 2017, 2021)
2. Roum – Aazour – Homsiyeh, Caza Jezzine, Mouhafazet South Lebanon; lower Barremian (Granier et al. 2016; Maksoud et al. 2017, 2021).

Of the examined specimens, all but one, *Protoita istvani*, sp. nov., are from the Hammana outcrop.

All the material was previously deposited at the National Museum of Natural History, Paris, France (MNHN) and is now deposited at the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

### Imaging

Relevant material was prepared following (Azar et al. 2003) between two coverslips, using Canada balsam as a mounting medium. Specimens were examined and scored under a Leica M205C stereo microscope with a 7.8–320× magnification. Imaging of specimens was performed with a Keyence VHX 5000 digital microscope. Images were stacked and scale bars placed using the proprietary software. Measurements were taken based on the stacked images in ImageJ (v. 2.1.0). All measurements are in micrometers (µm). Plates were generated in Adobe Photoshop 2022.

## Fossil biodiversity analysis

Fossil data for Chalcidoidea was pulled from the paleobioDB (McClennen et al. 2017), data was subsequently checked for errors and harmonized across all taxa for analysis in OpenRefine. Time series plots at the genus and family level were generated in R, with the DivDyn package (Kocsis et al. 2019). Fossil data was set based on its earliest possible age rather than oldest when an interval range is given for its occurrence, following the reasoning of Klopstein (2021).

## Terminology

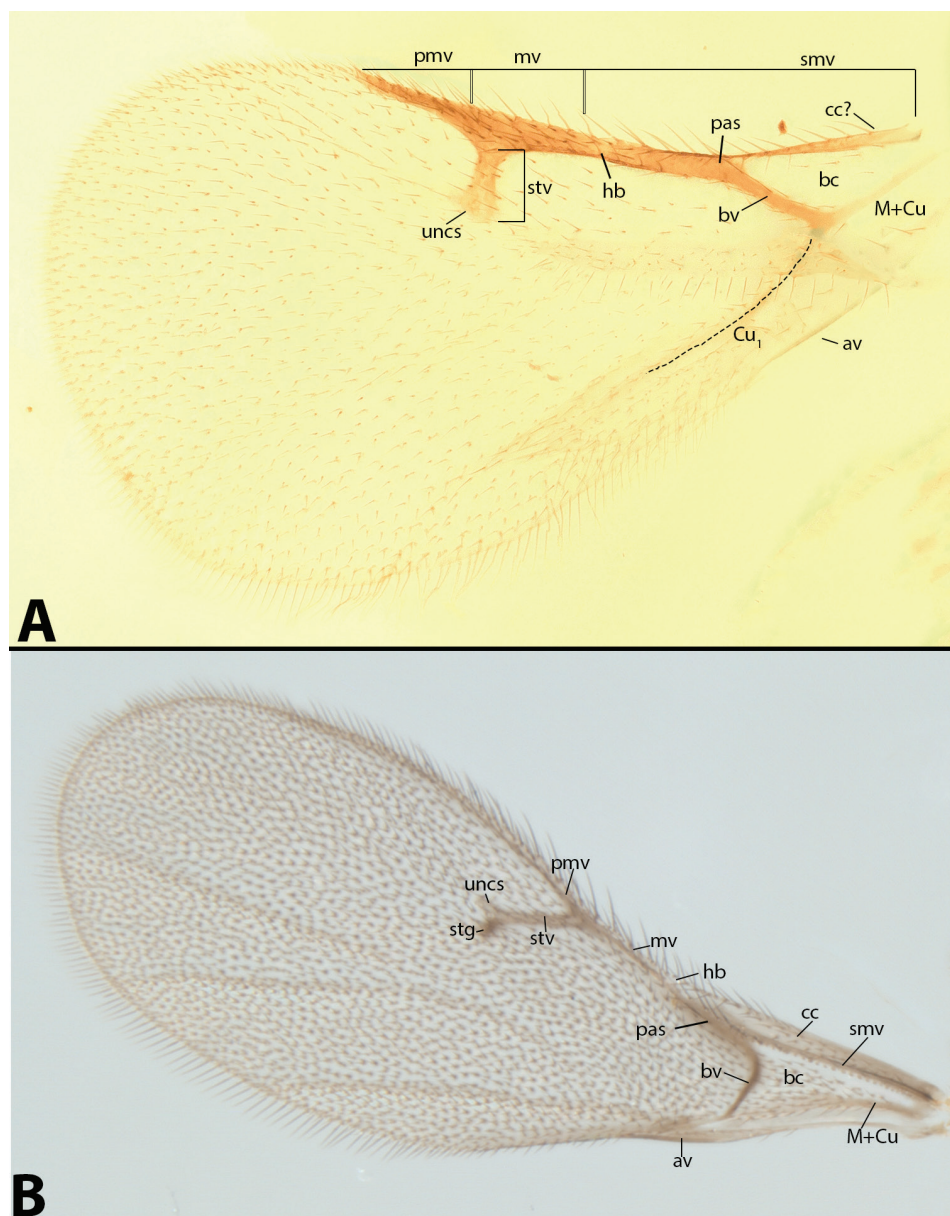
Terminology follows the Hymenoptera Anatomy Ontology (HAO) (Yoder et al. 2010), all term abbreviations will be noted at their first time of use in figure captions or in text. Additional wing terminology is derived from Heraty et al. (2013; Fig. 2), with modifications for clarity of venation variation present in the taxon based on HAO preferred synonyms. Measurements are given in micrometers.

## Notes on rationale for discretization of uncertain characters

Some morphological characters are of a continuous or difficult to discretize nature (e.g., clavomere segments) or their physical boundaries are not clearly defined in some taxa (e.g., marginal wing venation). The need for consistency and checkpoints of characters amongst all taxa are critical for their interpretation, especially within paleotaxonomy where structures can be degraded or obscured. Here we provide our rationale for discretizing such characters within Protoitidae.

**Marginal vein (mv)**—The marginal vein of Chalcidoidea is usually delimited between either the end of the costal cell (cc) proximally or the junction of the hyaline break and the point of intersection of the stigmal vein and postmarginal vein. In several specimens of Protoitidae the costal cell is not visible or folded in a way that it does not provide clear indication of the proximal starting point of the marginal vein. In these specimens we use the presence of a weakening of the wing venation at a junction similar to the hyaline break in higher chalcids, which often has sensilla that mark the beginning of the marginal vein (hb; Fig. 2A).

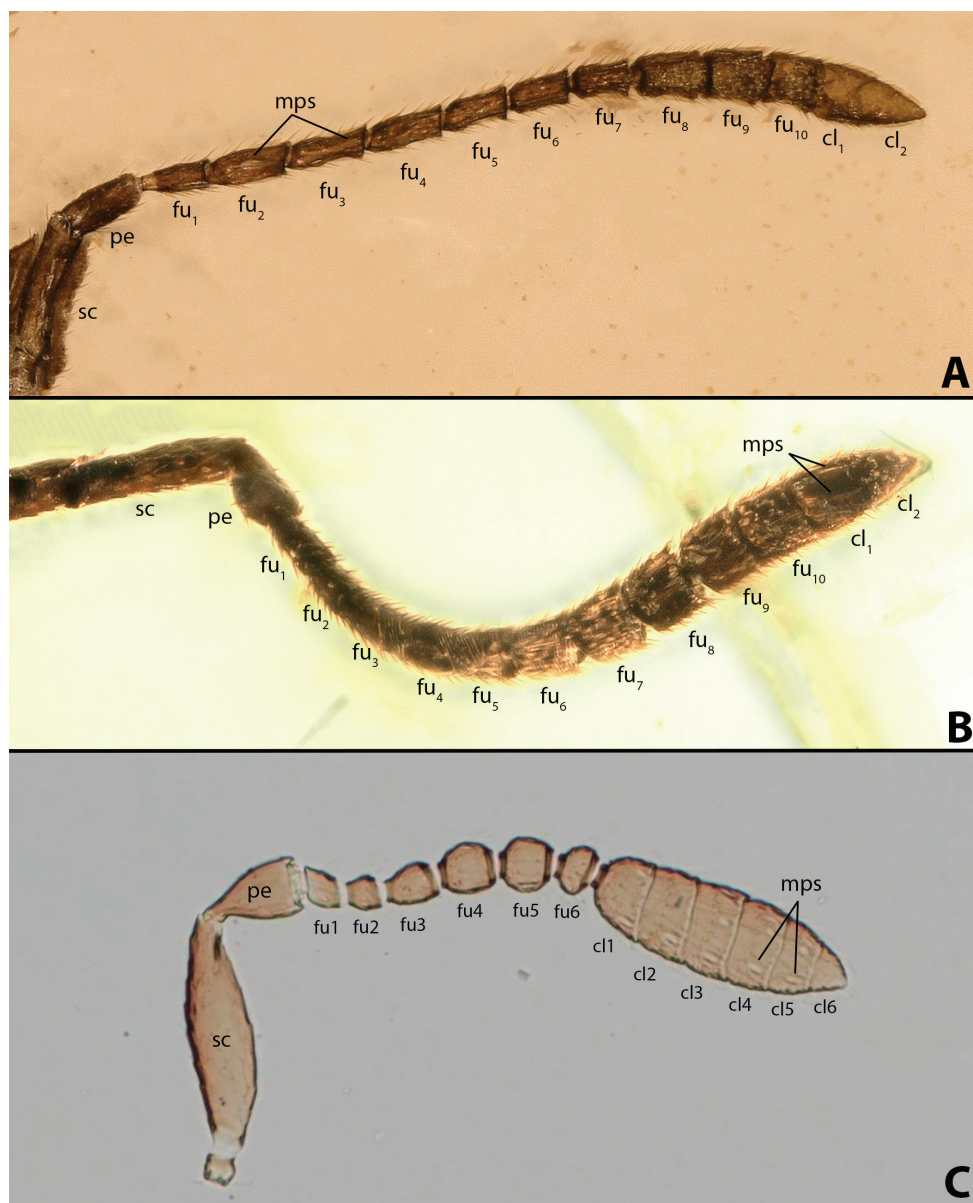
**Flagellomere (fl)/ funicle (fu)/ clavomere (cl)**—Within chalcid antennal terminology, flagellomeres are all the antennomeres beyond the pedicel, whereas funicular segments are defined as the flagellomeres located between the anellus or anelli (often ring-like segment(s) directly distal of pedicel that always lack MPS) and clava. Protoitidae lack an anellus, the basal flagellomere being longer than wide and having MPS, so for the sake of clarity when discussing antennal segments “flagellomere” is used for all segments beyond the pedicel including clavomere(s), and funicle for all segments between pedicel and clava. The claval segments of several taxa are often difficult to discern because of a gradual increase in flagellomere width through the entire length of the flagellum. Likewise, many fossil taxa described are based on singletons so shape and closeness of antennal segments are difficult



**Figure 2.** Fore wing morphology and terminology **A** *Cretaxenomerus vitreus*, sp. nov. **B** *Rotoita* sp. (Baeomorphidae). **av** = anal vein; **bc** = basal cell; **bv** = basal vein; **cc** = costal cell; **Cu<sub>1</sub>** = cubital vein; **hb** = hyaline break; **M+Cu** = medio-cubital crossvein; **mv** = marginal vein; **pas** = parastigma; **pmv** = postmarginal vein; **smv** = submarginal vein; **stv** = stigmal vein; **uncs** = unicus.

to state as true or as taphonomic artifacts. Within this work, we assign and count claval segments starting at those without a clear ‘gap’ at the joint with the subsequent segment (Fig. 3A, B). Nearly all protoitids have at minimum a 2-segmented clava due to the partial fusion of  $fl_{11}$  and  $fl_{12}$  (Fig. 3A, B:  $cl_1, cl_2$ ). *Cretaxenomerus vitreus* and *C. tenuipenna* have no





**Figure 3.** Antennal morphology **A** *Protoita noyesi*, sp. nov. **B** *Cretaxenomerus curvus*, sp. nov. **C** *Rotoita basalis* (Baeomorphidae). **cl<sub>n</sub>** = claval segment n; **fu<sub>n</sub>** = funicular segment n; **mps** = multiporous plate sensilla; **pe** = pedicel; **sc** = scape.

distinction or fusion in the terminal flagellomeres and thus the terminal flagellomere ( $fl_{12}$ ) is considered the clava. In many species there is a dimensional variation in the terminal five or six flagellomeres, however consistent identification of these as claval segments is difficult within fossils where the angle of the antennae may obfuscate the closeness of two segments (for comparison with Baeomorphidae antennae see Fig. 3C).

## Results

### Systematic palaeontology

#### Order Hymenoptera Linnaeus, 1758

#### Superfamily Chalcidoidea

#### Family Protoitidae Ulmer & Krogmann, fam. nov.

<https://zoobank.org/D3E42A23-E578-4343-87E7-78A4B0B86E55>

#### Type genus. *Protoita*, gen. nov.

**Diagnosis.** Antenna 14-segmented (Fig. 3A, B); clava 1–3 segmented, terminal two flagellomeres differentiated by a line of weakness (partially fused) when clava multi-segmented (Fig. 3A, B); MPS present on all flagellomeres. Clypeus inflected dorsally and laterally with an arched groove at margin (Figs 6G, 7C, 8E, 10C). Malar sulcus present. Lower tentorial bridge present, about as broad as distance between lower margin of occipital foramen and dorsal margin of hypostomal foramen. Postgenal bridge absent (Fig. 5A). Pronotum dorsally narrow, almost entirely concealed by mesonotum medially in dorsal view (Figs 5D, 6C, 7A, 8B, 10D, 11D); lateral panel externally reaching base of tegula. Mesonotum about 4× as long as mesoscutellum (Figs 4D, 5D, 6C, 7A, 8B, 11D, 13A, 14A). Prepectus laterally evident as elongate, vertical sclerite partly covered by posterior-most margin of lateral panel of pronotum (Fig. 16A, B). Mesopleuron oriented dorsoventrally, abutting ventrally on a lower plane than coxae (Fig. 8B); mesodiscrimen deeply invaginated. Fore wing with basal vein completely sclerotized (Fig. 2A). M+Cu pigmented at least distally and usually sclerotized. Marginal vein strongly sclerotized and 2–3× as wide as submarginal vein. Parastigma usually as wide as or nearly as wide as marginal vein (Fig. 2A). Costal cell reaching far beyond junction of submarginal vein and basal vein. Retinaculum pigmented. Hind wing with three hamuli of equal length and orientation, the distal hamulus not extending beyond midpoint of hind wing. Meso- and metacoxae abutting, separated widely from procoxa by mesopleuron (Figs 6A, C, 8B, 11D, 13A). Protibial spur curved and apically cleft; probasitarsus with basitarsal comb nearly always present (Figs 4C, 7D, 10E, 11F, 14D:cal). Metatibia with two apical spurs with shorter spur about 1/3 length of longer spur (Figs 8A, 9A, 11C). All tarsi 5-segmented; basitarsi about as long as or slightly shorter than tarsomeres 2–4 (Figs 4A, 5A, 6A, 8A, 10E, 11F, 15C). Metasoma with short petiole. Hypopygium reaching end of metasoma.

#### Key to genera of Protoitidae, fam. nov.

- 1 Metasoma in dorsal view triangular in shape and broadly attached to mesosoma (Figs 4A, 5A, 7A); syntergum approximately equal in length to preceding tergite (Figs 4G, 6F); cerci digitiform. Body length less than 1 mm ..... ***Protoita* gen. nov.**
- Metasoma in dorsal view ovoid, with distinct constriction between meta- and mesosoma (Figs 9A, 12A, 13A, 14A); syntergum nearly always elongate (single

exception *Cretaxenomerus deangelis* with syntergum very short and narrow) (Figs 8D, 10F, 12D, 13B, 15B); cerci button-like. Body length greater than 1 mm. .... *Cretaxenomerus* Nel & Azar, 2005

***Protoita* Ulmer & Krogmann, gen. nov.**

<https://zoobank.org/7B0689EB-29B3-4D83-AB1C-3C32F8EC1CF2>

**Diagnosis.** Small, less than 1 mm in length. Head transverse in dorsal view, wider than mesosoma and with temple narrow. Metasoma sessile, broadly associated with mesosoma, and in dorsal view triangular in shape; syntergum no longer than preceding tergite; cerci digitiform. Female with exerted ovipositor at most  $\frac{1}{4}$  as long as length of metasoma.

**Key to species of *Protoita*, gen. nov.**

- 1 Head globular or of about equal dimensions (Figs 4E, 7A).....2
- Head narrowed antero-posteriorly in dorsal view (Figs 5A, 6D, G). ....3
- 2 Terminal clavomere equal in length to preceding clavomere (Fig. 4B). Head in lateral view triangular (Fig. 4A); occiput deeply impressed (Fig. 4E). with basitarsal comb sparse, only present on proximal half of tarsomere (Fig. 4C) ..... ***Protoita noyesi* sp. nov.**
- Terminal clavomere  $\frac{1}{2}$  length of preceding clavomere (Fig. 7B); head in dorsal and anterior view globular, slightly broader than long (Fig. 7A, C). Foreleg with basitarsal comb present along entire length (Fig. 7D)..... ***Protoita petersi* sp. nov.**
- 3 Antenna with clava 3-segmented; funicular segments all about equal in dimensions (Fig. 5A, C). Mandibles bidentate (Fig. 5E). Foreleg without basitarsal comb. Stigmal vein at 90° angle with marginal vein (Fig. 5A). Male (Fig. 5B)..... ***Protoita bidentata* sp. nov.**
- Antenna with clava 2-segmented; funicular segments 1–3 4× as long as wide (Fig. 6A, B). Mandibles tridentate (Fig. 6G). Fore leg with basitarsal comb. Stigmal vein at 45° angle with marginal vein (Fig. 6A, C). Female (Fig. 6F)..... ***Protoita istvani* sp. nov.**

***Protoita noyesi* Ulmer & Krogmann, sp. nov.**

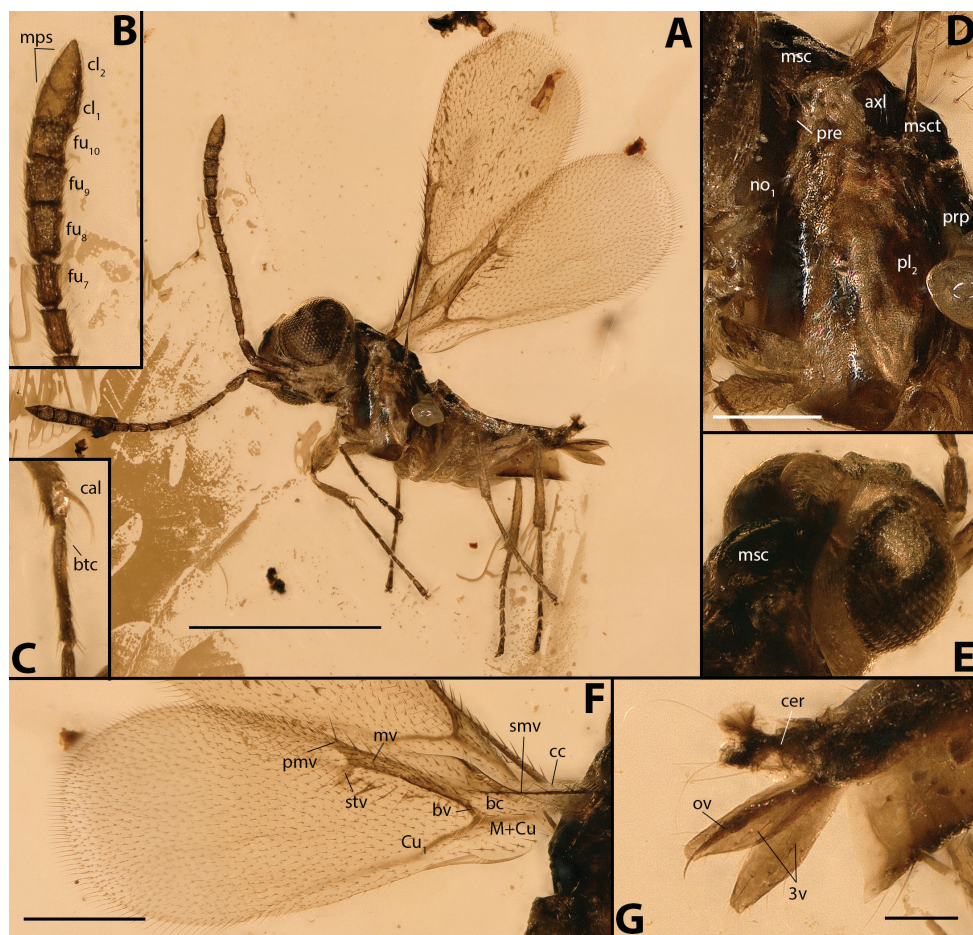
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Figs 3A, 4, 16B

**Diagnosis.** The female of *Protoita noyesi* differs from those of other species in the genus by the following combination of characters: occiput impressed relative to vertex (Fig. 4E). Flagellomere 8–12 with micropilosity on ventrum. Ovipositor sheaths broadened at midpoint before tapering distally (Fig. 4G).

**Description. Female.** Body length 876. Body uniformly brown except legs light brown. Wings with light brown infumation, uniformly setose. Right mesopleuron





**Figure 4.** *Protoita noyesi*, holotype **A** lateral habitus **B** apical part of antenna **C** fore leg basitarsus **D** mesosoma, lateral **E** head, posterior **F** fore wing **G** ovipositor complex and terminal metasomal segments. Scale bars: 500  $\mu$ m (**A**); 200  $\mu$ m (**F**); 100  $\mu$ m (**D**); 50  $\mu$ m (**G**). **3v** = 3<sup>rd</sup> valvulae; **axl** = axillula; **btc** = basitarsal comb; **cal** = calcar; **cer** = cerci; **msc** = mesoscutum; **msct** = mesoscutellum; **no**<sub>1</sub> = pronotum; **ov** = ovipositor; **pl**<sub>2</sub> = mesopleuron; **pre** = prepectus; **prp** = propodeum.

with bluish metallic tint. **Head** wedge shaped in lateral view, wider than mesosoma in dorsoventral view (Fig. 4A, E), width 301, length 249. Postorbital carina present. Temple very narrow (Fig. 4E). Vertex concave. Occiput impressed. Antennal scrobes depressed. Toruli closer to inner margin of eye than each other. Antennal insertion at midline of eye. Genal margin with 3 setae on ventral edge. Clypeus inflexed, dorsally merging with interantennal projection. Mandibles on higher plane from face. Mandibular dentition 3:3. Maxillary palps 2–3 segmented (specimen position makes exact count impossible). Labial palps damaged. **Antenna** length 586. Radicle as long as basal width of scape. Scape distally laterally compressed, 2.5 $\times$  as long as wide. Pedicel 2.25 $\times$  as long as wide. Funicles 1–4 at least 2.6 $\times$  as long as wide; fu7 2 $\times$  as long as wide. Clava at least

2 segmented. All clavomeres with micropilosity on ventral side. **Mesosoma** (Fig. 4D) length 263. Lateral panel of pronotum narrow, not touching tegula. Mesonotum length 185. Mesoscutum partially collapsed. Prepectus present as vertically narrow triangular sclerite. Mesopleuron about 2.6× as long as wide (281:105); pleural suture present as depression. Axillae relatively small; axillulae with dorsal flange extending over wing base slightly (Fig. 4D). Mesoscutellum posteriorly sloped. Dorsellum band-like, width 28. Propodeum sloping posteriorly, at 45° angle relative to dorsal plane of mesosoma. **Wings** (Fig. 4F). Fore wing length 826, width 330. Longest marginal seta of fore wing 42. Submarginal vein length 350. Marginal vein wide and strongly sclerotized, length 69, width 22. Cubital vein sclerotized along basal 1/3 of its length, then present as pigmented fold, length 200. Basal vein sclerotized, length 27. Stigmal vein short, length 30. Uncus elongate, extending distally further than postmarginal vein (possible artifact); 5 uncal sensillae present. Postmarginal vein slightly shorter than marginal vein. Basal cell with 2–3 rows of setae. Hind wing slender; length 598, width 35. Length of longest marginal seta of hind wing 37. **Legs** with barsitarsal comb of fore leg present as sparse setation only on proximal half of tarsomere (Fig. 4C:bt). Trochanter of mid leg elongate relative to fore- and metatrochanter. **Metasoma** length 410. Gaster wedge-like. Metasoma broadly associated with mesosoma; petiole (Mt<sub>1</sub>) not visible. Mt<sub>2-9</sub> visible. 4 sternal segments visible with hypopygium equal in length to preceding 3 segments, protruding laterally and reaching end of metasoma. Ovipositor slightly extruded; ovipositor sheaths flattened and broadest in middle (Fig. 4G).

**Male.** Unknown.

**Holotype.** Female. Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 407AB.

**Type condition.** Specimen in good condition with slight detachment from amber along the mesopleuron, and bubble formed around propodeal spiracle.

**Etymology.** The specific epithet is a patronym in honor of Dr John Noyes for his lifelong contributions to chalcidology.

### *Protoita bidentata* Ulmer & Krogmann, sp. nov.

<https://zoobank.org/35C89B66-DAA3-4CE6-9DD5-9F9D1716E03B>

Fig. 5

**Diagnosis.** *Protoita bidentata*, the only species of the genus known from the male, differs from all other species in the genus by the following combination of characters: Body and antenna bicolored (Fig. 5A). Mandibular formula 2:2 (Fig. 5E:md). Clava 3-segmented (Fig. 5C). Stigmal vein of fore wing extending at a right angle to wing margin (Fig. 5A). Basitarsal comb of fore leg lacking.

**Description. Male.** Body length 855. Head, scape, pedicel and fu<sub>1</sub>–fu<sub>4</sub> brown. Mesosoma, metasoma and fu<sub>5</sub> to tip of clava dark brown. Legs pale. Sculpture on head, meso- and metasoma alutaceous. Wings hyaline, uniformly pilose, damaged beyond postmarginal

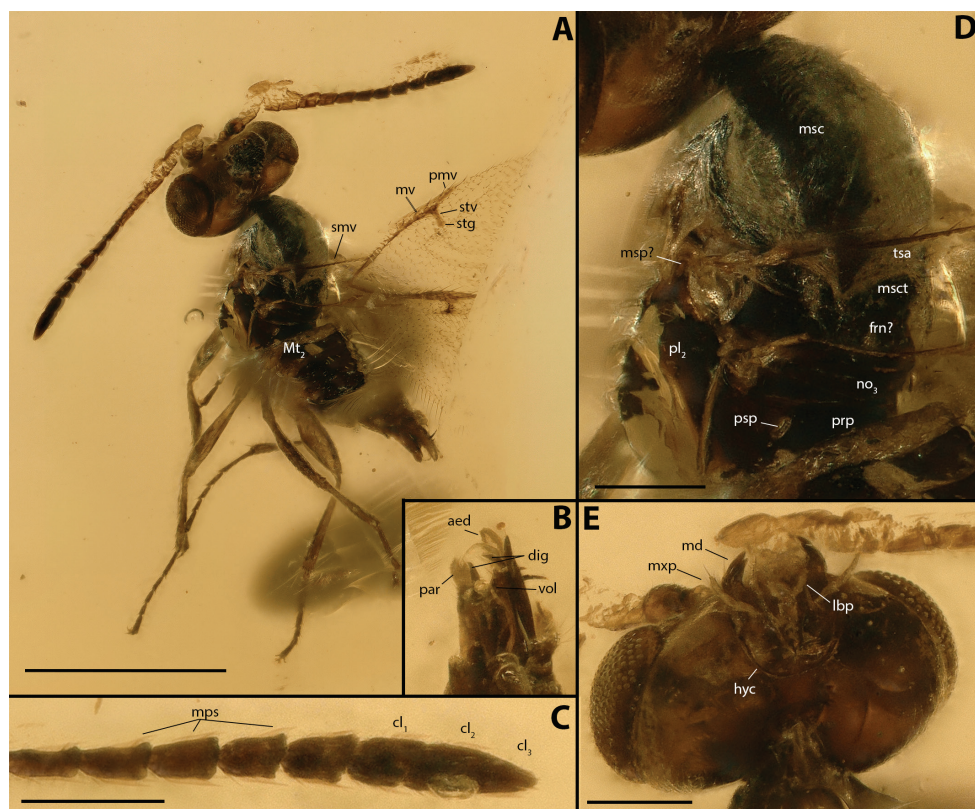
vein (Fig. 5A). **Head** strongly transverse,  $2\times$  as wide as long in dorsal view (360/179). Temples very short, about  $0.15\times$  as long as eye length. Lower tentorial bridge wide, about as wide as long; postgenal bridge absent; hypostomal carina complete (Fig. 5E:hyc). Occipital carina present (Fig. 5E). Antennal scrobe slightly depressed. Interantennal region convex. Antennal insertion closer to inner eye margin than each other (Fig. 5A). Clypeus not visible. Dentition 2:2, extending out from facial plane (Fig. 5E:md). Maxillary palps 3-segmented (Fig. 5E:mxp). Labial palps 2-segmented (Fig. 5E:lbp). Maxilla wider than labium. **Antenna** length 533. Pedicel and scape partly damaged.  $Fu_1$  about or slightly less as wide as pedicel, other flagellomeres gradually widening distally,  $fu_{1-6}$  not less than  $2\times$  as long as wide,  $fu_{7-9}$  less than  $2\times$  as long as wide. Clava 3-segmented, clava length 85 (Fig. 5C). MPS present on all segments including terminal segment; MPS extend beyond the distal edge of the segment. Claval segments equilateral and closely associated relative to funicle segments; clava without micropilosity (Fig. 5C). **Mesosoma** length 346. Transcutal articulation present as weak line of separation (Fig. 5D:tsa). Mesopleuron large, partially obscured by bubble (Fig. 5D:pl<sub>2</sub>); separated from metapleuron by suture. Axillae not pronounced; axillulae slightly flanged (Fig. 5D). Mesonotum length 224. Mesoscutellum convex, length 44,  $2\times$  as long as wide (Fig. 5D:msct). Metanotum narrow, band-like, width 21 (Fig. 5D:no<sub>3</sub>). Propodeum partially obscured by abdomen, relatively short, as long as or slightly longer than mesoscutellum (Fig. 5D:prp); propodeal spiracle visible, oval, posteriorly angled, closer to anterior margin of propodeum than its diameter (Fig. 5D:psp). **Wings**. Fore wing damaged beyond midline. Fore wing width 323. Longest marginal seta length 46. Submarginal vein length 379. Marginal vein narrow, length 81, width 24. Cubital vein narrow, weakly pigmented. Basal vein sclerotized, length 60. Stigmal vein straight,  $90^\circ$  relative to dorsal wing margin, stigmal vein length 44. Uncus present with ephemerall line extending distally. Postmarginal vein length 53. Hind wing length 440, width 28. Longest marginal seta of hind wing 35 (Fig. 5A). **Legs**. Protibial calcar long, curved, apically bifurcate. Basitarsus of fore leg ventrally curved; no basitarsal comb. **Metasoma** length 313. Metasoma broadly associated with mesosoma; petiole obscured (Fig. 5A).  $Mt_{2-9}$  visible; all equal in length except  $Mt_2$ , dorsally slightly shorter. 3 sternal segments visible, each about  $2\times$  as long as tergal segment average length. Cerci between  $Mt_8$  and  $Mt_9$ , digitiform, about  $2\times$  as long as digitiform base. **Genitalia** length externally 97. Genital capsule externally protruding. Paramere present; single apical parameral setae present. Intervosellar process broad, extends equally in length to aedeagus. Aedeagus broad with 2 sets of sensillae (Fig. 5B:aed). Digitus with 2 digital processes (Fig. 5B:dig).

**Female.** Unknown.

**Specimens examined.** *Holotype*: male, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 182.

**Type condition.** Specimen with distal  $\frac{1}{3}$  of its wings missing and basal antennomeres damaged.





**Figure 5.** *Protoita bidentata*, holotype **A** dorsolateral habitus **B** male genitalia, ventral **C** terminal funicular segments and clava **D** mesosoma, dorsolateral **E** head, posteroventral. Scale bars: 500  $\mu$ m (**A**); 100  $\mu$ m (**C–E**). **aed** = aedeagus; **dig** = digitus; **frn** = frenum; **hyc** = hypostomal carina; **lbp** = labial palp; **md** = mandible; **msp** = mesothoracic spiracle; **Mt<sub>n</sub>** = metasomal tergum; **mxp** = maxillary palp; **no<sub>3</sub>** = metanotum; **par** = paramere; **psp** = propodeal spiracle; **tsa** = transcutal articulation; **vol** = volsella.

**Etymology.** The specific epithet is derived from the mandibular formula of the species.

**Notes.** *Protoita bidentata* is the only species in the genus described from a male. While it is the only taxon with two mandibular teeth, sexual dimorphism in this character is very rare in Chalcidoidea, likely the female of *P. bidentata* is also bidentate. Unlike dentition, antennal shape and claval segments are quite often sexually dimorphic in extant chalcids, and in *Cretaxenomerus curvus* where the male is known we can see a drastic variation in flagellar shape and claval number. *P. bidentata* is the only species known within *Protoita* with 3 claval segments, and within all of Protoitidae only *C. deangelis* is also known to have 3 claval segments however that species is described from a female.

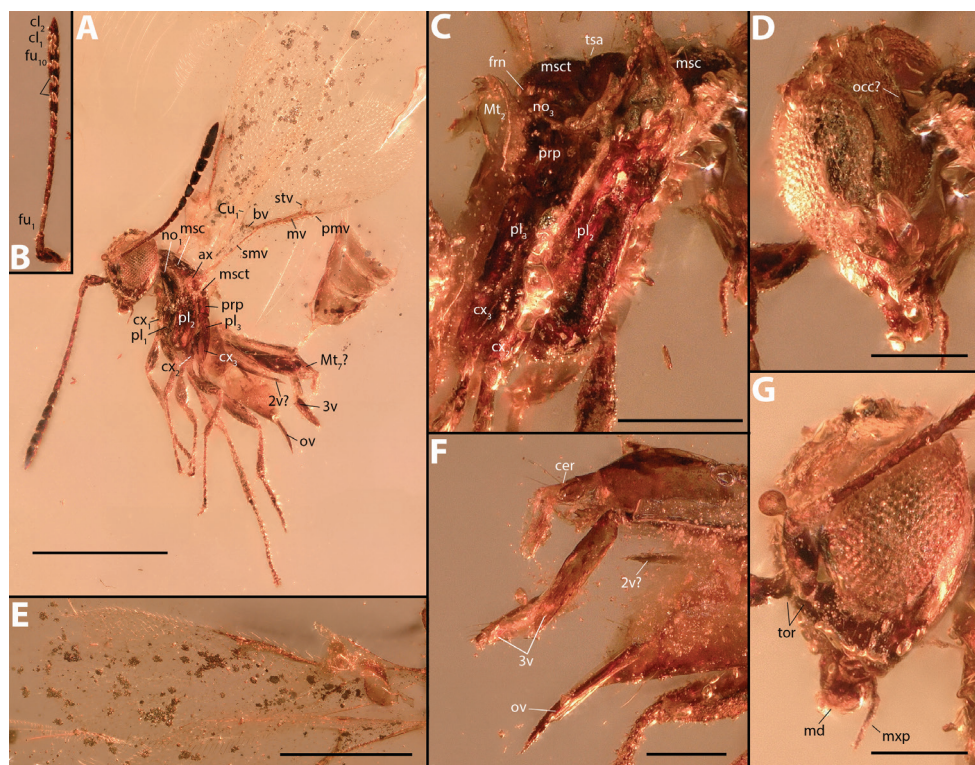
***Protoita istvani* Ulmer & Krogmann, sp. nov.**

<https://zoobank.org/7550D3A4-0E73-444C-9692-E6AFA6915815>

Fig. 6

**Diagnosis.** The female of *P. istvani* differs from all others in the genus by the following combination of characters: Head flattened antero posteriorly, disc-like (Fig. 6D, G).  $Fl_{1-3}$  elongate, about  $4\times$  as long as wide (Fig. 6B). Clava 2-segmented (Fig. 6B).

**Description. Female.** Body length 918. Coloration auburn with dark antennae. Eyes white. Wings hyaline, uniformly setose. Metasoma damaged, tergal segments detached from body (Fig. 6A). **Head** broad, wider than mesosoma in dorsal view, anteroposteriorly narrow, head longer than wide in lateral view (Fig. 6D, G). Frons  $2\times$  as long as face (Fig. 6F, G). Eyes large,  $0.8\times$  height of head, about  $1.6\times$  as high as long. Malar sulcus present; malar space short, only about  $0.15\times$  as long as eye height (Fig. 6D). POL slightly shorter than LOL. Toruli equal in distance from each other as to inner eye margin. Maxillary palps 3-segmented (Fig. 6G:mxp) **Antenna** length 676. Scape  $2\times$  as long as pedicel, gradually broadened from base (Fig. 6B). Pedicel same length or slightly shorter than  $fu_1$ , about  $1.5\times$  as wide as  $fu_1$  width. Flagellomeres gradually widening;  $fu_{1-3}$  about  $4\times$  as long as wide,  $fu_6$   $3\times$  as long as wide,  $fu_{7-10}$  elongated, but less than  $2\times$  as long as wide. Clava 2 segmented. MPS present on all segments (Fig. 6B). **Mesosoma** length 299. Mesosoma in lateral view heavily sloped; nearly  $135^\circ$  relative to mesosoma (Fig. 6C). Mesonotum roughly  $0.5\times$  as long as mesosoma. Notauli present as simple depressions. Mesopleuron dorsoventrally elongate,  $2.4\times$  as long as wide (Fig. 6C:pl<sub>1</sub>). Axilla not advanced, not extending beyond the anterior margin of mesoscutellum (Fig. 6A:axl). Mesoscutellum  $\frac{1}{3}\times$  as long as mesonotum. Metanotum band-like,  $0.3\times$  as long as mesoscutellum (Fig. 6C:no<sub>3</sub>). Propodeum is only slightly longer than mesoscutellum (Fig. 6C:prp). **Wings.** Fore wing length roughly  $1.1\times$  as long as body,  $3.2\times$  as long as wide. Marginal setae of fore wing short, length of longest seta 26. Cubital vein ephemeral, roughly  $1.8\times$  as long as basal vein. Basal vein pigmented. Submarginal vein long and narrow, length 393. Marginal vein narrow, about  $0.2\times$  as long as submarginal vein. Postmarginal vein short and tapering, slightly shorter than marginal vein (63:77) (Fig. 6E). Stigmal vein at  $80^\circ$  angle to wing margin. Uncus present. Hind wing obscured by fore wing. **Legs.** Tarsomere 4 on all tarsi very short relative to other tarsal segments (Fig. 6A). Basitarsal comb of fore leg present. Hindtibia elongate, equal in length to tarsi (Fig. 6A). Forecoxa greatly impressed into prosternum (possibly an artifact). Hind coxa elongated, about  $3.1\times$  as long as broad (Fig. 6C:cx<sub>3</sub>). **Metasoma**  $1.3\times$  as long as mesosoma. Metasoma broadly associated with mesosoma; remnants of  $Mt_2$  visible (Fig. 6C). Most of tergal and sternal segments damaged. Only 3 tergites countable, all with transverse setal row posteromedially. Two elongate sensillae visible off of terminal sternite. Metasomal cerci digitiform (visible only on left side ; Fig. 6F:cer). Ovipositor length 140, not extending beyond distal point of ovipositor sheath; ovi-



**Figure 6.** *Protoita istvani*, holotype **A** lateral habitus **B** antenna, lateral **C** mesosoma, lateral **D** head, posterior **E** fore wing **F** ovipositor complex and terminal metasomal segments **G** head, lateral. Scale bars: 500  $\mu$ m (**A**); 250  $\mu$ m (**E**); 150  $\mu$ m (**C**); 100  $\mu$ m (**D**, **F**, **G**). **2v** = 2<sup>nd</sup> valvifer; **cx**<sub>n</sub> = coxa; **occ** = occipital carina; **pl**<sub>3</sub> = metapleuron; **tor** = toruli.

positor sheaths roughly equal in length to ovipositor, uniform width along entire length, about 4.2 $\times$  as long as wide (Fig. 5F:3v).

**Male.** Unknown

**Material examined. Holotype:** female, Roum – Aazour – Homsiyeh, Caza Jezzine, Mouhafazet South Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: HAR26.

**Type condition.** Specimen with bubbles surrounding MPS on several flagellomeres, mesosoma detached from the amber, and metasomal tergites damaged because they are detached.

**Etymology.** The specific epithet is a patronym in honor of István Mikó, the first author's mentor and close friend who instilled in him his passion for entomology and morphology.



***Protoita petersi* Ulmer & Krogmann, sp. nov.**

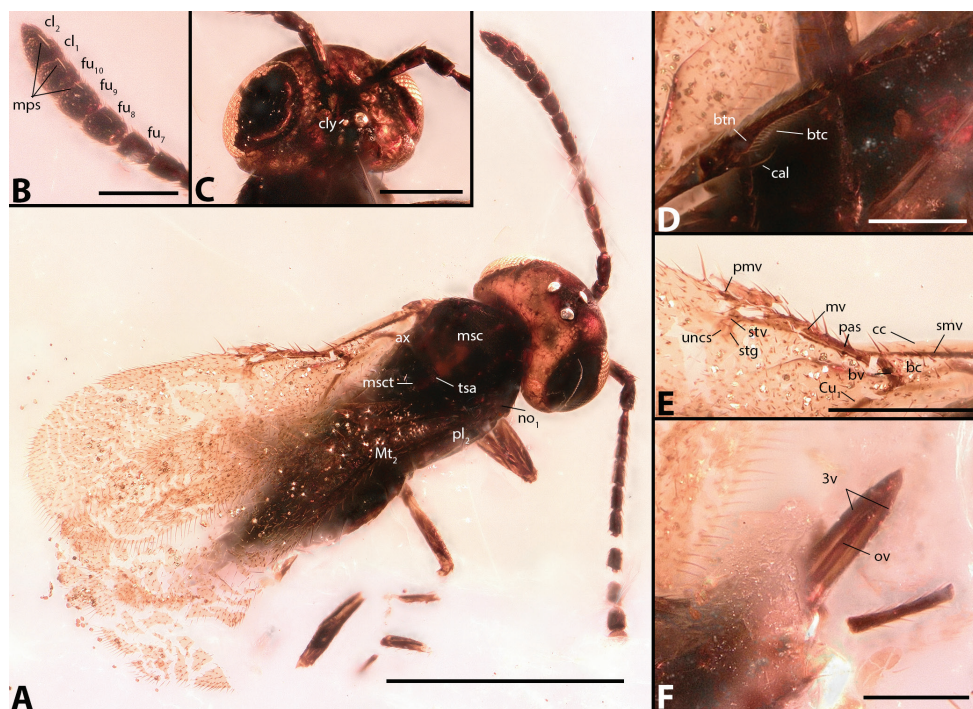
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Fig. 7

**Diagnosis.** The female of *P. petersi* differs from others of the genus by the following combination of characters: Head not as transverse as in other species, only about 1.6× as wide as long in dorsal view (Fig. 7A). Clava 2 segmented; terminal clavomere 0.5× as long as preceding clavomere (Fig. 7B). Postmarginal vein of fore wing equal in length to stigmal vein, both short; and basal vein very short and wide (Fig. 7E). Hind wing marginal setae not longer than width of hind wing.

**Description. Female.** Body length 913. Body dark brown legs, except coxae, and part of mesepimeron. Head, especially frons, vertex and back of head, base of  $fu_1$  light brown to dark yellow. Wings hyaline, uniformly pilose. **Head** ovular, only 1.6× as wide as long, wider than widest point of meso- or metasoma in dorsal view (Fig. 7A). Frons 1.5× as long as face. Ocelli equilateral, POL=OOL. Malar sulcus faintly present. Antennal scrobe weakly defined (Fig. 7A, C). Interantennal projection pronounced (Fig. 7C). Toruli near lower eye margin, slightly sunken into face. Toruli more than one diameter from eye margin and about same distance from one another (Fig. 7C). Dental formula 3:3. Maxillary palp at least 2 segmented (Fig. 7C). **Antenna** length 549. Scape about 3.5× as long as wide, gradually broadening from base to end. Pedicel 1.8× as long as wide.  $Fu_1$  tapering proximally at insertion into pedicel,  $fu_{1-4}$  about 2.3× as long as wide,  $fu_7$  only about 1.2× as long as wide (Fig. 7A). Clava at least 2 segmented,  $cl_1$  wider than  $fu_7$ , claval length 187; all clavomeres with sensillary patch ventrally (Fig. 7B). MPS present on all segments in one row lengthwise (Fig. 7B). Pilosity uniform along all flagellomeres. **Mesosoma** length 359. Lateral panel of pronotum with 4 setae along dorsolateral margin. Mesoscutum convex, obscuring pronotum medially in dorsal view. Mesonotum large,  $\square$  x as long as mesosoma in dorsal view (Fig. 5A). Notauli not externally visible (when a strong underlight is used distinct strips of thickened sclerite may be seen corresponding to notauli and mesoscutal sulcus, possibly an artifact). Transcutal articulation complete. Mesoscutellum convex, band-like approximately  $\frac{1}{3}$  x as long as mesonotum. Axillae advanced (Fig. 7A). Metano-propodeal complex obscured by wings and bubbles. **Wings.** Fore wing 2.9× as long as wide. Longest marginal seta 38. Cubital vein 211. Basal vein short, 0.17× as long as cubital vein. Submarginal vein 229. Marginal vein slightly less than  $\frac{1}{2}$  as long as submarginal vein (104), width only 17. Stigma oriented at 40° angle with wing margin. Uncus present as cluster of uncil sensillae (Fig. 7E). Postmarginal vein approximately equal in length to stigmal vein (38:39) (Fig. 7E). Hind wing elongate, 0.66× as long as fore wing, 7.75× as long as wide. Marginal setae of hind wing long, 1.5× as long as width of hind wing, length of longest visible sensilla 58. Marginal vein of hind wing less than  $\frac{1}{2}$  x as long as hind wing. **Legs.** Basitarsal comb of fore leg present (Fig. 7D:btc); slight basitarsal notch present. (Fig. 7D:btn) **Metasoma.** Metasoma roughly equal to mesosoma in length, attached broadly to mesosoma; petiole obscured.  $Mt_2$  as broad as broadest point of mesosoma and only about 0.5× as long as  $Mt_3$ ;  $Mt_3$ - $Mt_8$  about same length (Fig. 7F). 7 tergal segments countable. Ovipositor length 148, only partially extruded, enveloped by ovipositor sheaths (Fig. 7F:3v).





**Figure 7.** *Protoita petersi*, holotype **A** dorsal habitus **B** apical flagellomeres, lateral **C** head, ventral **D** fore leg **E** fore wing venation **F** ovipositor complex. Scale bars: 500  $\mu$ m (**A**); 150  $\mu$ m (**E**); 100  $\mu$ m (**B–D**). ax = axilla; btn = basitarsal notch; cly = clypeus.

#### Male. Unknown

**Specimens examined.** *Holotype*: female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 874A.

**Type condition.** Specimen with right antenna damaged beyond flagellomere 5, right hind leg damaged at midpoint of femur, and right fore wing damaged beyond midpoint of marginal vein.

**Etymology.** The specific epithet is a patronym in honor of our friend and colleague Dr Ralph Peters, for his work on the early diversification of Chalcidoidea.

#### *Cretaxenomerus* Nel & Azar, 2005

**Diagnosis.** Body larger than 1 mm. Head usually long in dorsal view with temples well developed. Metasoma separated from mesosoma by distinct petiole or constriction, and in dorsal view ovoid; female with an elongate syntergum, longer than preceding tergite (Mt<sub>7</sub>) (except *C. deangelis*).

Key to species of *Cretaxenomerus*

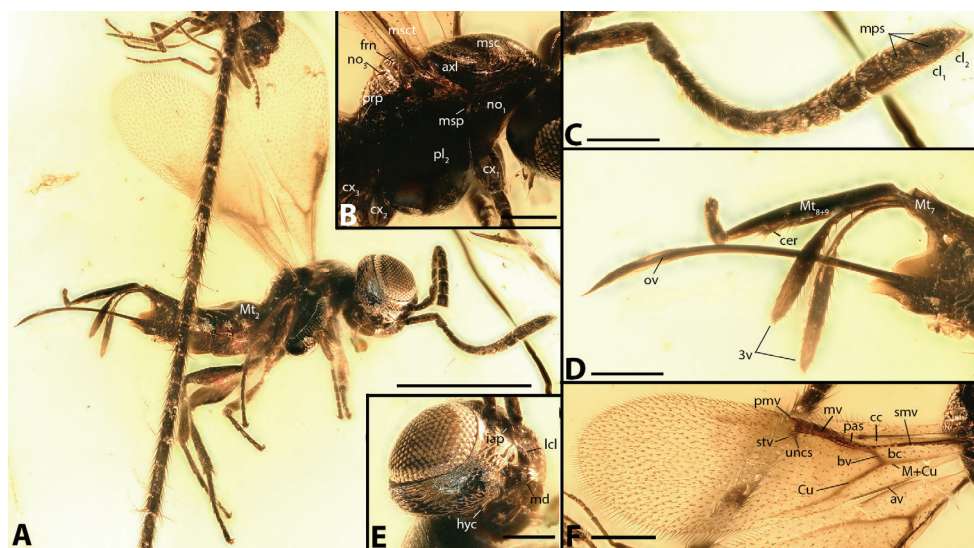
- 1 Syntergum longer than 1/2 length of ovipositor (Figs 8D, 12D, 15B). Ovipositor sheaths spatulate distally (Figs 8D, 12D) ..... **2**
- Syntergum shorter than or equal to 1/2 length of ovipositor (Figs 10F, 13B). Ovipositor sheaths uniformly broad (Figs 10F, 13B) ..... **4**
- 2 Syntergum articulating with preceding tergum at an angle (Fig. 8A, D). Cubital vein extending beyond tip of postmarginal vein (Figs 8F, 9D) ..... ***Cretaxenomerus curvus* sp. nov.**
- Terminal tergum not articulating with preceding tergum at an angle (Figs 10F, 12D, 13B). Cubital vein extending to tip of or less than length of postmarginal vein (Figs 10B, 11A, 12C, 13D). ..... **3**
- 3 Head at least 2× as broad as long (Fig. 15A). Terminal tergum broadening posteriorly (Fig. 15B). Hind basitarsus with only sparse setation (Fig. 15C).  $Fu_1$ – $fu_3$  2× as long as wide (Fig. 15A). ..... ***Cretaxenomerus jankotejai***
- Head about as broad as long, globular. Terminal tergum of uniform width along entire length (Fig. 12D). Hind basitarsus with dense setation (Fig. 12D).  $Fu_1$ – $fu_3$  3× as long as wide (Fig. 12B). ..... ***Cretaxenomerus mirari* sp. nov.**
- 4 Flagellum with 1-segmented clava (Figs 11B, 13C). ..... **5**
- Flagellum with 2–3 segmented clava (Figs 10C, 14C) ..... **6**
- 5 Fore wing spatulate, 2.5× as long as wide (Fig. 11A). Basitarsal comb absent (Fig. 11F) ..... ***Cretaxenomerus vitreus* sp. nov.**
- Fore wing narrow, 3.5× as long as wide (Fig. 13D). Basitarsal comb present (Fig. 13A). ..... ***Cretaxenomerus tenuipenna* sp. nov.**
- 6 Head longer than wide (Fig. 14A). Clava 3-segmented (Fig. 14C). Basitarsal comb of fore leg present (Fig. 14D). Fore wing with costal cell about equal in width to marginal vein (Fig. 14B). Syntergum not longer than preceding tergite (Fig. 14A). ..... ***Cretaxenomerus deangelis* sp. nov.**
- Head wider than long (Fig. 10C). Clava 2-segmented (Fig. 10C). Basitarsal comb of fore leg absent (Fig. 10E). Fore wing costal cell narrower than marginal vein (Fig. 10B). Syntergum nearly 2× as long as preceding tergite (Fig. 10A, F) ..... ***Cretaxenomerus brevis* sp. nov.**

***Cretaxenomerus curvus* Ulmer & Krogmann, sp. nov.**

<https://zoobank.org/CF8C92D9-DD42-4E47-AA86-78ED85561736>

Figs 3B, 8, 9, 16B

**Diagnosis. Female.** Females differ from those of all other species within the genus by the following combination of characters: Syntergum hinged at joint with elongated  $Mt_7$ , reaching more than  $\frac{3}{4}$  length of ovipositor sheath (Fig. 8D:  $Mt_{8+9}$ ); fore wing with postmarginal vein about equal in length to stigmal vein and cubital vein extending beyond tip of postmarginal vein (Fig. 8F). **Male.** Same as female except flagellomeres all as wide as long; clava 2-segmented (Fig. 9B).



**Figure 8.** *Cretaxenomerus curvus*, holotype (874D) **A** lateral habitus **B** mesosoma, lateral **C** antenna, lateral **D** ovipositor complex and terminal abdominal segments **E** head, lateroventral **F** fore wing. Scale bars: 500  $\mu$ m (**A**); 150  $\mu$ m (**F**); 100  $\mu$ m (**B–E**). iap = interantennal process; lcl = lateral clypeal line; Mt<sub>8+9</sub> = syntergum.

**Description. Female.** Body length 1314 (HT) – 1407 (PT). Overall body color black with a blue sheen on the gena of HT when examined at certain angles except tegulae, legs excluding coxae, and second half of ovipositor sheath dark brown, tip of ovipositor sheath light brown, and with legs almost black. Wings hyaline except fore wing slightly brownish in HT (possible artifact) and partly brownish in PT 881B; with sparser pilosity proximally on wing surface. Head, mesosoma and metasoma coriaceous to alutaceous except areolate posterior part of mesoscutellum and propodeum. **Head** ovate, 1.5 $\times$  as wide as long (Fig. 8E). Vertex and temple of head curved strongly, back of head concave, closely associated with mesosoma. Temple about 0.3–0.25 $\times$  as long as eye length. Eye broadly oval, almost as long as high. Ocellar triangle equilateral, POL=LOL=OOL. Malar sulcus faint, but present. Shallow internantennal projection (Fig. 8E:iap). Toruli closer to inner margin of eye than each other and very close to dorsal margin of clypeus, well below center of eye, hence lower face short. Clypeus dorsally with raised rim, inwardly inflexed, with row of setae just below dorsal clypeal margin (Fig. 8E). Anterior tentorial pits situated well below dorsal margin of clypeus. Dentition 3:3, mandibles on different plane from face (Fig. 8E). Maxillary palp 3 segmented, distal segment longer than basal segment (Fig. 8E). **Antenna** length 637 (HT)–671 (PT). Antenna 14-segmented. Radicle raised from face. Fu1-2 at least 2 $\times$  as long as wide. Clava 2-segmented (Fig. 8C); clava 1.5 $\times$  as long as wide. MPS present on all flagellomeres with single row on each segment; MPS on terminal segment not extending beyond tip. All segments uniformly pilose (Fig. 8C). **Mesosoma** length 380 (PT)–401 (HT). Pronotum with bristle on posterolateral corner. Mesoscutum obscuring pronotum medially in

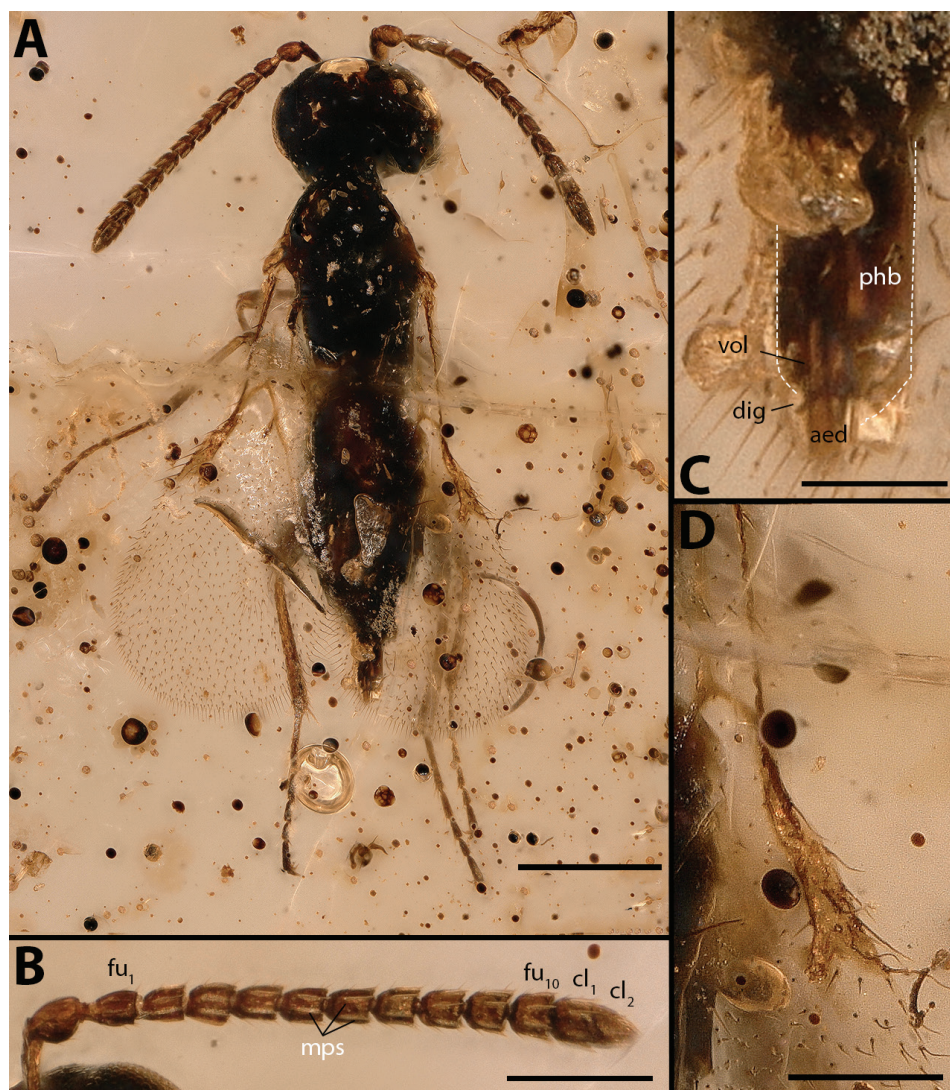
dorsal view. Lateral part of prepectus slender and straight, dorsally covered by posteriormost corner of lateral pronotum, slightly broadened ventrally (Fig. 16A:pre). Mesonotum large, roughly  $2/3\times$  as long as mesosoma. Notauli present and simple impressions. Mesopleuron  $2\times$  as high as long in lateral view (Fig. 8,B). Suture present between meso- and metapleuron (Fig. 8A). Transcutal articulation present and complete. Axillae reduced, axillulae extending further anterior than posterior edge of mesonotum (Fig. 8B:axl). Mesoscutellum short, about  $1/5$  length of mesonotum. Dorsellum band like. Propodeum strongly sloped. **Wings.** Fore wing  $2.4\times$  (PT)– $2.7\times$  (HT) as long as wide. Pilosity sparse in basal part of wing relative to disc (Fig. 8F). Basal cell dorsally with one median row of hairs only. Longest marginal seta of fore wing 38. Cubital vein extending beyond length of postmarginal vein, length 377 (Fig. 8F). Basal vein short, length 43. Submarginal vein length 342. Marginal vein strongly sclerotized and broad, length 96, width 29; marginal vein with 6 marginal sensillae present. Stigmal vein present, equal in length to postmarginal vein, at  $45^\circ$  angle with wing margin (Fig. 8F). Uncus present; 5 uncal sensillae in cluster. Postmarginal vein very short, about  $0.25\times$  as long as marginal vein (Fig. 8F). Hind wing elongate and narrow  $6.8\times$  as long as wide. Hamuli count 3, proximal hamular hook longer than other 2. Hamuli and venation of hind wing only extend  $1/3$  length of hind wing. **Legs.** Hind femur slightly broadened medially (Fig. 8A). Fore tibia with curved clefted spur. Hind tibia with two spurs, shorter spur about  $0.75\times$  as long as longer one. Basitarsus of fore leg ventrally curved; basitarsal comb present, bristles of comb very short (Fig. 8A). **Metasoma** length 407, nearly equal in length to mesosoma. Six ( $Mt_{2-7}$ ) tergal segments and syntergum ( $Mt_8+Mt_9$ ) countable, except the  $Mt_{3-7}$  all roughly equal in length from lateral view (Fig. 8A). Six sternal segments visible. Hypopygium flanged, extending beyond  $Mt_7$ . Syntergum articulating with  $Mt_7$  and covering ovipositor sheaths dorsally, syntergum length 273,  $Mt_7$  length 51 (Fig. 8A, D). Ovipositor  $1.2\times$  as long as metasoma; tip of ovipositor with 5 teeth; ovipositor sheaths stalk-like at base, distally spatulate with sensillae along margin, sheaths approximately equal in length to syntergum (Fig. 8D:3v). **Male.** Similar to female except the head is not as long (Fig. 9A). Interantennal process reaching over the  $2/3$  of eye height, antenna with only  $Fl_1$  about as  $2\times$  as long as wide (Fig. 9B). Clava 2-segmented (Fig. 9B). Postmarginal vein slightly longer than stigmal vein (Fig. 9D). Male genitalia extended; digitus with single digital spine (Fig. 9C:dig)

**Specimens examined.** **Holotype:** female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 874D. Locality information and depository of paratypes same as for holotype (Female–881B, 146U; Male–1614FA).

**Type condition.** Right antenna of holotype with terminal 3 segments missing. The amber piece of the holotype included a single inclusion of a Ceratopogonidae (Diptera).

**Etymology.** The specific epithet is derived from the Latin ‘curvus’ meaning curved or bent, in regards to the articulation of the syntergum of the species.





**Figure 9.** *Cretaxenomerus curvus*, male paratype (1614F) **A** dorsal habitus **B** antenna, lateral **C** male genitalia, ventral **D** fore wing venation. Scale bars: 250 µm (**A**); 100 µm (**B**, **D**); 50 µm (**C**). phb = phallobase.

**Notes.** The metasoma of paratype specimen 146U is damaged, preventing examination of the syntergum, however the wing venation and head shape place it as *C. curvus*. This is the only species described based on both sexes which provides some insight into the putative sexual dimorphisms within the genus. Notably, the variation in antennal shape and claval size which is a prolific form of dimorphism within extant chalcids. The female of *C. curvus* has a clear clava with multiple claval segments relative to the male which has all flagellar segments relatively stout and uniform with only the partial fusion of the terminal segments indicating a clava.

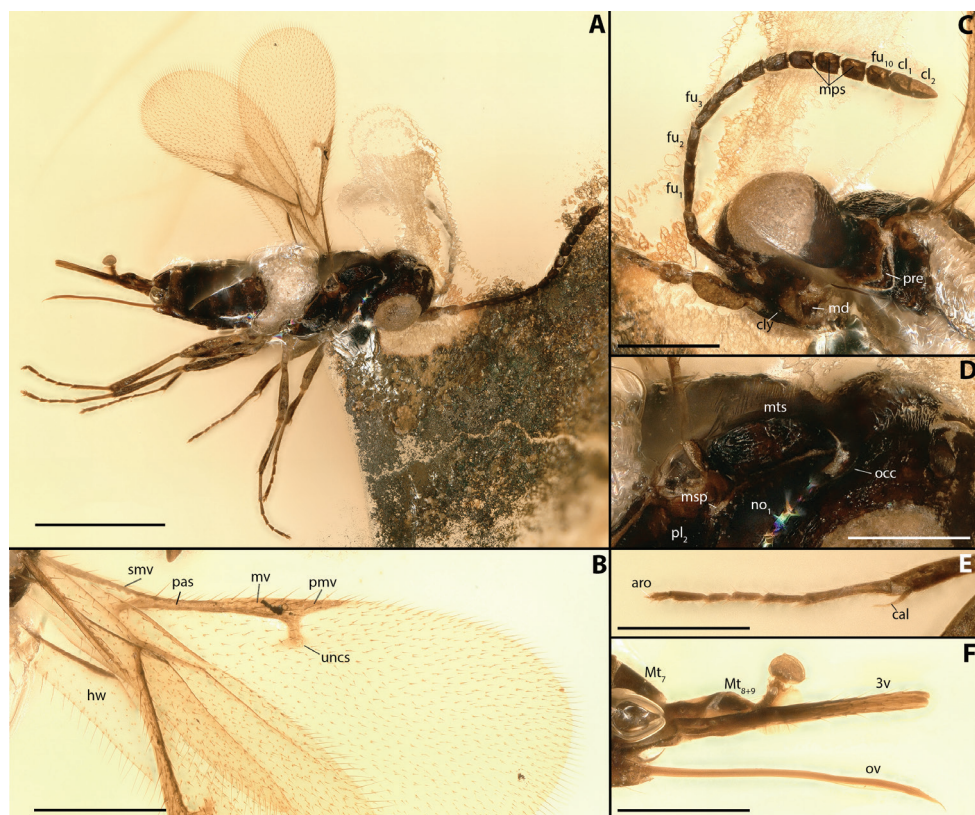
***Cretaxenomerus brevis* Ulmer & Krogmann, sp. nov.**

<https://zoobank.org/1BAEE43E-EAFA-4921-8B80-A4824EAA9B35>

Fig. 10

**Diagnosis. Female.** *Cretaxenomerus brevis* differs from all other species in the genus by the following combination of characters: scape laterally flattened, only 2.25× as long as broad; antenna with at least  $fu_1$ – $fu_4$  conspicuously longer than broad,  $fl_1$  about 3.75× as long as broad. Anterolateral margin of mesoscutum flanged. Arolium elongated and extending beyond tip of tarsal claws. Syntergum relatively short, extending about 1/3 length of ovipositor sheath.

**Description. Female.** Body length 1145. Uniformly dark brown, legs light brown, eyes white (likely an artifact of amber deposition) (Fig. 10A). **Head.** Ovular in shape, wider than long, length 201, width 313. Eye almost circular. Ocelli large, equilateral, POL=LOL=OOL. Temples relatively short, at most about 0.2× as long as eye length. Gena large, about 0.5× as long as eye length; no genal carina or sulcus present. Toruli closer to inner margin of eye than each other and very close to dorsal margin of clypeus, well below center of eye, hence lower face short (Fig. 10C). Clypeus dorsally with raised rim, inwardly inflexed; lower clypeal margin wide. Anterior tentorial pits situated well below dorsal margin of clypeus. Dentition 3:3. Maxillary palp count 2. **Antenna** length 706. Radicle pronounced. Scape laterally flattened, only 2.25× as long as broad. Pedicel semiglobular, only 1.5× as long as broad (possible artifact of compression), 0.5× as long as scape (Fig. 10C). All flagellomeres are longer than wide with  $fu_1$  longest one, length 98, about 3.75 as long as wide,  $fu_{10}$  about 1.5× as long as broad. Clava 2-segmented, 2.8× as long as broad (Fig. 10C). Micropilosity present on all claval segments (Fig. 10C). **Mesosoma** length 334. Notch in posterior most part of lateral panel of pronotum dorsal to prepectus with prothoracic spiracle (?) (Fig. 10D:msp). Mesonotum 238. Prepectus externally visible, thin, dorsally overlapped by lateral panel of pronotum, ventral portion curved anteriorly (Fig. 10C:pre). Notauli present as depression (Fig. 10D). Mesopleuron elongate, 1.5× as long as wide (250:164). Axillular rim with sharp carina delimiting mesoscutellum from frenum. Bubble obscuring propodeo-metanotal complex. **Wings.** Fore wing 2.8× longer than wide (981:343). Longest marginal seta 31. Cubital vein 174 (sclerotized part) and extending as pigmented fold beyond length of postmarginal vein. Basal vein 43, strongly sclerotized. Submarginal vein length 372, with 7 admarginal setae, basalmost 2 being longest. Marginal vein length 110, width 27, with 6 admarginal setae. Stigmal vein 61, at  $\approx 85^\circ$  to wing edge. Uncus with 5 uncal sensillae. Postmarginal vein 0.8× as long as marginal vein, tapering. Costal cell of fore wing very narrow. Hind wing slender, 10.6× longer than wide (647:61) (Fig. 10B). **Legs.** Basitarsomere equal in length to tarsomere 2–4; basitarsal comb absent. Arolium of pretarsus elongate, extending further distally than tarsal claws (Fig. 10E:aro). **Metasoma** length 555. Petiole obscured by bubble, however slendering of propodeum and expanding of metasoma suggests a constricted petiole. Metasoma with 6 countable tergal segments ( $Mt_{2-7}$ ) and syntergum ( $Mt_{8+9}$ );



**Figure 10.** *Cretaxenomerus brevis*, holotype **A** lateral habitus **B** fore and hind wing **C** head, ventrolateral, and antenna **D** mesonotum, dorsolateral **E** fore leg **F** ovipositor complex and terminal abdominal segments. Scale bars: 500  $\mu$ m (**A**); 200  $\mu$ m (**B**, **C**); 150  $\mu$ m (**D**–**F**). aro = arolium; hw = hind wing.

2 enlarged sternal segments countable. Hypopygium with longitudinal row of 6 setae along edge, concave distally and reaching end of Mt7. Syntergum relatively short (141), only  $\frac{1}{3}$  length of extruded ovipositor (Fig. 10F). Ovipositor length 383, tip of ovipositor with 5 teeth (Fig. 10F:ov); ovipositor sheaths equal in length to ovipositor, ovipositor sheath flattened but equal width along entire length (Fig. 10F:3v).

**Male.** Unknown.

**Material examined.** *Holotype*: female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 1228.

**Type condition.** A large bubble obscures the posterior of the propodeum and petiole. The head is damaged at the lateral clypeal line.

**Etymology.** The specific epithet is derived from the Latin word for ‘short’, referring to the comparatively short syntergum relative to the other species in the genus.



***Cretaxenomerus vitreus* Ulmer & Krogmann, sp. nov.**

<https://zoobank.org/A147EFF9-9000-4983-BD3F-1D2C927B7607>

Figs 2A, 11

**Diagnosis.** *Cretaxenomerus vitreus* differs from all other species in the genus by the following combination of characters: fore wings broadly spatulate, with postmarginal vein about 2× as long as stigmal vein (Fig. 2A). All tarsi with manubrium broadly spatulate (Fig. 11F:man).

**Description. Female.** Body length 1381. Body bilaterally damaged with some internal sclerite structures visible (Fig. 11A). Most of the right part of the specimen is missing including both scapes and right pedicel, the whole mouth complex, entire right hind leg, right midcoxa, forecoxa and femur and base of right fore wing and entire hind wing. Metasoma damaged with only Mt<sub>2-5</sub> and ovipositor sheaths and ovipositor present. Body light brown in coloration, eyes red. Wings hyaline, speculum less pilose than wing disc. **Head.** Head broad, approximately 1.4× as wide as long, posteromedially depressed. Eyes large, broadly oval, slightly taller than wide (Fig. 11A). Ocellar triangle equilateral, ocelli raised and angled from head capsule; ocelli large (Fig. 11A). No facial sulci or occipital carina present. **Antenna** length 805. All flagellomeres longer than broad, fu<sub>1-2</sub> about 2.8× as long as broad, fu<sub>3</sub> 2.0× as long as broad (Fig. 11A). Clava 1-segmented (Fig. 11B). MPS present on all segments, extending beyond distal margin of segment, including on apical segment; MPS at least on fu<sub>1-4</sub> in two rows. Pilosity sparse and uniform on all flagellomeres. **Mesosoma** length 480, pronotum medially obscured, with setal line along mesonotal margin. Mesoscutum 0.7× length of mesosoma. Prepectus elongate and slender, overlapped anteriorly by lateral pronotal panel (Fig. 11D, E:pre). TSA complete across mesonotum (Fig. 11D:tsa). Mesopleuron large, 1.75× as long as wide; transpiral line present as narrow line. Metapleuron small, differentiated from mesopleuron by carina. Axillae not well defined. Mesoscutellum narrow and band-like, □ length of mesoscutum. Frenum discernable as shift in scutellar sculpturing with marginal foveal rim, roughly ¼ length of mesoscutellum (Fig. 11D:fre). Dorsellum damaged. Propodeum ⅓ length of mesoscutum; supracoxal flange developed, but very narrow; propodeal spiracle ovoid (Fig. 11D:psp). **Wings.** Fore wing spatulate, 3× longer than wide. Longest marginal seta length 40. Costal cell narrow. Submarginal vein broad and distally tapering, length 458. Cubital vein pigmented and tubular after intersection with basal vein for about length of basal vein then ephemeral distally, tubular portion equal in length to basal vein (Fig. 2A). Basal vein strongly pigmented and broad, □ length of entire cubital vein. Marginal vein strongly pigmented, ≈ ⅓ length of submarginal vein. Width of marginal vein ½ length of marginal seta. Stigmal vein broad, ½ length of postmarginal vein, oriented 90° relative to wing margin. Stigma spatulate with distinct uncus; uncus sensillae count 4 (Fig. 2A:uncs). Postmarginal vein elongate and tapering, equal in length to marginal vein. Hind wing approximately ½ length of fore wing, 16× as long as wide. Longest marginal seta of hind wing longer than width of hind wing. Marginal vein of hind wing ½ length of hind wing. **Legs.** Hindlegs slightly longer than mid



**Figure 11.** *Cretaxenomerus vitreus*, holotype **A** lateral habitus **B** apical flagellomeres, lateral **C** metasoma, lateral **D** mesosoma, lateral **E** prepectus **F** fore leg. Scale bars: 500  $\mu$ m (**A**); 100  $\mu$ m (**C**–**F**).

and fore legs which are equal in length (Fig. 11A). Basitarsus of all legs roughly equal in length to tarsomere 2–4; basitarsal comb of fore leg absent (Fig. 11F). Legs with sparse pilosity. Tarsal manubrium spatulate, as broad as tarsal claws (Fig. 11F:man). **Metasoma.** Only  $Mt_{2,5}$  preserved, all equal in length (Fig. 11C). Medial longitudinal setal line present on all tergal segments, counting of setal lines retained in the amber indicate 6 tergal segments countable (Fig. 11C). Ovipositor length 248. Ovipositor sheath equal in length to ovipositor; broadened along entire length; setae arising from surface of ovipositor sheath, margin bare.

**Male.** Unknown.

**Material examined. Holotype:** female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 534C.

**Type condition.** Face and mandibles absent from specimen. Mesosoma bisected and cleared with scleritic components visible on left side, internal components visible on right. Metasoma with first few terga present, and marginal setal line of other segments still present to indicate placement. Right hind leg with only distal tarsomeres remaining.

**Etymology.** The specific epithet is the Latin word for ‘glassy’ or ‘transparent’ in regards to the unique taphonomy of the specimen that appears as though it were cleared.

**Notes.** Damage to the specimen provides for a unique examination of both external and internal scleritic structures; however, damage to the abdomen has resulted in the loss of the terminal segments and syntergum. The lack of a multi-segmented clava is shared with *Cretaxenomerus tenuipenna* sp. nov.; however, the distinct difference in wing shape and venation separates these two specimens into distinct species.

***Cretaxenomerus mirari* Ulmer & Krogmann, sp. nov.**

<https://zoobank.org/CA9573B0-4C46-443C-9000-03F57E442982>

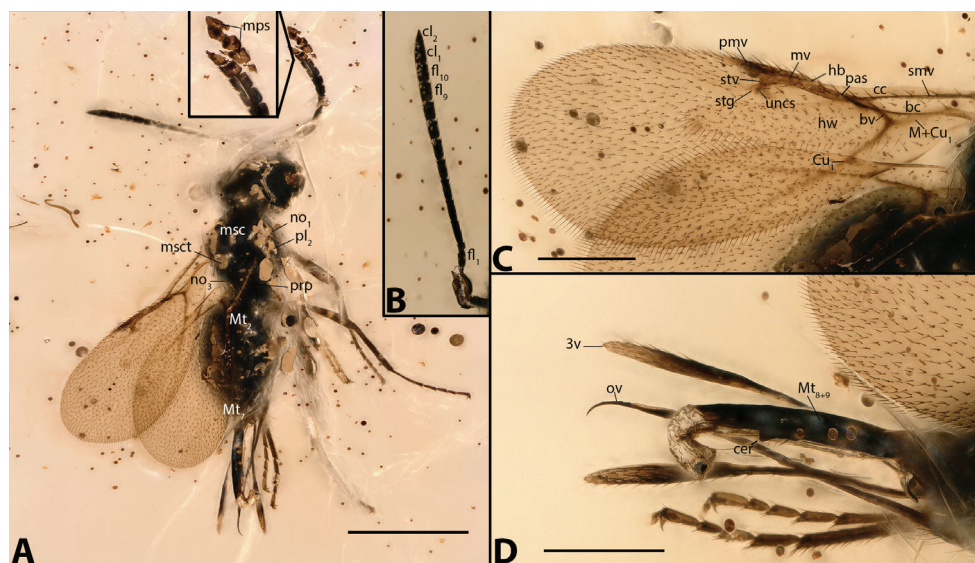
Fig. 12

**Diagnosis.** *Cretaxenomerus mirari* differs from all other species in the genus by the following combination of characters: Head very transverse in dorsal view. Clypeus not as inflexed. Mesoscutum broader than long. Hind basitarsus with dense comb-like setation (Fig. 12D). Syntergum straight, and longer than  $\frac{3}{4}$  the length of the ovipositor (Fig. 12D). Fore wing with a pronounced costal cell which is broader than the marginal vein, and cubital vein equal in length to distal tip of postmarginal vein (Fig. 12C).

**Description. Female.** Body length 1212. Coloration dark brown to black, slight metallic coloration on abdomen may be an artifact. Scape, legs and ovipositor sheaths dark brown, tip of ovipositor sheaths light brown. Wings lightly brownish infumated, wing venation brown. **Head.** Unusually long and low, about  $1.5\times$  as wide as long and low, about  $0.5\times$  as high as broad (Fig. 12A). Eye broadly ovoid, but horizontally oriented (longer than height). Temple about  $\frac{1}{4}$  as long as eye. Clypeus not deeply inflected. Epistomal sulcus and malar sulcus present. Toruli closer to inner eye margin than to each other.

**Antenna.** Length 699, approximately  $0.6\times$  as long as body. Scape  $2.85\times$  as long as broad. All flagellomeres longer than wide,  $fu_{1-3}$   $3.0\times$  as long as wide,  $fu_{4-10}$  about  $2.0\times$  as long as wide (Fig. 12B). Clava 2-segmented, length 88 (Fig. 12B). MPS present on all segments, slightly askew, not extending beyond apical edge of segment. Micropilosity laterally on  $cl_{1-2}$  and  $fu_{9-10}$ .

**Mesosoma.** Length 342. Mesonotum wider than long and  $0.6\times$  length of mesosoma. Prepectus narrow, dorsally hidden from dorsoposterior edge of lateral panel of pronotum. Axillae advanced. Mesopleuron obscured due to angle of specimen. Mesoscutellum short,  $0.2\times$  as long as mesonotum (Fig. 12A:msct). Dorsellum narrow and band-like,  $\frac{3}{4}$  length of mesoscutellum. Propodeum sloped, roughly  $2\times$  as long as mesonotum (Fig. 12A:prp). **Wings.** Base of the fore wing including speculum with sparser pilosity than disc. Fore wing length 1046,  $2.7\times$  as long as wide. Longest marginal seta of fore wing 39. Costal cell about  $2\times$  as long as marginal vein and postmarginal vein (Fig. 12C).



**Figure 12.** *Cretaxenomerus mirari*, holotype **A** dorsal habitus with magnified view of clava **B** antenna, lateral **C** fore wing **D** ovipositor complex and terminal metasomal segments. Scale bars: 500  $\mu$ m (**A**); 200  $\mu$ m (**C**, **D**).

Cubital vein very long, approximately  $\frac{1}{3}$  length of fore wing, strongly pigmented. Basal vein length 44, strongly pigmented. Submarginal vein length 367, costal cell of fore wing well developed. Marginal vein slightly longer than  $\frac{1}{4}$  length of submarginal vein; strongly pigmented and broad, width 23. Stigmal vein short, length 33. Uncus with 4 uncinal sensillae (Fig. 12C). Postmarginal vein tapering towards wing margin,  $\frac{2}{3}$  length of marginal vein. Hind wing  $\square$  length of fore wing,  $6.7\times$  longer than wide. Longest marginal seta of hind wing 34. Venation and hamuli of hind wing not further than  $\frac{1}{2}$  length of wing (Fig. 12C). **Legs.** Basitarsal comb present on fore leg. Basitarsomere equal in length to tarsomere 2–4 on fore leg. Dense setation along hind basitarsus (Fig. 12D). **Metasoma** length 563,  $\approx 1.6\times$  as long as mesosoma. Constricted petiole.  $Mt_{2-7}$  countable. Hypopygium elongate, reaching nearly to end of metasoma. Elongate, medial, longitudinal setal row down ventrum of metasoma. Syntergum about  $0.5\times$  as long as metasoma and reaching up to about  $\frac{3}{4}$  of ovipositor sheath length, broadened after insertion of cerci, spatulate (Fig. 12D). Ovipositor ejected, about equal in length to metasoma; ovipositor tip with 3 teeth; ovipositor sheaths equal in length to ovipositor, stalk-like basally before widening distally and becoming spatulate with marginal setation (Fig. 12D).

**Male.** Unknown.

**Material examined. Holotype:** female, Hammana / Mdeyrj, Caza Baabda, Mouhazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 157G.



**Type condition.** Specimen complete, but terminal segments of the right antenna fragmented, and tarsal segments of the left fore leg longitudinally split; partial detachment from the amber along the right side of thorax and eye margin. Streaks in the amber make it difficult to clearly assess some characters.

**Etymology.** The specific epithet is derived from the Latin ‘mirari’, which is the origin of the English ‘mirage’ in regards to the haziness of the specimen within the amber from the taphonomic process.

**Notes.** *Cretaxenomerus mirari* shares several characters with *P. curvus*, namely the presence of 3 claval segments and a syntergal protrusion which is roughly  $\frac{3}{4}$  of length of the ovipositor. While it is possible that *P. mirari* has an articulating syntergum which is simply not observable due to taphonomic processes, a postmarginal vein that is longer than the stigmal vein and a clear costal cell, would suggest that *P. mirari* is a distinct species for the sake of identification and until more specimens are discovered which may contradict its current placement.

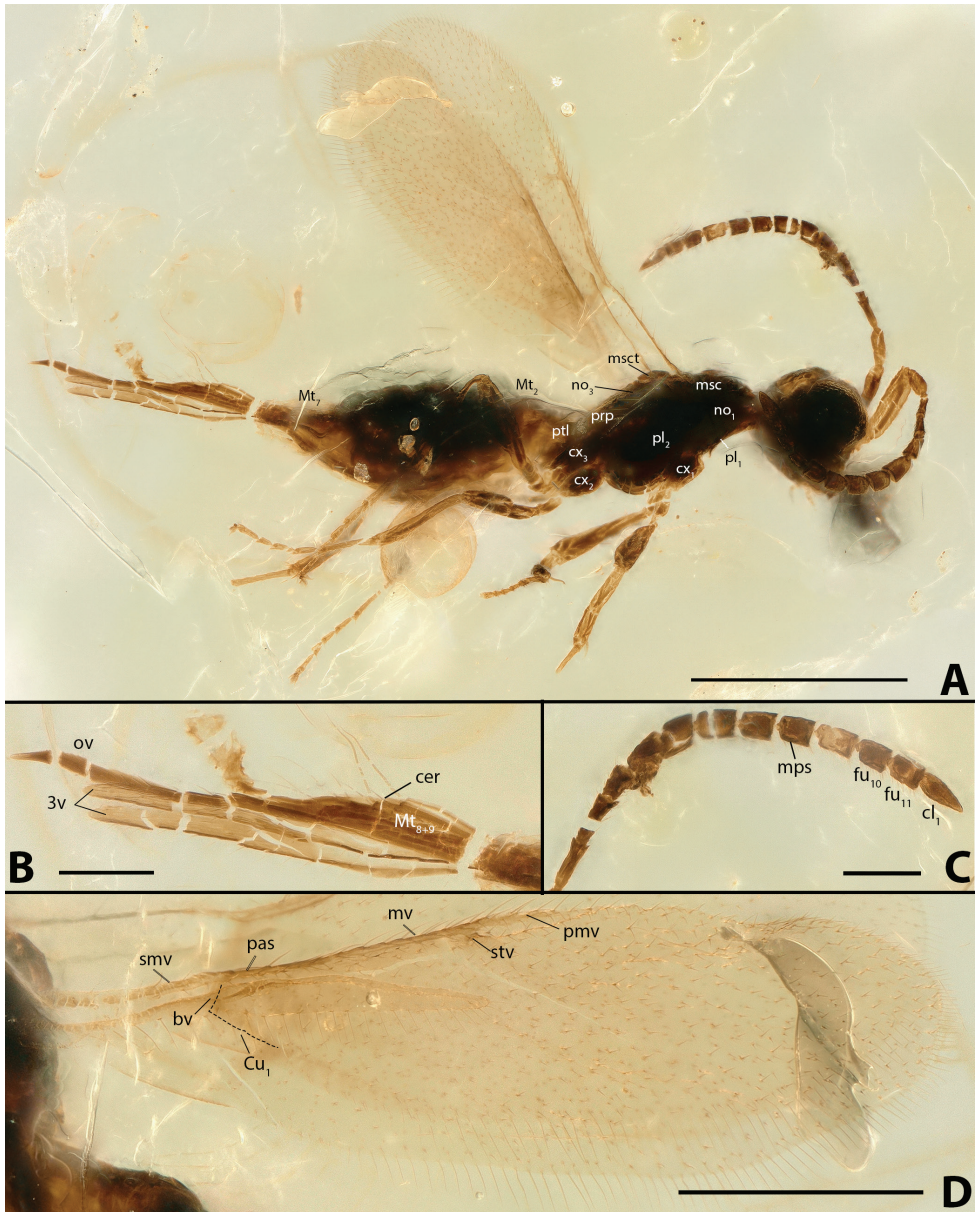
***Cretaxenomerus tenuipenna* Ulmer & Krogmann, sp. nov.**

<https://zoobank.org/021F799C-F0BD-48D4-B803-B207B9DDC43D>

Fig. 13

**Diagnosis.** *Cretaxenomerus tenuipenna* can be differentiated from all other species in the genus by the following combination of characters: scape conspicuously long, about as long as eye height,  $fu_{1-2}$  about  $2\times$  as long as wide, especially  $fu_1$  much narrower than pedicel, at least  $fu_4$  only slightly longer than wide and wider than pedicel, terminal claval segments loosely associated, without distinct fusion between  $cl_1$  and  $fl_{11}$ . Fore wing slender,  $3.5\times$  longer than wide. Foretibia without basitarsal comb. Propodeum not strongly sloped.

**Description. Female.** Body length 1256. Body dark brown, appendages light brown, may be taphonomic artifact. Wings hyaline with some slight brown infumation distally from basal vein, uniformly pilose. Right fore leg tarsal segments except about half of basitarsus and left hind tarsal segments 25 are missing, left antenna after pedicel and ovipositor broken on several places, both antennae with some cracks on scape and pedicel. **Head.** Globular, approximately equal in length and width (Fig. 13A). Face equal in length to frons. Temple rather short, about  $\square$  as long as eye length. Eye circular, about as high as pedicel length (Fig. 13A). Toruli equal distance from one another as to inner eye margin. No scrobal depression. Dental formula 3:3; mandibles on higher plane than face. Maxillary palps at least 2-segmented. **Antenna** long, more than half the length of body (712). Scape elongated, about  $3.4\times$  as long as wide and  $4\times$  as long as length of pedicel (Fig. 13A).  $Fu_{1-2}$  elongate relative to other funicles, both segments about  $2\times$  as long as wide, length of  $fu_1$  72 (Fig. 13C).  $Fu_1$  much narrower than pedicel; at least  $fu_4$  only slightly longer than wide and wider than pedicel. Clava 1-segmented, undifferentiated from prior flagellomeres (Fig. 13C). MPS extending past apical margin of flagellomeres. Pilosity uniform on all segments.



**Figure 13.** *Cretaxenomerus tenuipenna*, holotype **A** lateral habitus **B** ovipositor and terminal metasomal segments **C** antenna, lateral **D** fore and hind wing (showing beneath fore wing). Scale bars: 500 µm (**A**); 250 µm (**D**); 100 µm (**B**, **C**).  $pl_1$  = propleuron;  $ptl$  = petiole.

**Mesosoma** elongate, longer than high; length 390. Mesonotum roughly  $\frac{1}{2}$  length of mesosoma. Mesoscutum convex. Mesopleuron elongate, 1.6× as long as wide. Mesoscutellum 0.4× length of mesonotum. Metanotum band-like, 0.4× length of mesoscutellum (Fig. 13A). Propodeum elongate and sloped roughly 30°, roughly  $\frac{1}{2}$  length of

mesonotum. **Wings.** Fore wings elongate, 3.5× longer than wide, length 1041, width 292. Longest marginal seta 44. Basal vein and cubital vein ephemeral (Fig. 13D). Basal vein length 47. Submarginal vein length 399. Marginal vein about  $\frac{3}{8}$  length of submarginal vein and narrow; width 19. Stigma short, length 28. Postmarginal vein narrow,  $\frac{1}{2}$  length of marginal vein. Hind wing slender and elongate, 13× as long as wide, 0.5× as long as fore wing length (Fig. 13D). Ventral marginal setae of hind wing long, 0.8× width of hind wing. **Legs.** Basitarsus curved in first third; basitarsal comb of fore leg not visible. Hind trochanter as long as hindcoxa (Fig. 13A:cx<sub>3</sub>). **Metasoma** elongate, 1.5× as long as mesosoma. Attached to mesosoma narrowly by clear petiole (Fig. 13A:ptl). Mt<sub>2-6</sub> tergal segments countable. Syntergum 0.6× length of metasoma. Ovipositor length 620, 1.2× length of gaster; ovipositor about 2× as long as syntergum (Fig. 13B); ovipositor tip with at least 3 teeth visible; ovipositor sheaths uniformly flattened along its entire length (Fig. 13B).

**Male.** Unknown.

**Material examined.** *Holotype:* female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 623I.

**Type condition.** Specimen relatively complete; antennal segments partly fragmented and separated from taphonomic process; syntergum and ovipositor complex also fragmented; tarsal segments missing beyond basitarsus on left fore- and hind leg. Streaks and ripples in the amber obscured some characters during imaging.

**Etymology.** The specific epithet is a portmanteau of the Latin ‘*tenuis*’ for narrow and ‘*penna*’ for feather in regards to its slender wings.

**Notes.** *Cretaxenomerus tenuipenna* has several similarities with *C. brevis*, most pronounced being the shortened syntergum as well as *C. vitreus* in antennal structure. However, the wing shape would indicate it is likely a closely associated but distinct species.

### *Cretaxenomerus deangelis* Ulmer & Krogmann, sp. nov.

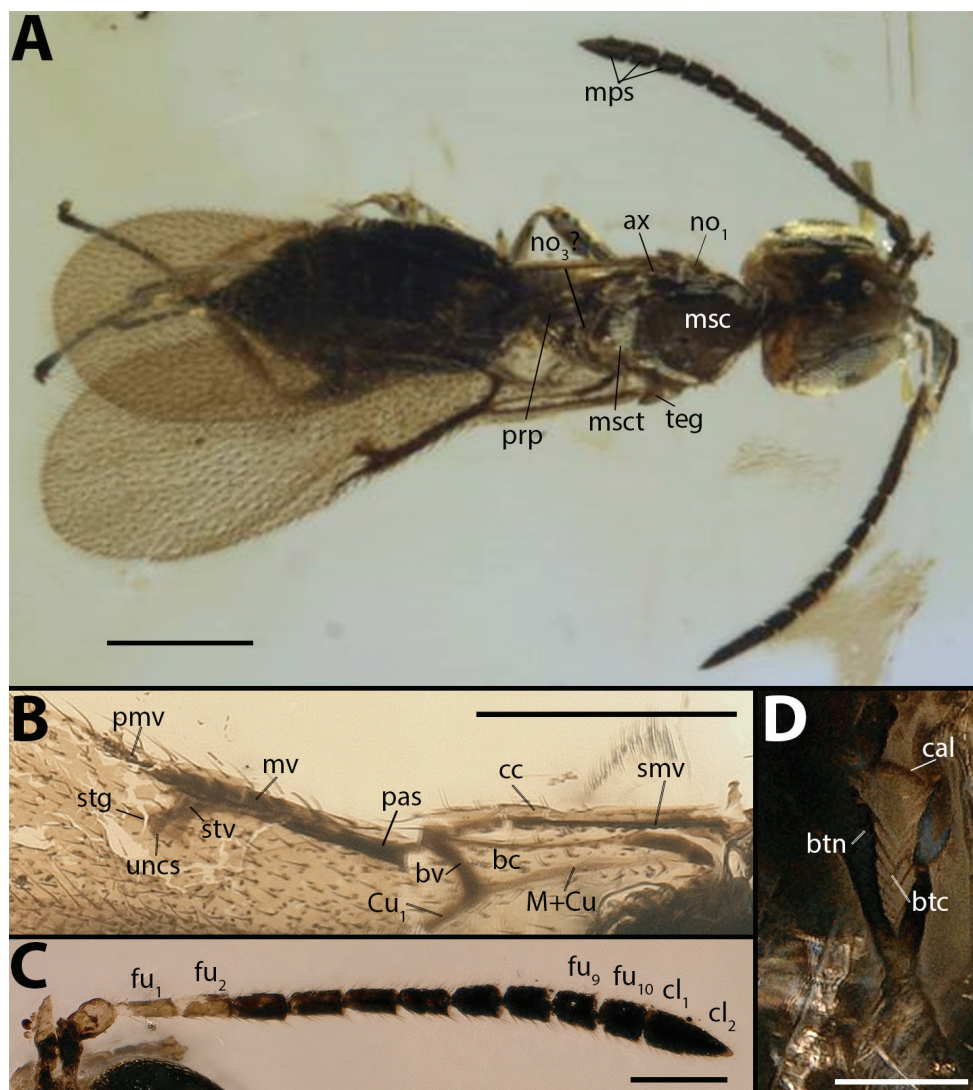
<https://zoobank.org/A30ADD01-7CA5-42D0-99A9-F16B6EE8669A>

Fig. 14

**Diagnosis.** *Cretaxenomerus deangelis* differs from all other species in the genus by the following combination of characters: shape of its head capsule, longer than wide in dorsal view. Mesoscutum with notauli. Fore wing basal cell narrow and marginal setation short. Syntergum short.

**Description. Female.** Body length 1179. Head capsule light-brown, body and appendages dark brown, aside from first two flagellomeres. Wing venation dark brown. Wing's damaged just distal to junction of smv and bv, first 2 flagellomeres damaged. Wings with slight brown infumation, uniform pilosity. **Head** elongate, about 1.3× as long as wide, wider than mesosoma in dorsal view (Fig. 14A). Temple large, at most  $\frac{1}{4}$  as long as eye length. Occiput very narrow and concave, about  $\frac{1}{3}$  as wide as head width.





**Figure 14.** *Cretaxenomerus deangelis*, holotype **A** dorsal habitus **B** fore wing venation and cells **C** antenna, lateral **D** fore leg basitarsus and tibia. Scale bars: 250 µm (**A**); 200 µm (**B**); 100 µm (**C**); 50 µm (**D**).

Malar sulcus well developed, connecting lower margin of eye and oral fossa. Antenna insertion around midline of eye. Frons protruding, on higher plane than face. Clypeus inflected. Mandibles on higher plane than clypeal margin. **Antennae** length 743. Scape probably short and broad, not visible due to damage.  $Fu_{1-6}$  narrow, longer than wide, but not elongate, equal in length to  $Fu_{7-10}$ . Clava 2-segmented, claval length 95. MPS present on all segments (Fig. 14C). Fine pilosity present, adpressed at 45° on all segments aside from pedicel and scape relative to surface. **Mesosoma** length 466. Mesoscutum 2.4× as long as mesoscutellum. Notauli well visible for its entire length. Prepectus narrow, dor-

sally overlapped by posterior-most corner of lateral panel of pronotum, laterally seen as narrow sclerite, well separated from mesonotum. Transscutal articulation medially present. Mesodiscrimen deeply invaginated. Tegula visible, bare of setation (Fig. 14A:teg). Lateral panel of metanotum with flange. Propodeum approximately equal in length to mesoscutellum (Fig. 14A). **Wings.** Fore wing length 1047, 3.3× as long as wide. Longest marginal seta length 22. Costal cell present, nearly equal in width to basal cell (Fig. 14B). Cubital vein length 229, pigmented along the entire length. Basal vein □ length of cubital vein, strongly pigmented and distally curved. Basal cell of fore wing proximally narrowed, wider at junction of M+Cu. Submarginal length 380. Marginal vein with uniform thickness along its length, short, about 0.2 as long as submarginal vein (Fig. 14B). Stigmal vein length 42, stigma and uncus present; 6 uncus sensillae present. Postmarginal vein equal in length to marginal vein; tapering distally (Fig. 14B). Hind wings obscured by fore wings. **Legs.** Basitarsomere of all legs elongate, slightly shorter than tarsomere 2–4. Basitarsal comb of fore leg present (Fig. 14D:btc) with a blunt protuberance present laterobasally (Fig. 14D:btn). **Metasoma** length 505. Mt<sub>2,7</sub> plus syntergum visible, syntergum about 0.15× as long as the rest of gaster, broadly attached to Mt<sub>7</sub>, articulation not visible (Fig. 14A). **Genitalia.** Ovipositor only slightly extended from body and slightly longer than syntergum, no more than Mt<sub>7</sub> plus syntergum length (Fig. 14A).

**Male.** Unknown.

**Material examined. Holotype:** female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number 810H.

**Type condition.** Due to the taphonomic process both antennae are detached from the head and both scapes, pedicels and first two flagellomeres are broken; the mesosoma is slightly deformed dorsolaterally; both wings are broken, the left wing just before the basal vein and the right wing beyond the basal vein, and with some additional ruptures on the disc of both wings.

**Etymology.** The specific epithet is a patronym in honor of Eric Deangelo, an early mentor and professor of one of the authors (JU) who introduced him to biology and research.

**Notes.** Due to the orientation of the specimen in the amber, the tip of the metasoma is obscured, so the syntergum could not be clearly examined, but there does not appear to be an elongate syntergum. Because *C. deangelis* apparently lacks an elongate syntergum, similar to *Protoita* but unlike other *Cretaxenomerus* females, this feature might support its placement into a third genus, although it shares more similarities with *Cretaxenomerus* species than *Protoita*. Without additional specimens to examine, we consider it premature to erect a third genus for the specimen due to its damaged state and obscured syntergum and place it tentatively in *Cretaxenomerus*. Even though the lack of an elongate syntergum is shared with *Protoita*, this lack of an apomorphy does not justify placement within *Protoita* as it shares more diagnostic features with *Cretaxenomerus* such as body length, a petiolar constriction at the waist and a head which is not wider than long in dorsal view.

*Cretaxenomerus jankotejai* Nel & Azar, 2005

Fig. 15

**Diagnosis.** *Cretaxenomerus jankotejai* can be differentiated from all other species in the genus by the following combination of characters: large body length, broad head, which is nearly 2× as wide as long (Fig. 15A), and a distinctly broadened posterior portion of its elongate syntergum (Fig. 15B: Mt<sub>8+9</sub>).

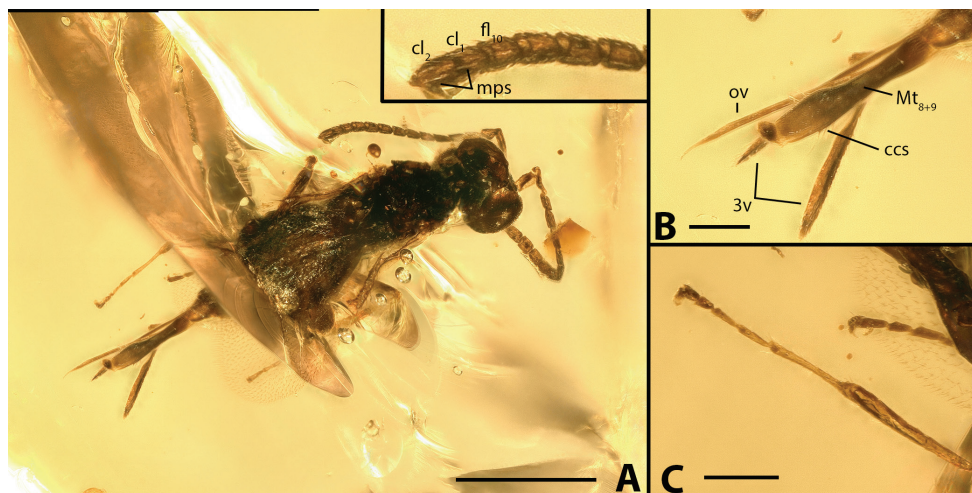
**Redescription. Female.** Body length 1490, uniformly dark brown in coloration, eyes white, wings hyaline with dense pilosity along wing disc, sparser at speculum. **Head** globose, length 160, 2× as wide as long (Fig. 15A). Ocelli large, LOL about equal to OOL. Toruli slightly closer to one another than inner eye margin. Malar sulcus present. Maxillary palps 2–3 segments. **Antenna** length 776. Fu<sub>1-3</sub> 2× as long as wide, fu<sub>4-10</sub> about 1.5× as long as wide (Fig. 15A). Clava 2 segmented, undifferentiated from funicles (Fig. 15A-inset). MPS present on all flagellomeres, as single long sensillae around circumference of segment in single row (Fig. 15A-inset). **Metasoma** length 370. Lateral panel of pronotum large and triangular. Mesonotum without notauli. Mesoscutum about 1.5× as long as mesoscutellum. Prepectus visible as a narrow strip in anterior half of mesopleuron. Mesopleuron dorsoventrally elongate. Axillulae striate. Metanotum short, length 30, medially overlapped by mesoscutellum (Fig. 15A). **Wings.** Obscured by malformation around specimens, make measurements of wing length not possible. Costal cell narrow. Basal vein short, strongly pigmented. Cubital vein lightly pigmented anterior to junction with basal vein and more strongly pigmented posterior to junction. Submarginal vein length 259. Marginal vein broad, 1/3 length of submarginal vein (Fig. 15A). Postmarginal vein very short, equal in length to shortened stigmal vein. **Legs.** Basitarsomere of all legs very long, approximately equal in length to following 4 tarsomeres combined (Fig. 15C). Tarsomere 4 noticeably shorter than others on all legs. Protibial calcar simple; basitarsal comb of fore leg present. **Metasoma** length 553, 917 with syntergum. Clear number of metasomal segments obscured. Metasoma connected with mesosoma by narrow petiolus (Fig. 15A). Syntergum widest in the posterior 1/3 of its length (Fig. 15B). Cerci with 3 cercal sensillae (Fig. 15B:ccs). Ovipositor extending only slightly beyond length of syntergum; ovipositor sheaths narrow basally before becoming spatulate in the posterior 1/4 of its length.

**Male.** Unknown.

**Material examined. Holotype:** female, Hammana / Mdeyrij, Caza Baabda, Mouhafazet Mount Lebanon; lower Barremian. In amber mounted in Canada Balsam. Deposited at Natural History Museum of the Lebanese University, accession/specimen number: 972A.

**Type condition.** Specimen complete; dorsum of head partially detached; a large transverse crack in the amber obscures portions of the metasoma distally.

**Notes.** Nel and Azar (2005) described the elongate syntergum and associated ovipositor complex as a “tubular structure”, and suggested it was an early variant of the unique telescoping ovipositor system of Platygastroidea. Reexamination of the specimens indicates that this structure is not tubular but shaped as a narrow channel and



**Figure 15.** *Cretaxenomerus jankotejai*, holotype **A** dorsal habitus, with inset showing close up of terminal flagellomeres **B** ovipositor complex with elongate syntergum **C** mesotibia and tarsus showing tarsal length. Scale bars: 500 µm (**A**); 100 µm (**B**, **C**). ccs = cercal sensilla.

the presence of frass at the end of it suggests it is the true ending of the abdomen and alimentary canal rather than the ovipositor, which is clearly seen on (Fig. 15B). Along with the wing venation and tarsal characters we transfer *Cretaxenomerus jankotejai* from Scelionidae to Protoitidae.

## Discussion

The classification of Protoitidae within Chalcidoidea is based on at least two of three putative external synapomorphies for the superfamily, with the most conspicuous being the specialized morphology and placement of MPS along all flagellar segments. Although multiporous plate sensilla occur within several lineages of Proctotrupomorpha, Chalcidoidea are unique in having the MPS raised, ridge-like, along the flagellomere and with the apical end of the sensilla raised above and often projecting beyond the apical margin of the flagellomere (Figs 5C, 7B, 9B, 11B) (Barlin and Vinson 1981; Basibuyuk and Quicke 1999). Likewise, the MPS of Protoitidae can be seen in lateral view as raised above the surface of the flagellum and often extending beyond the distal apices of the segment, including the distalmost clavomere (best seen in Fig. 9B). A second external synapomorphy that supports superfamilial placement of the newly described family is the presence of a free prepectus that is external between the pronotum and mesopleuron (Fig. 16). The structure and evolution of the prepectus within Chalcidoidea was examined in great detail by Gibson (1986, 1999). A free, external prepectus was hypothesized as the derived structure relative to the rest of Proctotrupomorpha, in which the prepectus is fused with the posterior margin of the pronotum to form a





**Figure 16.** Prepectus of Protoitidae **A** *Cretaxenomerus curvus*, mesosoma, lateral **B** *Protoita noyesi*, mesosoma, ventrolateral. Scale bars: 100  $\mu$ m (**A, B**).

“tongue and groove” articulation with the anterior margin of the mesopleuron (Gibson 1999, fig. 2) such that the pronotum is immovable relative to the mesopleuron and typically is more or less triangular in shape in lateral view. Because most Chalcidoidea have a free prepectus between the pronotum and mesopleuron (secondarily fused with the pronotum in most Perilampidae and Eucharitidae) the pronotum is moveable relative to the mesothorax and not laterally triangular in shape, at least if the prepectus is comparatively large between the pronotum and mesopleuron. A comparatively narrow and partially concealed prepectus is found in Baeomorphidae and some Mymaridae and this structure is hypothesized as the groundplan structure for the superfamily (Gibson 1986; Heraty et al. 2013). The prepectus of Protoitidae is likewise a vertically elongate sclerite that is partially overlapped dorsally by the posteriormost edge of the lateral panel of the pronotum. It is visible in only a few specimens, most clearly in *P. vitreus* (Fig. 11E) and *P. noyesi* (Fig. 16B), in part due to the unique taphonomy of the specimen, but the structure of the pronota in all the fossil taxa indicates the prepectus is small and narrow because the pronotum is very short dorsally so not readily visible in dorsal view and is much more extensive laterally (e.g. Figs 7A, 8B, 11D).

It should be noted that the prepectus is free, external and triangular in Diversinitidae, which represents the condition in most larger “hard-bodied chalcids” (Haas et al. 2018) and putatively the most-derived condition within Chalcidoidea. The occurrence of Diversinitidae in Upper Cretaceous Burmese amber is significant because the only other lineages represented in the Cretaceous fossil record are smaller “soft-bodied” families that lack a distinctly triangular, external prepectus, such as Baeomorphidae and some Mymaridae. This indicates that the shift from stem- to crown-group lineages in Chalcidoidea occurred much earlier than previously anticipated. Based on fossil evidence we find a minimum age of this shift well within the Lower Cretaceous period at a time period between 130 million years (occurrence of Protoitidae) and 100

million years (occurrence of Diversinitidae) rather than at the Paleocene-Eocene thermal maximum as suggested by previous authors (e.g., Heraty and Darling 2009; Peters et al. 2018). An earlier crown-group diversification during the late Jurassic was recently suggested by Cruaud et al. (2023).

Within Chalcidoidea, Protoitidae cannot be included in Mymaridae, which are regarded as the earliest extant lineage of Chalcidoidea, morphologically by the structure of the ovipositor (Quicke et al. 1994; Gibson and Huber 2000) and more recently by molecular studies (Heraty et al. 2013; Peters et al. 2018; Cruaud et al. 2023). Putative mymarids are also found in Lebanese amber (Azar pers. comm.), further confirming Mymaridae as being present under its current concept at that time. Likewise, classification of protoitids in Baeomorphidae is unfounded based on tarsal formula (four in Baeomorphidae vs. five in Protoitidae), and shape of the protibial spur, short and straight in Baeomorphidae, while elongate and curved in Protoitidae. Based on outgroup comparisons (selected from Blaimer et al. 2023), a 5-segmented tarsi is likely the groundplan feature in Chalcidoidea with 4 segments being the derived state. 5-segments being most common in both Mymarommatoidea and Diaprioidea. Within Mymaridae both 4- and 5-segmented tarsi may be found. The number of flagellomeres vary greatly in extinct baeomorphid species (Gumovsky et al. 2018), but extant baeomorphid females and males of *Baeomorpha* have 12-flagellomere antennae as do Protoitidae. Protoitidae in general have a putatively small breadth of claval numbers (1–3 segmented) which is a similar range to the extinct *Baeomorpha*. Despite the similar range, *Baeomorpha* have a larger number of claval segments (4–6 segmented clava) (Gumovsky et al. 2018). Likewise, the curvature of the basal vein in Baeomorphidae is chalcid like (basally-curved), and the marginal vein is much thinner than in Protoitidae (Fig. 2). Moreover, some specimens of Protoitidae have traces of metallic coloration on the gena or laterally on the mesonotum, which might indicate a relationship of Protoitidae to crown-group hard-bodied lineages rather than to Mymaridae or Baeomorphidae (Fig. 16B).

Protoitidae do share some features with Baeomorphidae and some Mymaridae, namely the shape of the prepectus, which is comparatively narrow, dorsoventrally elongated and anteriorly overlapped by the lateral panel of the pronotum (Fig. 16). The presence of MPS on the 1<sup>st</sup> flagellomere is known only for male Mymaridae within extant Chalcidoidea (Heraty et al. 2013). A probable hypothesis is that MPS on flagellomere 1 in both sexes was the groundplan state within Chalcidoidea, with subsequent loss in mymarid females and both sexes of other chalcids. The MPS present on flagellomere 1 in both sexes of Protoitidae is likely a retained symplesiomorphy of the family. Absence of flagellar MPS from Mymarommatoidea, the hypothesized sister lineage of Chalcidoidea, and irregular presence and structure of MPS for other Proctotrupomorpha prevents any definitive statement of character polarity more broadly.

Gibson (1986) regarded the possession of 13 antennomeres as a ground plan feature for Chalcidoidea and interpreted 14 antennomeres in *Diglochis* (Pteromalidae) and some males of Eucharitidae as secondarily derived. Some authors have considered a terminal spine or what has been termed a terminal button on the antennal clava as remnants of a 14<sup>th</sup> antennomere and have thus considered a 14-segmented antenna as the ground

plan condition for Chalcidoidea (Graham 1969; Onagbola and Fadamiro 2008b). The presence of a 14-segmented antennae in the oldest known chalcid fossils supports this view, i.e., that a flagellum consisting of 12 flagellomeres was the ground plan structure of Chalcidoidea and the terminal button of some extant chalcids is, indeed, a highly reduced 12<sup>th</sup> flagellomere. A 12-segmented flagellum has been previously hypothesized as a grouplan character in Gibson (1986). Even at the early stage of Lower Cretaceous diversification of Chalcidoidea there has been a reduction in number of flagellomeres to 7 (as exhibited by *Baeomorpha caeleps* Gumovsky (2018)), a derived character state which is otherwise not known from Cretaceous Chalcidoidea. Cretaceous mymarids have 8 (*Enneagmus*, *Carpenteriana*), 10 (*Myanmymar*) or 11 (*Macalpina*, *Triadomerus*) flagellomeres (Poinar and Huber 2011). Diversinitidae females have an 11-segmented flagellum, whereas males have a 12-segmented flagellum, suggesting the fusion of the terminal segments occurred early in the evolution of Chalcidoidea in at least females (Haas et al. 2018). This partial fusion of the terminal button along with MPS on the terminal button of, for example, *Chromeurytoma* (Megastigmidae) or *Pseudotorymus* (Torymidae), a character shared with Protoitidae and Diversinitidae, provides further evidence that this was previously a separate segment. The initial indicators of this fusion can be seen in several species of Protoitidae based on the simple line of weakness dividing the terminal two flagellomeres (Fig. 3A, B).

All species of Protoitidae, aside from *P. bidentata*, have tridentate mandibles. Although there has been no formal investigation of the character polarity of mandibular dentition for Chalcidoidea, variation in the mandibular formula amongst the most basal lineages, Mymaridae and Baeomorphidae, makes it a structure difficult to assess for phylogenetic significance. The extinct genera of Mymaridae have no consistent pattern in dentition, varying from 2–4 teeth (Huber 2017b). Among extant Baeomorphidae, *Rotoita* Bouček & Noyes has bidentate mandibles (Bouček and Noyes 1987, fig. 2) similar to those of *P. bidentata* (Fig. 5D), whereas *Chiloe* Gibson & Huber has bidentate mandibles but with the upper tooth broad and serrate (Gibson and Huber 2000, fig. 4). Within the extinct Baeomorphidae, both bidentate (*Baeomorpha popovi*) and tridentate (*Baeomorpha liorum*) mandibles have been observed (Gumovsky et al. 2018; Huber et al. 2019). Amongst extinct lineages, the mandibles of all diversinitids are bidentate (Haas et al. 2018), indicating 2 or 3 teeth certainly are the most common mandibular structures amongst early chalcids, and perhaps supporting bidentate mandibles as the groundplan structure for Chalcidoidea.

Both the basal and cubital veins of Protoitidae are sclerotized or at least pigmented, unlike for most other Chalcidoidea. Within Chalcidoidea, basal and cubital fore wing veins are also pigmented in Baeomorphidae, a few Pteromalidae (Miscogasterinae, Trigonoderinae), a few Melanosomellidae, Leucospidae, some Megastigmidae and sporadically in many other groups (Krogmann and Burks 2009). However, other chalcids have the basal vein curved strongly basally (Fig. 2B), whereas the basal vein in protoitids joins the cubital vein at a straight angle without curving or curving only slightly proximally (Fig. 2A). A straight or proximally oriented basal vein is most common in the relictual lineages of Proctotrupomorpha (Rasnitsyn and Kühnle 2020) such as Peleciniidae, Vanhorniidae,

Heloridae and Roproniidae, and the Australasian genera of Proctotrupidae, such as *Austroserphus* and *Austrocodrus*. This straight or proximal curvature of the Rs+M vein (putatively homologous with the basal vein of Chalcidoidea) is seen for Evaniomorpha when venation is not reduced as well as for Ichneumonoidea and Symphyta (Sharkey and Roy 2002), which would indicate a proximally curving Rs+M vein as plesiomorphic with the redirection of the vein occurring in more derived Proctotrupomorpha.

All protoitids are characterized by a syntergum which results from the fusion of  $Mt_8$  and  $Mt_9$ . This is a derived feature found also in most extant Chalcidoidea, but which likely evolved convergently multiple times (Krogmann and Burks 2009). The unique shape of the elongated syntergum is an autapomorphy of *Cretaxenomerus* among extinct chalcids.

We observed in several *Cretaxenomerus* females six distinct metasomal tergal sclerites preceding the syntergum, with  $Mt_7$  being slightly elongate to articulate with the syntergum ( $Mt_{8+9}$ ). The point of fusion between  $Mt_{8+9}$  is likely at about the posterior  $\frac{1}{3}$  of the elongated tergum where there is a pair of lateral notches before the structure abruptly narrows slightly again, corresponding to the position of the cerci (Fig. 8D:cer).

The syntergum is sexually dimorphic, being elongate only in females, and likely functioning as a dorsal protection for the elongate ovipositor sheaths. In several females, such as a paratype of *P. curvus*, where the ovipositor is extended, the syntergum is shifted up, articulating with the base of the ovipositor, and terminal tergite ( $Mt_7$ ). The membranous anal tube can be seen projecting from the apex of the syntergum, suggesting it to be the true distal point of the abdomen (Figs 8D, 10F, 12D). This is in contrast to the platygastroid ovipositor system (Austin and Field 1997), with which the structure was initially mistaken for in the original description of *Cretaxenomerus jankotejai* Nel & Azar, 2005.

Within *Cretaxenomerus* there is continuous variation in the structure of the syntergum. Within the “short-syntergum” species, consisting of *C. brevis* and *C. tenuipenna*, the ovipositor sheaths are continuous in width along their entire length (Figs 10F, 13B), compared to the spatulate-like sheaths of the “long-syntergum” group, such as *C. curvus* and *C. mirari*, which broaden distally into paddle-like structures along a narrow proximal stalk (Figs 8D, 12D). The structural diversity of the metasoma indicates a broad spectrum of oviposition capabilities and that the early Chalcidoidea described herein were able to occupy a diverse range of ecological niches. The function of the modified syntergum is uncertain, in part due to lacking comparison in extant taxa, although likely involved in assisting with oviposition or protection of the ovipositor. Egg parasitism is known from early chalcid lineages of Mymaridae and putatively in Baecomorphidae (Munro et al. 2011; Peters et al. 2018). The additional presence of micropilosity along the claval and distal flagellar segments in Protoitidae, provides some support for parasitism of concealed hosts, character often associated with the lifestyle Podagrioninae, mantid eggs parasitoids (Janšta et al. 2018).

There is a clear divide in the Chalcidoidea fossil record between the Cretaceous and Eocene, corresponding with the division of early “soft-bodied” chalcids and the larger “hard-bodied” lineages (Fig. 1). Cruaud et al. (2023) places the divergence points of



the major chalcid lineages within the Lower Cretaceous, which corresponds with the fossil record, with Mymaridae persisting as an early crown-group lineage from the Cretaceous throughout the fossil record but Baeomorphidae presenting itself as a “Lazarus taxon”, with a disjointed record between the Cretaceous and extant lineages (Jablonski 1986). The presence of Protoitidae and Diversinitidae in the Lower Cretaceous also confirms an early crown group diversification, with the two families likely representing late stem group lineages. Diversinitidae shares several synapomorphies with other members of the younger “hard-bodied” clade that provides further support for an Upper Cretaceous diversification. One hypothesis based on the known fossil record is an early diversification of Chalcidoidea within the Cretaceous, followed by the extinction of several lineages (including Protoitidae and Diversinitidae), possibly during the subsequent K-T extinction (Labandeira 2005), and then a subsequent radiation of other chalcidoid lineages during the paleocene-eocene thermal maximum. This secondary radiation corresponds with the diversification of herbivorous insects (Curanno et al. 2008), which led to the rapid diversification of parasitoids (Nyman et al. 2007). This may also provide some rationale for the seemingly disjunct apomorphies of surviving lineages of the earlier diversification event (Baeomorphidae and Mymaridae) relative to the rest of Chalcidoidea. Research into fossils within the paleocene may elucidate this transition and provide better resolution to the stem-group to crown-group transition.

The most recent biogeographic theories on the origin of Chalcidoidea suggest an Eastern Gondwanan origin for the group with the rapid radiation of the group occurring in Southern Gondwana (Cruaud et al. 2023). This is based quite heavily on the density of early lineages occurring in Burmese amber such as Mymaridae and Baeomorphidae (Gumovsky et al. 2018), with crown group taxa appearing with more regularity in the southern gondwanan Cenozoic records. The presence of Protoitidae in Northeastern Gondwanan Lebanese amber presents a new piece of evidence for an Eastern Gondwanan origin. Lebanese amber also contains early putative Mymaridae (Azar pers. comm.), which suggests *Cretaxenomerus* was at least present in tandem with an extant lineage. We suggest an addendum to the present theory of Cruaud et al. (2023) based on this new evidence. An Eastern Gondwanan origin to Chalcidoidea led to the presence of early crown groups and relictual families of Chalcidoidea, including the “hard-bodied clade”. These groups spread both north and south. Northern lineages such as the fossil *Baeomorpha* and Protoitidae were not successful and disappeared early in the evolution of Chalcidoidea whereas southern groups proliferated during the climatic shifts of the early Cenozoic. This would also account for the curious distribution of Baeomorphidae, which has a purely Southern Gondwanan extant distribution (New Zealand and Chile) and heavily Laurasian fossil record. Likewise, the presence of Diversinitidae in mid Cretaceous Burmese deposits (Haas et al. 2020) may suggest an early unsuccessful radiation attempt in Chalcidoidea prior to the eocene-paleocene thermal boundary with the bottleneck leading to the morphological “gap” between early relictual lineages such as Baeomorphidae, Mymaridae, Diversinitidae, and Protoitidae and the larger post gap megara diation event. Only with continued investigation of the fossil record of Chalcidoidea can we begin to uncover the true origins and early diversification of one of the largest insect lineages.

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## Supplementary material I

### Fossil Chalcidoidea occurrence data

Authors: Jonah M. Uimer

Data type: csv

Explanation note: Curated occurrence and metadata of fossil Chalcidoidea taxa used for generating time series plots.

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