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**Annales de Paléontologie**

**New evanioid wasps (Hymenoptera: Evaniidae; Praeaulacidae) from the mid-Cretaceous  
Kachin amber**

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## ABSTRACT

Two evanioid wasps are described from specimens entrapped in Kachin amber. The first species, *Sinuevania pouilloni* sp. nov., allows a revision of the diagnosis of the genus *Sinuevania*. The complex forewing venation (plesiomorphy) of this new species suggests that the genus *Sinuevania* belongs to the stem group of the family Evaniidae. Together with the new praeaulacine wasp *Praegastrinus edithae* gen. et sp. nov., *Sinuevania pouilloni* sp. nov. shows that the diversity of the superfamily Evanioidea in the mid-Cretaceous Kachin amber remains underestimated. New fossils of evaniid wasps from the Albo-Cenomanian amber of Charente-Maritime (France) are expected to extend the diversity and distribution of several genera. Based on the recent discovery, but not yet published, of new praeaulacid specimens from the mid-Cretaceous, we propose reclassifying *Mesevania* within the Praeaulacidae (Praeaulacinae).

## RÉSUMÉ

Deux guêpes évanioides sont décrites à partir de spécimens piégés dans l'ambre du Kachin. La première espèce, *Sinuevania pouilloni* sp. nov., permet une révision de la diagnose du genre *Sinuevania*. La nervation complexe de l'aile antérieure (plésiomorphie) de cette nouvelle espèce suggère que le genre *Sinuevania* appartient au groupe souche de la famille des Evaniidae. Avec la nouvelle guêpe praeaulacine *Praegastrinus edithae* gen. et sp. nov., *Sinuevania pouilloni* sp. nov. montre que la diversité de la superfamille des Evanioidea dans l'ambre du Crétacé moyen du Kachin reste sous-estimée. De nouveaux fossiles de guêpes évaniides de l'ambre albo-cénomaniens de Charente-Maritime (France) devraient étendre la diversité et la répartition de plusieurs genres. Sur la base de la découverte récente, mais non encore publiée, de nouveaux spécimens de praeaulacidés du Crétacé moyen, nous proposons de reclasser *Mesevania* au sein des Praeaulacidae (Praeaulacinae).

Keywords: Burmese amber, Evanioidea, evolution, systematic, diversity, taxonomy

Mots clés : Ambre birman, Evanioidea, évolution, systématique, diversité, taxonomie

## 1. Introduction

Evanioid wasps stand out distinctly from all other extant and extinct Hymenoptera lineages due to the attachment of their metasoma, which is situated high on the propodeum and well above the metacoxae (e.g., Goulet and Huber, 1993). Notably, the superfamily Evanioidea serves as an excellent example of having a stem group far more diverse and species-rich in the deep time than its crown group, with five out of its eight constitutive families having gone extinct (Jouault et al., 2022: fig. 8). Therefore, at the family level, this superfamily exhibited a greater diversity during the Mesozoic than in the Cenozoic. The monophyly of the superfamily is consistently supported in recent phylogenetic studies even when considering fossil taxa (e.g., Li et al., 2018; Parslow et al., 2020; Jouault et al., 2022). According to the latest time-calibrated analysis, the superfamily emergence can be traced back to the Late Triassic or the Early Jurassic. However, the oldest species belonging to this superfamily are from younger Middle Jurassic deposits, and the oldest representatives of the crown group are only recorded during the Early Cretaceous (Jouault et al., 2022: fig. 8).

Extant evaniid wasps are widespread and relatively diverse, with approximately 580 extant species placed in 21 genera. It is worth noting that this diversity is likely underestimated (Deans, 2005; Mullins et al., 2012). There is limited knowledge about the biology of modern evaniids even if their larvae are known to be predators of cockroach eggs found in oothecae (Edmunds, 1954; Huber, 1995). The specific metasomal configuration of evaniid wasps – the metasoma is short, flag-shaped, and attached high on the mesosoma by a long and thin petiole – is the origin of the common names for Evaniidae, often referred to as ensign wasps, nightshade wasps, or hatchet wasps. The stem Evaniidae are estimated to have originated during the Late Jurassic, while their

crown group likely emerged around the boundary between the Cretaceous and Paleogene periods. The family Evaniidae has a rather rich fossil record, with the oldest known species dating back to the late Hauterivian, numerous species documented up to the Miocene, and an important diversity in Burmese amber (e.g., Rasnitsyn et al., 1998; Nel et al., 2002; Deans et al., 2004; Jennings et al., 2012; Shih et al., 2020; Rosse-Guillevic and Jouault, 2023). However, the diversity of Cretaceous evaniids is still greatly underestimated.

The family Praeaulacidae is the earliest diverged clade within the superfamily Evanioidea, with their origin likely dating back to the latest Triassic or Early Jurassic, even though the earliest known species are from Jurassic deposits (Li et al., 2018; Jouault et al., 2022). Interestingly, they are well documented in compression or imprint fossil deposits but less so in amber (see Jouault et al., 2022: tabl. 1). Recent descriptions of mid-Cretaceous amber species suggest a rich morphological and taxonomic diversity within this family during that ‘period’, including representatives from the Nevaniinae and Praeaulacinae subfamilies (e.g., Li et al., 2015, 2023; Jouault et al., 2020; Jouault and Rosse-Guillevic, 2023). Praeaulacid wasps are characterized by their retention of plesiomorphic wing venation and morphology, featuring numerous antennomeres and crossveins (Rasnitsyn, 1972, 1975; Jell and Duncan, 1986). Although their ecology and behavior remain unknown, the diversity in their metasomal attachments and morphology suggests a specialization as parasitoids (Zhang and Rasnitsyn, 2007).

In this study, we introduce two new evanioid wasps, respectively belonging to the Evaniidae and Praeaulacidae families, discovered in mid-Cretaceous Kachin amber.

## **2. Material and methods**

### *2.1. Burmese amber*

The amber pieces containing the specimens studied herein derive from the deposits of Noije Bum in the Hukawng Valley (26°29' N, 96°35' E), Kachin State, northern Myanmar (see detailed map in

Grimaldi and Ross, 2017: fig. 2). Radiometric data established an early Cenomanian age ( $98.79 \pm 0.62$  Mya) for Kachin amber, based on zircons from volcanic clasts found within the amber-bearing sediments (Shi et al., 2012). Some ammonites, found in the amber-bearing bed, and within amber, corroborate a late Albian/early Cenomanian age of these sediments (Yu et al., 2019; Cruickshank and Ko, 2003). The specimens were accessed by Jean-Marc Pouillon, who donated them for study and housing in the Geological Department and Museum of the University of Rennes, France (IGR), under collection numbers IGR.BU-085 and IGR.BU-086.

## *2.2. Amber preparation, specimen imaging, and terminology*

The amber pieces were polished with a grinding polisher (Buehler MetaServ 3000), with thin silicon carbide sanding paper. The specimens were examined and photographed with a Nikon SMZ25 stereomicroscope with an attached Nikon D800 camera. Images taken with the Nikon D800 camera have been enhanced using Capture NXD software. All images are digitally stacked photomicrographic composites of several individual focal planes, which were obtained using Helicon Focus 6.7. The figures were composed with Adobe Illustrator CC2018 and Photoshop CC2018. The wing venation and terminology are adapted from Goulet and Huber (1993), and the surface sculpturing follows Harris (1979).

The published work and nomenclatural acts are registered in ZooBank with the following LSID: [urn:lsid:zoobank.org:pub:92B4B8CB-F727-40B9-9A8B-966DCAE941CF](https://zoobank.org/pub:92B4B8CB-F727-40B9-9A8B-966DCAE941CF)

## **3. Systematic palaeontology**

**Order Hymenoptera Linnaeus, 1758**

**Suborder Apocrita Gerstaecker, 1867**

**Superfamily Evanioidea Latreille, 1802**

*Remarks.* The new specimens are attributed to the superfamily Evanioidea because of their metasoma articulated high on the propodeum and well above the metacoxae (e.g., Goulet and Huber, 1993).

#### **Clade Neoevanioides Engel, 2006**

#### **Clade Evaniiformes Grimaldi and Engel, 2005**

#### **Family Evaniidae Latreille, 1802**

*Remarks.* The antennae with 11 flagellomeres and the hind wings lacking rs-m and cu-a crossveins exclude affinities of the new specimen with the family Praeaulacidae (e.g., Rasnitsyn, 1988; Li et al., 2015, 2023; Jouault et al., 2020; Jouault and Rosse-Guillevic, 2023). The Othniodellithidae have a cephalic horn (apomorphy), and antennae with numerous flagellomeres (Engel, 2017; Jouault et al., 2022). These characters are absent from the new specimen precluding its placement in the latter family.

Affinities with the family Gasteruptiidae are ruled out because the new fossil lacks the characteristic U-shaped notauli and the clavate metatibiae found in gasteruptiid wasps (Engel and Wang, 2016). The new specimen has forewings with a complete 2rs-m crossvein, which precludes affinities with the Anomopterellidae (Li et al., 2013). The new specimen can be differentiated from the Andreneliidae because of its oligomeric antennae (11 flagellomeres vs. at least 15 in *Andrenelia*), and its forewings with a thin pterostigma and the vein Rs more than twice shorter than the vein M (vs. of similar length) (Rasnitsyn and Martínez-Delclòs, 2000). The family Andreneliidae is found closely related to the Evaniidae but this position and the validity of the family are not certain (Rasnitsyn, 2013; Jouault et al., 2022). The new fossil has elbowed antennae (vs. not elbowed in Baissidae) and antennae with 11 flagellomeres (vs. 12 for baissid female) which precludes its placement into the Baissidae (Engel, 2013). The new specimen differs from the Aulacidae because it lacks propleura forwardly extending beyond the pronotum and forming as a

neck-like extension, has 13 antennomeres (vs. 12 antennomeres in aulacid female), and lacks the metasomal terga 1 and 2 fused into a long (here tube-like) petiole (Li et al., 2018). It further differs from the Aulacidae because of its short ovipositor (vs. relatively long in Aulacidae).

**Genus *Sinuevania* Li, Rasnitsyn & Ren, 2018 (in Li et al., 2018)**

**Included species:** *Sinuevania mira* Li, Rasnitsyn & Ren, 2018 (in Li et al., 2018) (type species); other species: *Sinuevania pouilloni* sp. nov.

**Emended diagnosis:** Female fully winged and of small to medium body size. Antennae with 11 flagellomeres. Mesosoma strongly sclerotized, compact and moderately high. Forewing with more than four enclosed cells; C and Sc+R tubular; M+Cu arched; 1M more than twice longer than 1Rs, slightly curved; 1Rs reaching Sc+R slightly anterior to pterostigma; Rs+M long, overpassing middle of pterostigma, contacting 1m-cu; 2r-rs long, inclined towards wing apex; 2rs-m, 3rs-m and 2m-cu present, not fully sclerotized; 1cu-a postfurcal; free M and Cu present; first medial cell trapezoidal, elongate; second medial cell (2m-cu) rectangular; second submarginal cell (2rm) smaller than third submarginal cell (3rm); marginal cell elongate, ending before wing apex. Hind wing without venation except Sc+R, without jugal lobe. Legs with preapical tarsomere of fore and mid legs extremely short; pretarsal claws short, with a preapical tooth; arolium present. Metasoma with petiole tubular, gaster slightly shorter than mesosoma; ovipositor thin, exposed, longer than petiole.

**Remarks:** Using the keys to the fossil genera of Evaniidae in Li et al. (2018) and Shih et al. (2020), the specimen keys to *Lebanevania* Basibuyuk & Rasnitsyn, 2002 because of its forewing venation complete, with 2rs-m, 3rs-m and 2m-cu all present, and 1cu-a distinctly postfurcal. The genus *Lebanevania* is known from only one species (i.e., *Lebanevania azari* Basibuyuk & Rasnitsyn, 2002) described from the Barremian Lebanese amber (Basibuyuk et al., 2002). Our new specimen presents numerous differences with *Lebanevania*, either in terms of general morphology or wing venation. Basibuyuk et al. (2002) noted that the genus *Lebanevania* is quite distinctive from other

evaniids, *inter alia*, because of its long fore trochanter and its non-tubular petiole. In the new specimen, the fore trochanters are also long, but the petiole is distinctively tubular. Additionally, the new specimen can be differentiated from the genus *Lebanevania* at least because of its forewings with 1Rs much shorter than 1M; 1M distinctly curved towards the apex of the wing; 2r-rs distinctly inclined; cell 2m-cu elongate; M after Rs+M extremely short (i.e., no conspicuous M abscissa between the cells 1m-cu and 2rm).

The new specimen differs from most other Cretaceous evaniid genera (i.e., *Botsvania* Rasnitsyn & Brothers, 2007; *Burmaevania* Shih et al., 2019; *Cretevania* Rasnitsyn, 1975; *Curtevania* Li et al., 2018; *Grimaldivania* Basibuyuk et al., 2000; *Iberoevania* Peñalver et al., 2010; *Newjersevania* Basibuyuk et al., 2000; *Praevania* Rasnitsyn, 1991; *Protoparevania* Deans, 2004; *Sorellevania* Engel, 2006) in having a complex forewing venation with 2m-cu, 2rs-m, and 3rs-m present.

We observed a striking resemblance between the new specimen and the genus *Sinuevania* (Li et al., 2018). However, *Sinuevania* was initially ruled out in the keys due to the putative absence of the 2m-cu crossvein (Li et al., 2018). It is important to note that the wing membrane where the 2m-cu crossvein should be located is damaged in the type specimen of this genus, making it impossible to definitively confirm or refute the presence of this crossvein. Intriguingly, there is an indication that the vein M forms an angle at the expected position of 2m-cu, suggesting the presence of this crossvein in the type specimen of *S. mira*. Given the close similarities between the new fossil and the type specimen of *Sinuevania*, we decided to revise the genus diagnosis instead of introducing a new genus, as doing so would complicate future research on Cretaceous evaniids.

***Sinuevania pouilloni* sp. nov.**

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Figs. 1–2

**Type material:** Holotype IGR.BU-085 (JMP018; ♀, in an amber piece measuring 10 × 4 × 7 mm); syninclusion: a specimen of the genus *Alavesia* sp. (Diptera: Atelestidae); deposited in the Geological Department and Museum of the University of Rennes, France.

**Etymology:** The specific epithet is a patronym honouring Jean-Marc Pouillon, for his generous donation to the MHNE. The specific epithet is to be treated as a noun in the genitive case.

**Locality and horizon:** Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

**Diagnosis:** Medium size species (body about 4.15 mm long). Forewing with 2r-rs longer than 1Rs, distinctly inclined; 2Rs short and straight; cell 2rm triangular, longer along 2rs-m, distinctly shorter than cell 3rm.

**Description:** Head rounded, about 0.97 mm high (in full-face view, mandibles included); gena width at most one-third of eyes width; compound eyes large, glabrous, slightly reniform, occupying most part lateral surface of head, 0.61 mm high (in full-face view) and 0.52 mm wide (measured laterally); ocelli arranged in an equilateral triangle; clypeus swollen medially; malar space longer than basal mandibular width; mandibles stout, with conspicuous sharp teeth (at least three on each), about 0.34 mm long (in full-face view); maxillary palps at least 0.6 mm long, length of measurable palpomeres from apex to base (in mm): 0.22, 0.12, 0.18; distance between toruli about 0.1 mm, between toruli and eyes about 0.07 mm. Antennae articulated at about head midlength, not inserted on swelling or shelf, with short scape (i.e., distinctly shorter than first flagellomere); scape about 0.32 mm long and 0.08 mm wide, subcylindrical; pedicel pear-shaped, about 0.13 mm long, widening distally, slightly longer than wide, shorter than first flagellomere; first flagellomere cylindrical and longer than following ones, flagellomeres shortening towards apex, widening distinctly from fifth flagellomere respective length of flagellomeres (in mm, from base to apex): 0.40, 0.33, 0.27, 0.22, 0.21, 0.21, 0.20, 0.19, 0.18, 0.16, 0.28; occipital carina present and complete. Mesosoma about 1.63 mm long and 1.35 mm high (in lateral view), with areolate mesopleura and



more distinctively areolate metapleura and propodeum; pronotum short, posteriorly delineated by a ridge; notauli conspicuous, and narrow (i.e., distance between them along scutellum short). Forelegs femur about 0.67 mm long, tibia about 0.70 mm long, tarsomere lengths (from basitarsus to apex, in mm): 0.35, 0.22, 0.16, 0.05, 0.15. Midlegs with trochanter 0.38 mm long, femur 0.86 mm long, tibia 0.85 mm long, tarsomere lengths (from basitarsus to apex, in mm): 0.46, 0.22, 0.16, 0.05, 0.15. Hind leg distinctively longer than fore- and mid-legs; coxa at least 0.54 mm long; trochanter about 0.67 mm long, widening towards apex; femora 1.45 mm long, slightly swollen medially; tibia about 1.58 mm long, widening towards apex; tarsomere lengths (from basitarsus to apex, in mm): 0.74, 0.45, 0.40, 0.17, 0.20. Tibial spurs formula: 1-2-2, foretibia with spur bifid.

Forewing 3.31 mm long and 1.1 mm wide; pterostigma broadest at level of 2r-rs (about 0.1 mm wide); costal cell distinctively broader than C, widening towards apex; radial cell distinctly longer than wide; submarginal cell pentagonal about 2.5× longer than wide; marginal cell about 3.7× longer than wide; first medial cell more than 3× longer than wide; 2rs-m antieriad 2m-cu along M; second submarginal cell 1.5× longer than wide; third submarginal cell about twice as long as wide, with 3rs-m arched; second medial cell about 2.8× longer than wide, with 2m-cu slightly sigmoidal. Hind wing about 1.5 mm long, with five distal hamuli.

Metasoma with petiole about 0.55 mm long, petiole with a ventral tooth-like projection distally (a common feature for evaniids); gaster pear-shaped, about 1.47 mm long, sternites widening and shortening towards apex; ovipositor and ovipositor sheath protruding from abdomen for about 1 mm.

**Remarks:** Compared to *S. mira*, *Sinuevania pouilloni* sp. nov. is much larger (body length about 2.8 mm in *S. mira* vs. 4.15 mm in *Sinuevania pouilloni* sp. nov.). Although this difference in size can be the result of the amount of food received at the larval stage, its combination with the other differences listed hereafter is considered diagnostic. The two species also differ in their forewing venations. *Sinuevania pouilloni* sp. nov. has a crossvein 2r-rs longer than 1Rs while in *S. mira* 2r-rs

is shorter than 1Rs; 2Rs is long and distinctively curved in *S. mira* while short and straight in *Sinuevania pouilloni* sp. nov.; the cell 3rm is elongate in *Sinuevania pouilloni* sp. nov., while comparatively much shorter in *S. mira*; the cell 2rm is triangular in *Sinuevania pouilloni* sp. nov., while rectangular in *S. mira*.

## **Clade Protoevanioides Jouault et al., 2022 (= Praeaulacidae + Othniodellithidae)**

### **Family Praeaulacidae Rasnitsyn, 1972**

**Remarks:** The numerous antennomeres (i.e., more than 20), the complete forewing venation (with two rs-m and two m-cu crossveins), and its hind wing venation with rs-m and cu-a present preclude the placement of the new fossil within the extant families Gasteruptiidae, Evaniidae, and Aulacidae. The high number of antennomeres ruled out affinities with the Baissidae. Note that the current rank (i.e., family) of the Baissidae might be challenged because no apomorphy has been found to support its monophyly (Rasnitsyn, 2013; Li et al., 2018; Jouault et al., 2022).

The specimen cannot be attributed to the family Anomopterellidae because it possesses forewings with a complete 2rs-m crossvein, while absent in anomopterellid wasps (Li et al., 2013). The new fossil can be differentiated from the Andreneliidae, at least, because it has a comparatively thin pterostigma (Rasnitsyn and Martínez-Delclòs, 2000). Note that the position and the validity of this family are not certain, but until the discovery of additional material, a synonymization seems hazardous (Jouault et al., 2022).

The placement of the new genus within the family Praeaulacidae is supported by its hind-wing venation with Rs, rs-m, and cu-a present (in the most developed evanioid hind-wing venation only R, Rs, M+Cu, M, Cu, A, and rs-m are present), but also because its antennae have a high number of flagellomeres (Li et al., 2015, 2023). Even the Othniodellithidae have a different conformation of the hind wings with the Cu often fused with the cu-a (Engel et al., 2016; Engel,

2017; Jouault et al., 2022). Nevertheless, the new fossil cannot be placed within the latter family because it lacks the typical cephalic horn (an apomorphy) of the Othniodellithidae (Engel et al., 2016; Engel, 2017; Jouault et al., 2022). Note that the Othniodellithidae have been found nested within the Praeaulacidae (Jouault et al., 2022), a result that may question their familial rank.

The family Praeaulacidae encompasses the three subfamilies Praeaulacinae, Cretocleistogastrinae, and Nevaniinae. The one-segmented petiole of the new fossil prevents its placement in the Nevaniinae, which possesses a two-segmented petiole (Zhang and Rasnitsyn., 2007; Li et al., 2014a; Jouault et al., 2020). The new specimen can also be differentiated from the Nevaniinae because its forewing has a vein M+Cu longer than the combined length of the veins 1Rs and 1M, vs. shorter than M+Cu in the Nevaniinae (Zhang and Rasnitsyn, 2007).

The forewing venation of the new specimen is also useful to rule out affinities with the subfamily Cretocleistogastrinae. The new species has a forewing with a thin pterostigma vs. wide in Cretocleistogastrinae, a crossvein 3rs-m completely preserved vs. completely lost, and a 2M well developed vs. absent (Rasnitsyn, 1990; Zhang and Zheng, 2000). Therefore, we place the new fossil within the subfamily Praeaulacinae.

### **Subfamily Praeaulacinae Rasnitsyn, 1972**

#### **Genus *Praegastrinus* gen. nov.**

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**Type species:** *Praegastrinus edithae* sp. nov.

**Etymology:** The genus name is a combination of the latin prefix *prae* (meaning before), and the suffix '*gastrinus*' often used for praeaulacid genera. Gender masculine.

**Diagnosis:** Head quadrate (in full face view), short, and medium-sized; antennae with 21(?)

antennomeres; frons with bi-lobed ledge covering each torulus dorsally (apomorphy). Mesosoma thin and slightly higher than long; hind tibiae not clavate; tibial spurs formula 1-2-2; tarsal claws simple. Forewing with pterostigma long and thin; 1M shorter than 1Rs; 1Rs long (i.e., 1Rs longer than its distance to pterostigma), inclined, and reaching Sc+R close to pterostigma; 1cu-a interstitial; 2r-rs nearly straight, reaching Rs at cell 2rm mid-length (well before 2rs-m), originating near middle of pterostigma (slightly before middle of pterostigma); 2rs-m present, slightly sinusoidal; cell 2rm trapezoidal, longer than wide, with parallel sides (i.e., 3Rs and 3M); 3rs-m oblique and arched; cell 3rm shorter than cell 2rm, pear-shaped; 1cu-a interstitial with M+Cu fork; cells 1mcu and 2rm in contact by 2M; cells 1mcu and 2mcu trapezoidal and longer than wide; 2m-cu reaching M distad 2rs-m (i.e., in cell 3rm), closer to 2rs-m than 3rs-m along M; 2cu-a long (about  $0.6 \times 2Cu$  length). Hind wings with 1Rs long and nearly straight; rs-m shorted than cu-a; 1M nearly straight; 2M well developed; cu-a reaching Cu distad M+Cu fork; A not overpassing cu-a. Metasoma distinctly longer than mesosoma; first segment petiole-like (i.e., long and thin) and ventrally inflated in its distal half; second segment conical, shorter than petiole.

**Remarks:** The genera *Archeogastrinus* Jouault & Rosse-Guillevic, 2023, *Habraulacus* Li et al., 2015, *Hadraulacus* Li et al., 2023, *Mesevania* Basibuyuk & Rasnitsyn 2000, and *Paleosyncrasis* Poinar, 2019 are the only praeaulacine genera described from the mid-Cretaceous Kachin amber (Basibuyuk et al., 2000; Li et al., 2015, 2023; Poinar, 2019; Jouault and Rosse-Guillevic, 2023). Note that the characters listed in the diagnosis also allow differentiation from the other Praeaulacinae.

The fore- and hind wing venations of the new specimen allow a rapid differentiation with *Archeogastrinus*, *inter alia*, because it has a forewing with 1cu-a interstitial with M+Cu fork (vs. 1cu-a distad M+Cu fork in *Archeogastrinus*); 1Rs longer than 1M vs. shorter than 1M; 2r-rs straight vs. curved, and distinctly anterior to 2rs-m vs. aligned with 2rs-m; cell 3rm short, pear-shaped vs. long and trapezoidal; a hind wing with 2M long (Jouault and Rosse-Guillevic, 2023).

Similarly, the new specimen cannot be placed within the genus *Habraulacus*, *inter alia*, because of its fore- and hind wing venations. The differences in the forewing venation between *Habraulacus* and the new specimen are somewhat less pronounced than with *Archeogastrinus*. Nevertheless, the new specimen differs from *Habraulacus* because of its forewing with 1Rs only slightly longer than 1M vs. more than twice the length of 1M in *Habraulacus*, its cell 3rm pear-shaped vs. rectangular, and the crossvein 2m-cu contacting M distad 2rs-m vs. nearly aligned. The most notable difference between the new specimen and the genus *Habraulacus* lies in the hind wing venation with, *inter alia*, 1Rs being more than  $3 \times$  the length of rs-m in the new specimen vs. 1Rs shorter than rs-m in *Habraulacus*, 2Rs absent vs. well developed, 1Cu longer than cu-a vs. shorter than cu-a, and A not overpassing cu-a vs. distinctively present after cu-a (Li et al., 2015).

The genus *Habraulacus* is easily differentiable from the other mid-Cretaceous praeaulacine genera because of its forewing lacking 2rs-m (vs. present in the others and in the new specimen), and its tibial spurs formula of 1-1-2 (vs. 1-2-2 for other genera with known formula and the new specimen) (Li et al., 2023). The genus *Mesevania* can be distinguished from most other praeaulacine genera because of its modified hind tibiae (i.e., swollen and resembling the condition found in the family Gasteruptiidae). This character can be specific to the female, maybe for parasitoid behavior, and cannot be used to exclude affinities with our specimen (a male). The wing venation of *Mesevania* is, at first sight, similar to that of the new specimen, and information for the hind wing venation is reduced. Together, these limitations complicate an in-depth comparison with our new specimen. However, the forewing venation of the new specimen appears to be different from that of *Mesevania* at least because cell 2m-cu is more elongated and nearly as long as cell 1m-cu (vs. shorter than 1m-cu in *Mesevania*); cell 3rm is about  $4 \times$  longer along M than along Rs (vs. about  $3 \times$ ), which result in a much more pronounced pear shape in the new specimen than in *Mesevania*; 2cu-a is also much longer in the new specimen (i.e.,  $0.6 \times$  the length of 2Cu) while it is extremely short in *Mesevania* (i.e., less than a quarter of 2Cu) (Basibuyuk et al., 2000). Note that a

reexamination of the type specimen of *Mesevania* will be needed to clarify the state of several key characters used for genera delineation in Praeaulacinae (e.g., hind wing venation).

Affinities with genus *Paleosyncrasis* are easily refuted because of the thin and elongate metasoma of the new specimen (vs. short and rounded in *Paleosyncrasis*), and the different hind wing venation with A not overpassing cu-a in the new specimen vs. overpassing cu-a, and the vein Rs not reemerging close to the wing margin vs. putatively reemerging (Poinar, 2019).

Note that the frons with a bilobed ledge covering each torulus dorsally is an apomorphic character of the new genus. In our current state of knowledge, it is difficult to establish a link with the cephalic horn of the Othniodellithidae.

***Praegastrinus edithae* sp. nov.**

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Figs. 3–5

**Type material:** Holotype IGR.BU-086 (JMP099; ♂, in an amber piece measuring 10 × 15 × 4 mm); syninclusion: an Apocrita; deposited in the Geological Department and Museum of the University of Rennes, France.

**Etymology:** The name of the new species honors Edith Pouillon for her generous hospitality during CJ's visit, and is to be treated as a noun in a genitive case.

**Locality and horizon:** Noiye Bum Hill, Hukawng Valley, Kachin State, Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.

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

**Description:** Head about 1.1 mm high (in full-face view, mandibles included); gena tapering towards mandibles, always shorter than eye width; compound eyes glabrous, 0.82 mm high and 0.42 mm wide (measured laterally), occupying most of lateral surface of head; ocelli arranged in an

isosceles triangle (posterior ocelli closer to anterior ocellus than to each other); supraclypeal area (i.e., area between clypeus and toruli) covered with minute, thin setae; clypeus slightly concave; malar space shorter than basal width of mandible; mandibles stout, each with three teeth, external edge rounded, about 0.3 mm long; maxillary palps at least 0.45 mm long; labial palps at least 0.34 mm long, length of measurable palpomeres from apex to base (in mm): 0.08, 0.08, 0.09; distance between toruli about 0.11 mm, between toruli and eyes about 0.16; antennae about 3.7 mm long; scape about 0.25 mm long and 0.07 mm wide, subcylindrical, slightly widening towards apex; pedicel about 0.15 mm long, slightly widening distally; occipital carina present and complete.

Mesosoma 1.4 mm long and 1.6 mm high (in lateral view), with pleura smooth; pronotum short; notauli simple, faintly impressed, converging posteriorly, but well separated posteriorly; medial line faint reaching about  $0.4 \times$  mesoscutum length. Forelegs femur about 0.80 mm long, tibia about 0.83 mm long, with spur bifid, tarsomere lengths (from basitarsus to apex, in mm): 0.62, 0.30, 0.17, 0.1, 0.15. Midlegs with femur 0.92 mm long, tibia 1.01 mm long, tarsomere lengths (from basitarsus to apex, in mm): 0.62, 0.27. Hind leg distinctively longer than fore- and mid-legs; femora 1.52 mm long, slightly swollen medially; tibia about 1.78 mm long, slightly widening towards apex.

Forewing 3.25 mm long and 1.25 mm wide; pterostigma broadest at level of 2r-rs (about 0.1 mm wide); costal cell distinctively broader than C, widening towards apex; radial cell distinctly longer than wide; 1M slightly arched; Rs+M faintly sigmoidal; submarginal cell pentagonal about  $2.25 \times$  longer than wide; 2r-rs  $1.13 \times$  longer than 2Rs; marginal cell about  $3.25 \times$  longer than wide; 3Rs more than  $3 \times$  the length of 4Rs; first medial cell more about  $3 \times$  longer than wide; 2M extremely short, shorter than 2cu-a ( $0.27 \times$ ); second submarginal cell about twice longer than wide; 2rs-m anteriorly 2m-cu along M; maximal length of third submarginal longer than its width, 4M shorter than 5M; 6M ending free in wing membrane; second medial cell about  $2.26 \times$  longer than wide, with 2m-cu and 3Cu nearly straight; 4Cu ending free in wing membrane.

Hind wing about 1.8 mm long and 0.6 mm wide, with three basal hamuli and at least three distal

present along C; 1Rs about four times longer than rs-m; 1Cu distinctly arched toward wing posterior margin, longer than cu-a; no free abscissa of Rs distad rs-m; M and Cu free abscissae present distad rs-m and cu-a crossveins.

Metasoma with petiole about 0.6 mm long, petiole slightly widening ventrally in its distal half; gaster conical, narrow, about 2.3 mm long (genitalia excluded), length of measurable sternites of gaster (in mm, from base to apex): about 0.51, 0.41, 0.32, 0.51, 0.43; all sternites widening and shortening towards apex; parameres longer than wide, paddle-shaped, protruding from abdomen for about 0.3 mm.

#### 4. Discussion

The presence of specific wing venation features, such as 2m-cu, 2rs-m, and 3rs-m, alongside distinct morphological characteristics like numerous antennomeres, has raised doubts regarding the classification of the genus *Mesevania* Basibuyuk & Rasnitsyn, 2000 within the family Evaniidae (e.g., Basibuyuk et al., 2000; Jouault, 2023; Jouault and Rosse-Guillevic, 2023). Further supporting its reclassification in the Praeaulacidae is the similarity in terms of wing venation observed between the praeaulacid genus *Paleosyncrasis* Poinar, 2019, *Mesevania*, and an as-yet-undescribed praeaulacid specimen discovered in mid-Cretaceous Kachin amber (C.J. pers. obs.). As a result, we propose reclassifying *Mesevania* within the family Praeaulacidae, designating it as a Praeaulacinae rather than an evaniid wasp.

The placement of *Mesevania* within the subfamily Praeaulacinae is supported by the lack of two-segmented petiole (vs. present in Nevaniinae), and M+Cu longer than the combined length of the veins 1Rs and 1M (vs. shorter). Similarly, its thin pterostigma (vs. wide in Cretocleistogastrinae), a crossvein 3rs-m completely preserved (vs. completely lost), and a 2M well developed (vs. never present) prevent a placement within the subfamily Cretocleistogastrinae.



## 5. Conclusion

The past diversity of evanioid wasps remains underestimated, a fact underscored by the discovery of *Sinuevania pouilloni* sp. nov. and *Praegastrinus edithae* gen. et sp. nov. Our recent examinations of institutional collections containing French Cretaceous amber provide further evidence for this assertion, as we have identified previously undocumented evaniid specimens (e.g., *Cretevania*). These findings promise to improve our knowledge regarding the past distribution and diversity of various genera. The mid-Cretaceous Kachin amber is a key deposit to unravel the evolution of this family and more broadly of the superfamily Evanioidea. This deposit is extremely interesting in that it contains representatives from both the stem and crown groups of the Evanioidea. The description of *Sinuevania pouilloni* sp. nov. clarifies the forewing venation of the genus and lets us assume that it belongs to the stem Evaniidae, primarily due to its complex forewing venation, which reflects plesiomorphic characteristics reminiscent of those observed in the Praeaulacidae. The description of *Praegastrinus edithae* gen. et sp. nov. with a unique bilobed frontal ledge suggests that the morphological diversity of evanioid wasps is much higher than previously estimated. This particular character may be indicative of a proximity with the Othniodellithidae, but this needs to be tested in a robust phylogenetic framework. Nonetheless, comprehensive studies are imperative to gain a more profound understanding of the evolution of the Evanioidea during the Cretaceous period.

## Disclosure of interest

The authors declare that they have no competing interest.

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Figure captions:

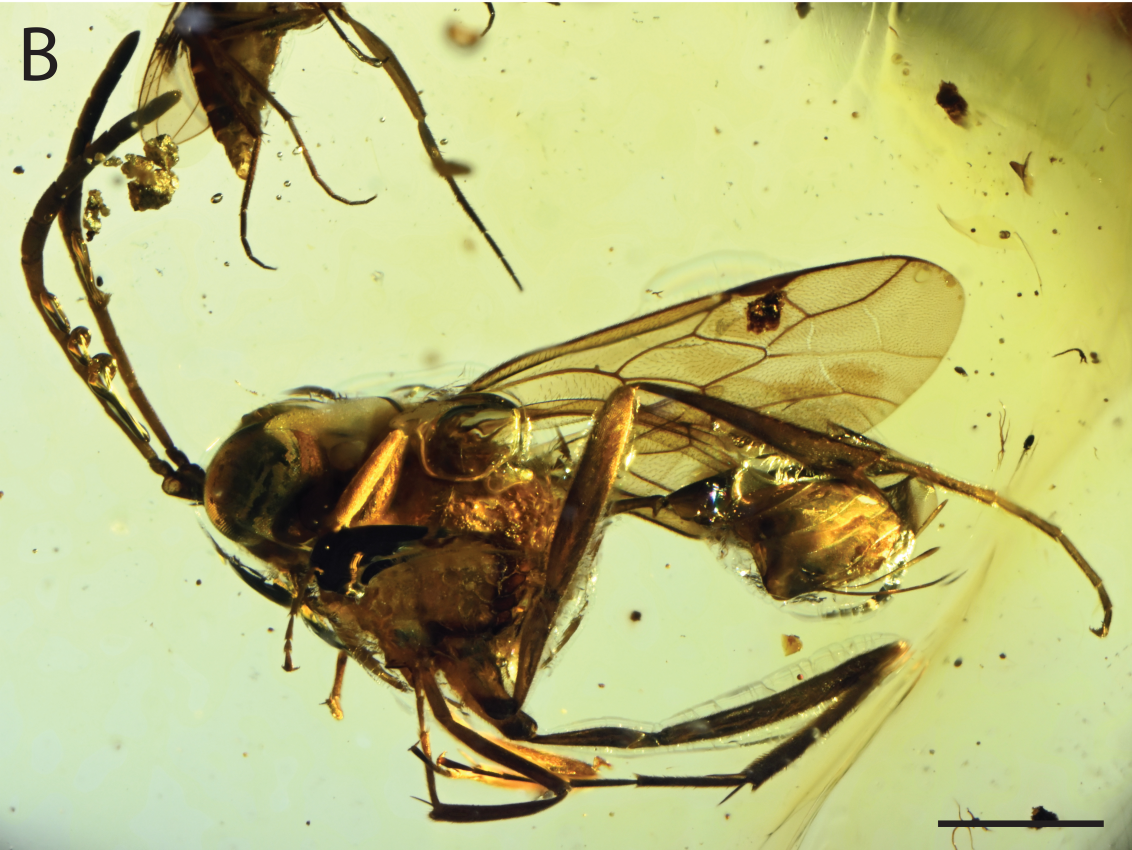




Figure 1. *Sinuevania pouilloni* sp. nov., holotype IGR.BU-085 (JMP018). A: Habitus in right lateral view; B: Habitus in left lateral view. Scale bars = 1 mm.

*Sinuevania pouilloni* sp. nov., holotype IGR.BU-085 (JMP018). A: Habitus en vue latérale droite;

B: Habitus en vue latérale gauche. Barres d'échelles = 1 mm.

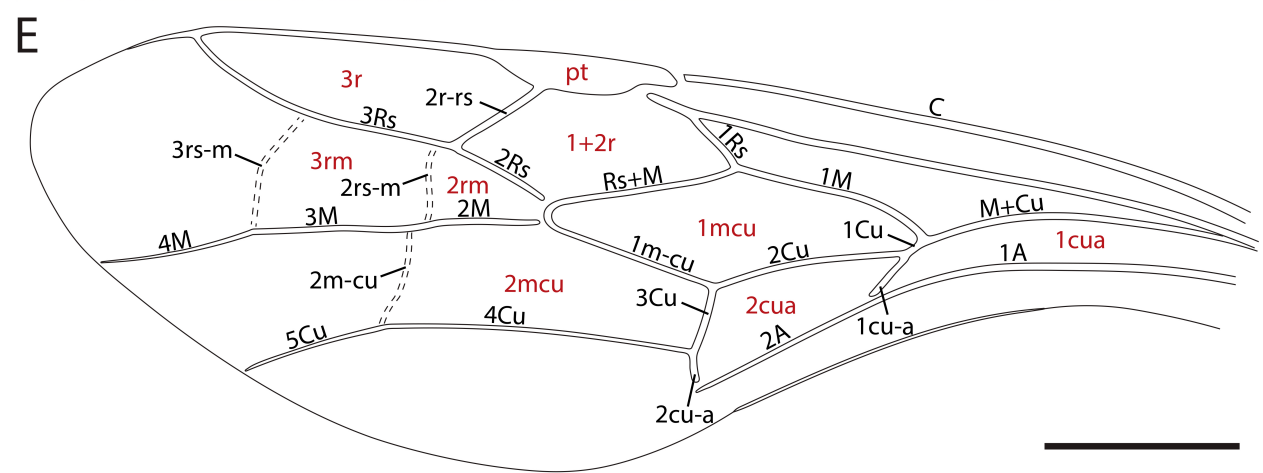
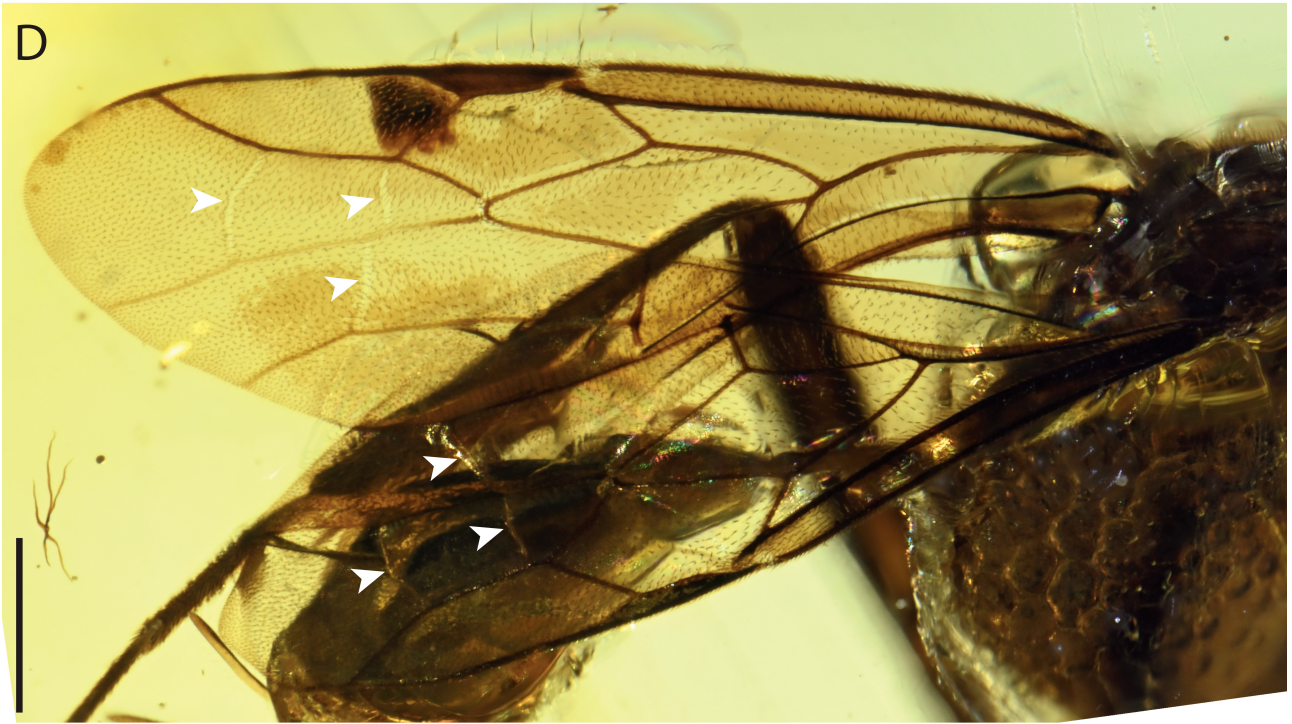
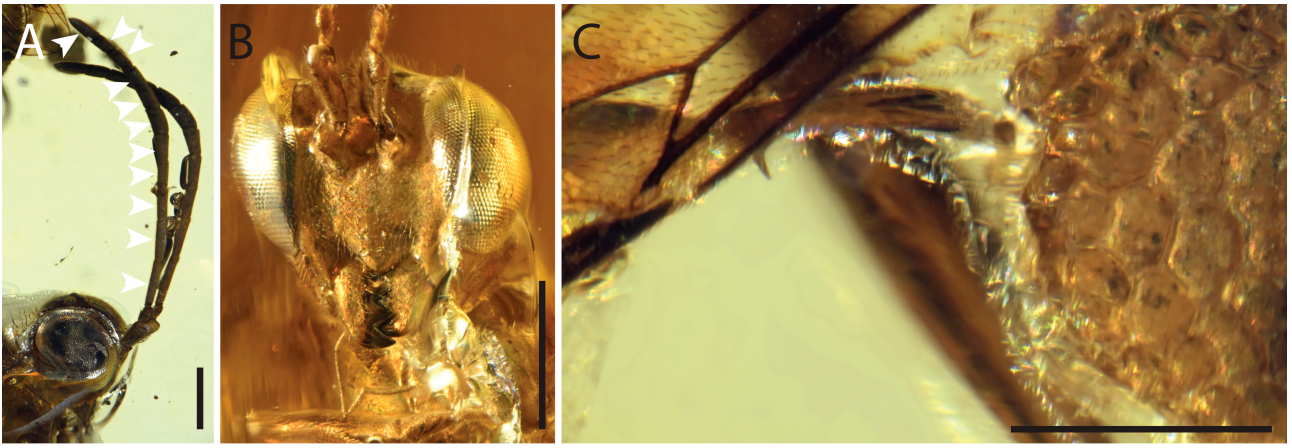


Figure 2. *Sinuevania pouilloni* sp. nov., holotype IGR.BU-085 (JMP018). A: Detailed view of antennae (arrows pointing to flagellomeres); B: Full-face view; C: Detailed view of propodeum and of petiole; D: Detailed view of the forewing venation (arrows pointing to veins 2rs-m, 3rs-m, and 2m-cu); E: Interpretative drawing of forewing venation with names of veins (dark) and cells (red) labelled. Scale bars: 0.5 mm.

*Sinuevania pouilloni* sp. nov., holotype IGR.BU-085 (JMP018). A: Vue détaillée des antennes (flèches pointant les flagellomeres); B: Vue de face; C: Vue détaillée du propodeum et du pétiole; D: Vue détaillée de la nervation de l'aile antérieure (flèches pointant les veines 2rs-m, 3rs-m, and 2m-cu); E: Dessin interprétatif de la nervation de l'aile antérieure avec les noms des nervures (noir) et des cellules (rouge) indiqués. Barres d'échelles = 0.5 mm.



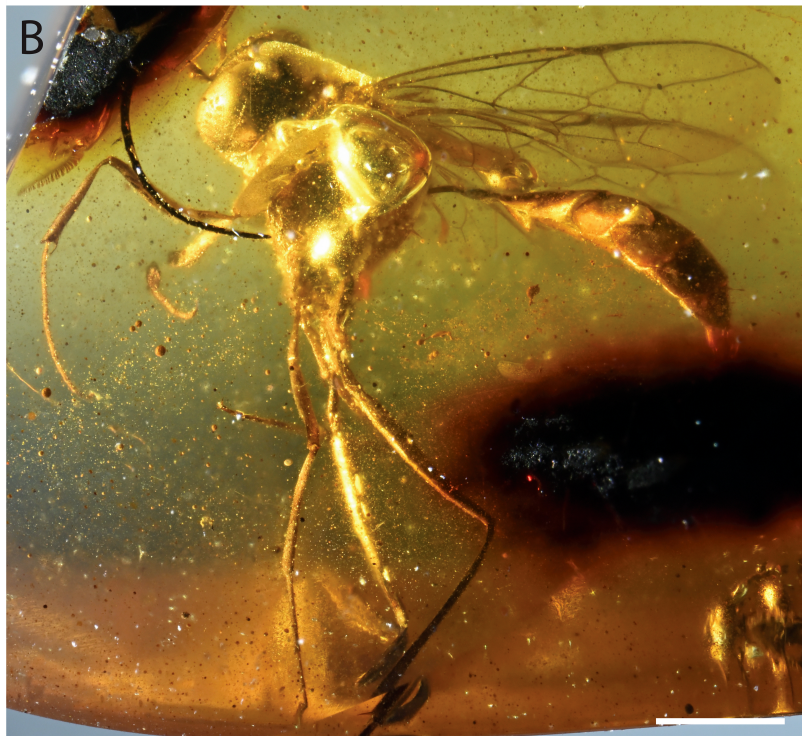
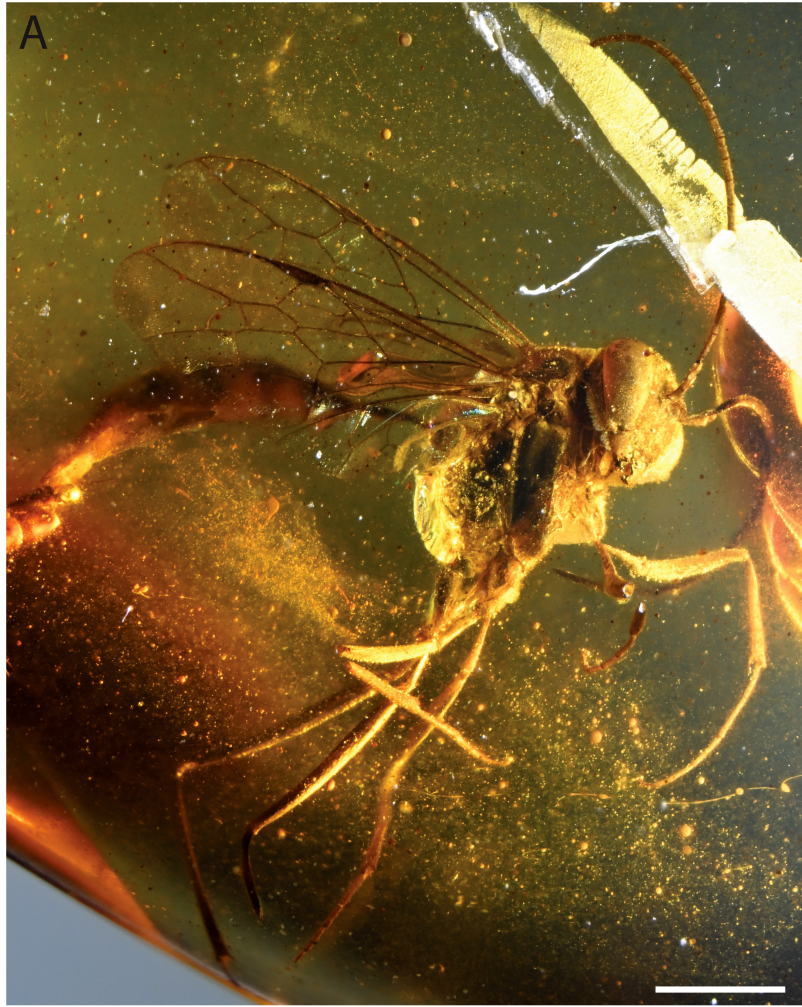


Figure 3. *Praegastrinus edithae* gen. et sp. nov., holotype IGR.BU-086 (JMP099). A: Habitus in right lateral view; B: Habitus in left lateral view. Scale bars: 1 mm.

*Praegastrinus edithae* gen. et sp. nov., holotype IGR.BU-086 (JMP099). A: Habitus en vue latérale droite; B: Habitus en vue gauche droite. Barres d'échelles = 1 mm.



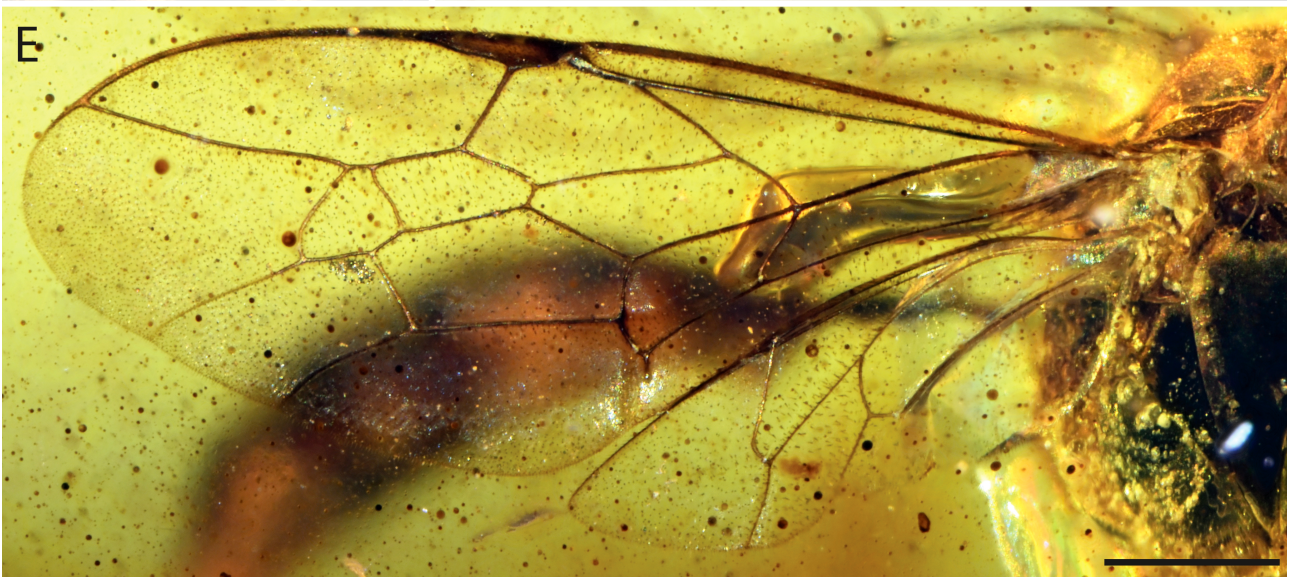
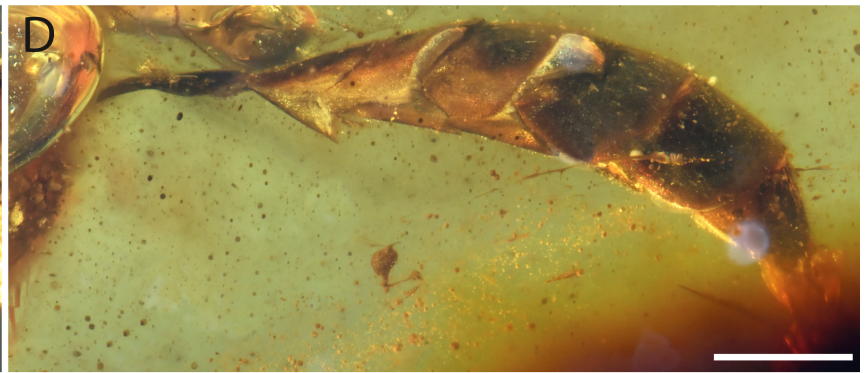
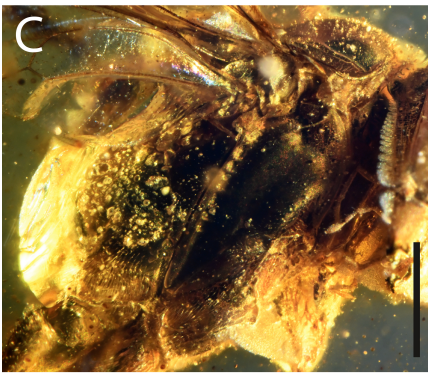
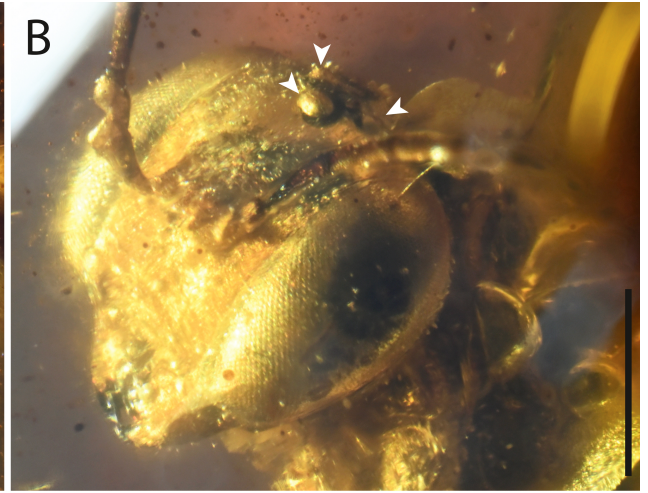
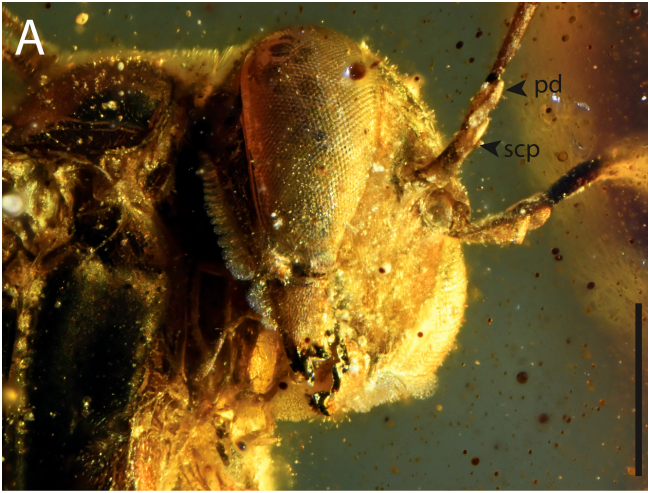


Figure 4. *Praegastrinus edithae* gen. et sp. nov., holotype IGR.BU-086 (JMP099). A: Detailed view of head (in right lateral view), with pedicel (pd) and scape (scp) indicated by dark arrows; B: Detailed view of head (in top left view), with ocelli indicated by white arrows; C: Detailed view of mesosoma in right lateral view; D: Metasoma in left lateral view; E: Detailed view of fore- and hind wing venations. Scale bars: 0.5 mm.

*Praegastrinus edithae* gen. et sp. nov., holotype IGR.BU-086 (JMP099). A: Vue détaillée de la tête (en vue latérale droite), avec le pedicel (pd) et le scape (scp) indiqués pour des flèches noires; B: Vue détaillée de la tête (en vue de dessus gauche), avec les ocelles indiqués par des flèches blanches; C: Vue détaillée du mesosoma en vue latérale droite; D: Metasoma en vue latérale gauche; E: Vue détaillée de la nervation des ailes antérieure de postérieures. Barres d'échelles = 0.5 mm.

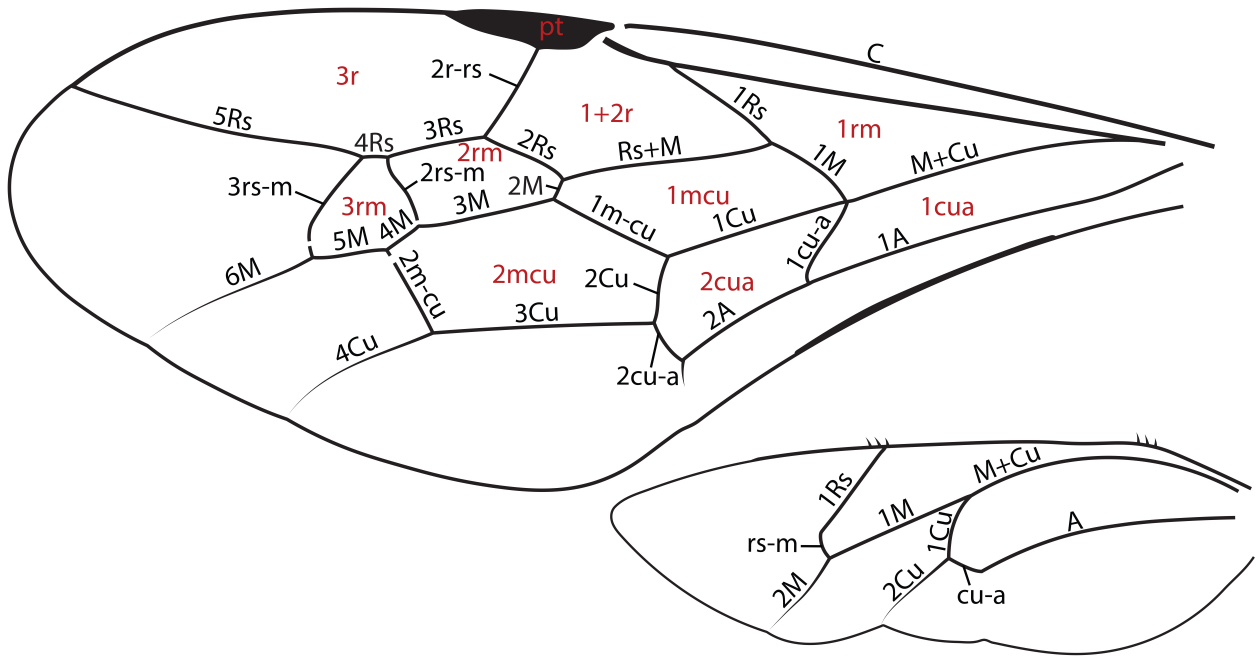




Figure 5. *Praegastrinus edithae* gen. et sp. nov., holotype IGR.BU-086 (JMP099). Interpretative line drawings of fore- and hind wing venations with names of cells (in red) and veins (in black) labelled. Scale bar: 1 mm.

*Praegastrinus edithae* gen. et sp. nov., holotype IGR.BU-086 (JMP099). Dessin interprétatif de la nervation des ailes antérieures et postérieures avec les noms des cellules indiqués en rouges et ceux des nervures en noir. Barre d'échelle = 1 mm.