



A new lineage of evaniiform wasps in Cretaceous amber from Myanmar (Hymenoptera: Evanioidea)

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Abstract

Evanioidea are distinctive parasitoid wasps with a comparatively rich fossil record extending to at least the Late Jurassic. Here we report a remarkable mid-Cretaceous species belonging to the clade Evaniiformes, exhibiting a mosaic of features characteristic of Evaniidae alongside traits more typical of plesiomorphic lineages outside of the evaniiforms. *Antevania hirsuta* gen. et sp. nov. is described and illustrated from a well-preserved female preserved in amber from Kachin, northern Myanmar. The genus is placed within the new family Antevaniidae fam. nov., and comparisons are provided with other living and fossil Evaniiformes, together with brief comments on its potential parasitoid biology.

Keywords: Cenomanian, Evaniidae, Evanioidea, Kachin, parasitoid, taxonomy

Introduction

The parasitoid wasp superfamily Evanioidea comprises three extant families, most readily recognized by the high articulation of the metasoma on the propodeum, positioned dorsally and variably separated from the more vertical posterior surface (Kieffer, 1912; Crosskey, 1951; Mason, 1993). Extant diversity is modest: Aulacidae include roughly 200 species, Gasteruptionidae slightly more than 500, and Evaniidae nearly 600. Aulacidae are endoparasitoids of wood-boring beetles or xiphydriid wood wasps, evaniids parasitize roaches, and Gasteruptionidae attack solitary bees and aculeate wasps (Gauld, 1995a, b; Huben, 1995; Jennings & Austin, 2004; van Noort & Broad, 2024). Among these, Evaniidae—commonly called ensign wasps—are distinguished by their reduced, laterally compressed, disklike metasoma, reminiscent of a ship's flag.

Despite their limited modern diversity, evanioids possess a rich fossil record, extending from the Late Jurassic to the Neogene (Grimaldi & Engel, 2005; Li *et al.*, 2018; Jouault *et al.*, 2021). Much of their early history is represented by an extensive stem assemblage of extinct lineages (e.g., Rasnitsyn, 1972; Zhang & Rasnitsyn, 2008; Oberprieler *et al.*, 2012; Engel, 2017; Li *et al.*, 2018; Jouault *et al.*, 2021), although early representatives of all three families are known by at least the mid-Cretaceous (e.g., Engel, 2017; Engel & Wang, 2016; Turrisi & Ellenberger, 2019). The clade Evaniiformes comprises the extant Evaniidae (Engel, 2017), traditionally defined by the “flaglike” gaster borne on a thin tubular petiole, reduced forewing venation (seven or fewer closed cells), and the absence of hind wing venation, among other traits (Kieffer, 1912; Crosskey, 1951; Mason, 1993; Huben, 1995). Several fossil genera conflict with this circumspection and are best regarded as stem groups (e.g., *Lebanevania* Basibuyuk & Rasnitsyn in Basibuyuk *et al.*, 2002; *Sinuevania* Li, Rasnitsyn, & Ren in Li *et al.*, 2018) relative to the crown clade of extant species.

Here we describe a remarkable new evaniiform family from mid-Cretaceous Kachin amber. The fossil, a well-preserved female in a largely clear piece of amber, exhibits a striking combination of plesiomorphic traits (e.g., non-geniculate antennae with a short scape, complete forewing venation, a greatly elongate ovipositor) with some noteworthy apomorphies (e.g., a long, arched basal typical of most Evaniidae; a distinctly separated jugal lobe). As in ensign wasps, the metasoma is laterally compressed and reduced to a disklike form articulating via a thin tubular petiole. The family, genus, and species are described and illustrated herein. We regard evaniiforms with complete wing venation as lying outside Evaniidae proper and, like the family described here, representing stem groups to the crown clade. Although phylogenetic relationships have been explored by several authors

(e.g., Li *et al.*, 2018; Jouault *et al.*, 2021), substantial discrepancies among proposed topologies highlight the need for further work and the likelihood that considerable extinct diversity remains undocumented. Indeed, each new fossil seems to blur the boundaries of Evaniidae (e.g., the debated inclusion of *Lebanevania*), and the present specimen would only exacerbate the confusion if forced into the family despite its elongate, coiled ovipositor and complete wing venation. Restricting Evaniidae to its traditional circumscription may therefore aid the practical delimitation of lineages within Evanioidea.

Material and methods

A single female of a remarkable evanioid (Fig. 1) was discovered in an ovoid piece of mid-Cretaceous (Cenomanian) amber from the mines around Tanai, Kachin, northern Myanmar. The long surfaces of the amber are uneven, slightly impacting some views. Further trimming and polishing was impossible owing to the closeness of the wasp to the amber surface on one side, and the closeness of a spectacular lacewing larva on the other (Fig. 1). A direct frontal view of the wasp is not possible owing to the position of the lacewing larva directly in front and slightly toward the opposing surface. The specimen is deposited in the vast amber collection of the Dr Peretti Museum Foundation, Meggen, Switzerland (PMF). The material was studied using a Nikon SMZ 1500 stereomicroscope and photographed and measured using a Keyence VHX-7100 digital microscope at the American Museum of Natural History, as well as a Keyence VHX-7000 in the PMF. The format and terminology generally follow that of Engel (2017).

Systematic palaeontology

Superfamily Evanioidea Latreille, 1802

Clade Evaniiformes Grimaldi & Engel, 2005

Antevaniidae fam. nov.

Type genus. *Antevania* gen. nov.

Diagnosis. Body densely hirsute on head (including mandibles), lower half of mesosoma, and legs. Head not compact against mesosoma, moveable on short neck; compound eyes large, ovoid, glabrous, nearly as wide as gena; ocelli in tight equilateral triangle at front of summit of head, separated from compound eye by at least 3× ocellar diameter, separated from each other by ocellar diameter; antenna not geniculate, with 13 antennomeres; scape short, length 2.6× width, shorter than flagellomere

l; occipital carina present and complete; malar space long, about as long as basal mandibular width; mandible densely hirsute; five maxillary palpomeres, basal palpomere tiny, remainder elongate, with third palpomere longest; three labial palpomeres.

Pronotum wholly declivitous, without defined collar, with short anterior neck, forming flat squarish plate abutting mesoscutum; mesoscutum with notauli complete but widely separated posteriorly, median mesoscutal sulcus absent.

Legs slender and long, with abundant long, erect setae; tibial spur formula 1-2-2, protibial spur slightly arched with minutely bifurcate apex; pretarsal claws with minute subapical tooth, arolium small.

Forewing venation comparatively complete, with 10 closed cells, marginal cell large, with apex pointed on anterior wing margin, 5Rs not strongly arching anteriorly, deep M+Cu fork and 1M long and gently arched; 1rs-m, 2rs-m, and 2m-cu present and tubular although unpigmented; 1cu-a strongly postfurcal. Hind wing with venation reduced to simple C+Sc+R; 3 distal hamuli; with deeply excised jugal lobe (partly bent forward and overlapping posterior of vannus as preserved).

Metasoma articulating to dorsal-facing surface of metasoma, articulation more widely separated from metanotum than angle to posterior-facing surface of propodeum; metasomal petiole long, slightly longer than gaster, tubular, with tergum and sternum fused; gaster reduced and slightly ovoid, laterally compressed; ovipositor elongate, much longer than body, coiled around metasoma, apex undulate-serrate.

Antevania gen. nov.

Type species. *Antevania hirsuta* sp. nov.

Etymology. The new genus-group name is a combination of the Latin preposition *ante*, meaning, “before”, and *Evania* Latreille, type genus of the superfamily. The gender of the name is feminine.

Diagnosis. As for the family (*vide supra*).

Antevania hirsuta sp. nov.

(Figs 1–4)

Holotype. ♀, PMF Ref. 061356, mid-Cretaceous Tanai amber, Kachin, Myanmar; deposited in the type collection of the PMF, Meggen, Switzerland.

Etymology. The specific epithet is the Latin adjective *hirsūtus*, meaning, “shaggy” or “hairy”, and refers to the dense, long pubescence of the species.

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

Description. ♀: Total body length (face to apex of gaster, as preserved) 5.12 mm; forewing length 4.12 mm. Integument dark brown to black throughout albeit



FIGURE 1. *Antevania hirsuta* gen. et sp. nov., female, holotype (PMF Ref-061356), left lateral habitus, an syninclusion of a large lacewing larva (at left).

lighter on antenna and ovipositor; wing veins dark brown to black, membranes hyaline and slightly infumate; body hirsute, with abundant setae on head, including mandible, mesosoma and legs, and in certain places on metasoma as specified below (in places setae have entangled with minute air bubbles, which at first glance may be mistaken to be pollen).

Head seemingly longer than wide, height (vertex to apex of closed mandibles) 1.45 mm [direct facial view not possible]; occipital carina complete (Fig. 2A); gena slightly broader than compound eye, width 0.40 mm; compound eye large, prominent, ovoid, glabrous (*i.e.*, without setae between ommatidia), length 0.67 mm, width 0.36 mm; ocelli prominent, arranged in small triangle forward on vertex above upper tangent of compound eyes, median ocellus separated from lateral ocelli by ocellar diameter, lateral ocelli separated ocellar diameter and from ocular border by 3× ocellar distance. Malar space long, about as long as basal mandibular width. Face without scapal basin. Antennal toruli separated by slightly less than torulus diameter, separated from compound eye by more than torulus diameter, situated in upper third of compound

eyes, widely separated from base of clypeus; antenna with 13 antennomeres; scape short, length 0.42 mm, width 0.16 mm; pedicel length 0.21 mm, width 0.11 mm; flagellum filiform, flagellomeres each longer than wide; flagellomere I longest, length 0.52 mm, width 0.12 mm; flagellomere II length 0.47 mm, width 0.13 mm; flagellomere III length 0.41 mm, width 0.13 mm; flagellomere IV length 0.41 mm, width 0.13 mm; flagellomere V length 0.39 mm, width 0.13 mm; flagellomere VI length 0.39 mm, width 0.13 mm; flagellomere VII length 0.38 mm, width 0.14 mm; flagellomere VIII length 0.38 mm, width 0.13 mm; flagellomere IX length 0.38 mm, width 0.12 mm; flagellomere X length 0.31 mm, width 0.11 mm; flagellomere XI length 0.39 mm, width 0.09 mm. Clypeus short and faintly arched in profile, supraclypeal area more noticeably arched in profile. Mandible slightly projecting [dentition not visible owing to abundant mandibular setae and orientation]. Maxillary palpus pentamerous, basal palpomere tiny, remainder elongate (Fig. 2A), with third palpomere longest. Labial palpus trimerous, palpomeres long, slender, subequal in lengths.

Mesosoma longer than high (Fig. 1), length 2.51 mm, maximum height 1.23 mm; pronotum without

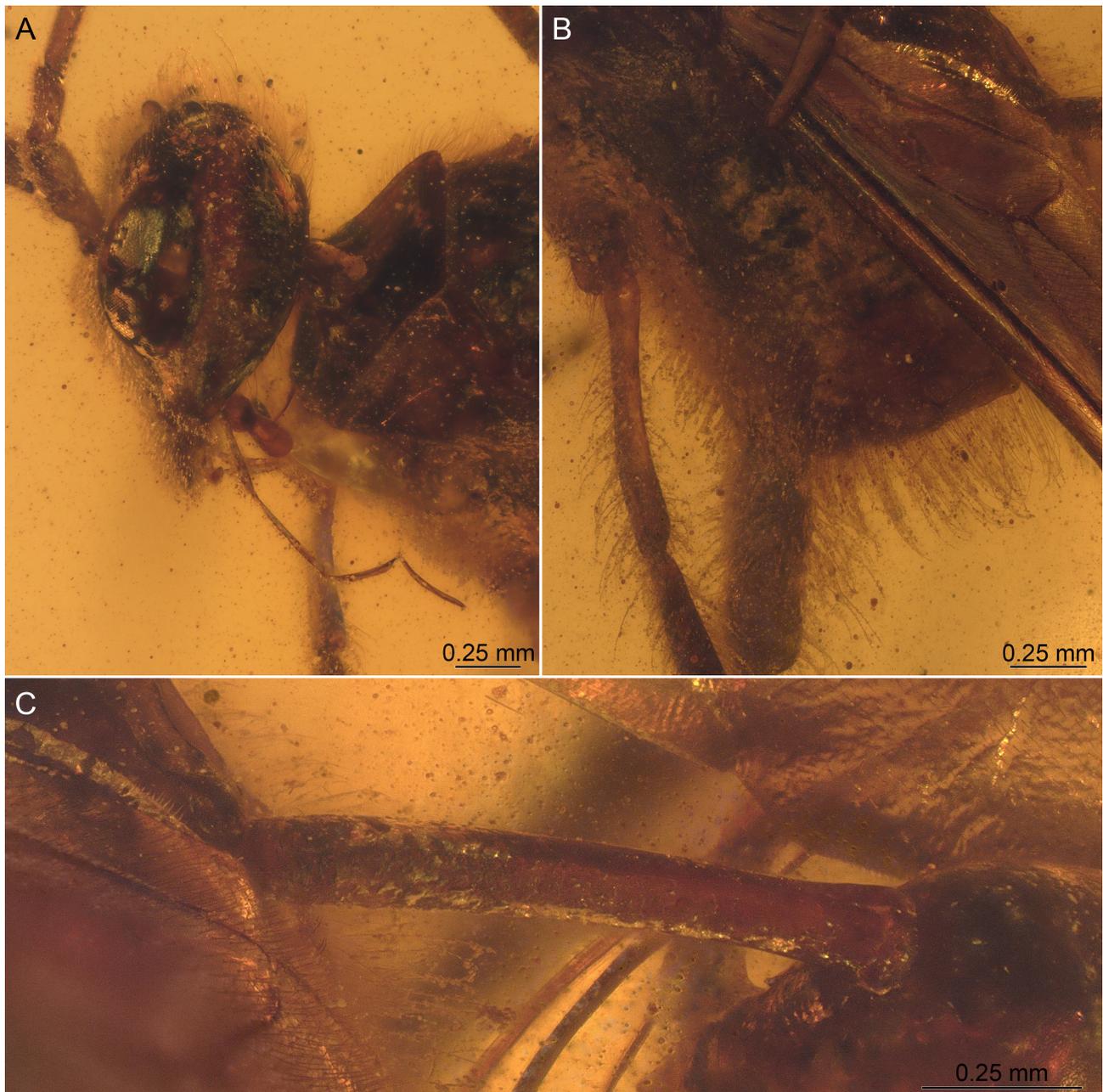


FIGURE 2. *Antevania hirsuta* sp. nov. (PMF Ref-061356). **A**, Left lateral view of head and prothorax. **B**, Detail of setation of mesosomal posterior. **C**, Detail of petiole.

defined, raised posterior dorsal-facing surface bordering mesoscutum, posterior border straight, elevated as thin ridge abutting and slightly above level of mesoscutum, laterally with prominent dorsoventral ridge posteriorly; prothoracic spiracle covered by posterolateral margin of pronotum; lateral surface of pronotum elongate triangular with a single line of weak elongate areolae formed by faint longitudinal ridges in upper portion, seemingly absent in lower portion, dorsal transverse ridge only about 0.75× length of lateral dorsoventral ridge; mesoscutum without transverse carinae or striae, imbricate, median line absent; separated from mesoscutellum by transverse row of small areolae, notauli impressed, complete but not meeting at

midline (widely separated); mesoscutellum slightly arched in profile, seemingly imbricate; metanotum a narrow strip, seemingly imbricate, neither areolate nor foveolate. Mesopleuron depressed in oblique line centrally, perhaps with faint ridging forming line of areolae within, if so, then remarkably faint [challenging to see with setation and darkness of integument], remainder of surface imbricate; metapleuron expanded, surface imbricate rounded and flanked above and behind by areolae of propodeum except short depressed line of areolae extending anteriorly but ending well before anterior margin. Propodeum areolate, with elongate dorsal surface.



FIGURE 3. *Antevania hirsuta* sp. nov., holotype (PMF Ref-061356). **A**, Forewing. **B**, Line drawing of fore- and hind wing venation.

Legs long (Fig. 1), with slender podites; metacoxa without distal lobe; pro- and mesotrochantelli indistinct; metatrochantellus + metafemur length 2.79 mm; tibial spur formula 1-2-2, protibial calcar minutely bifid apically, mesotibial spurs asymmetrical, one short, one long; metatibial spurs elongate, inner slightly longer than outer; metatibia length 2.12 mm, metatibia with thickened, narrow lamella on apical third of inner margin subapically; protarsomere IV shortest tarsomere [meso- and metatarsi incompletely preserved]; pretarsal claws with minute subapical tooth, arolium minute.

Forewing venation (Fig. 3) strong and complete, with 10 closed cells; costal cell comparatively wide; marginal cell large, broad, terminating on anterior wing margin and apex separated from wing apex by distance nearly equivalent to pterostigmal length; three submarginal cells, with first submarginal cell largest, second submarginal cell trapezoidal and exceptionally narrow on anterior margin, third submarginal cell squarish; second medial cell elongate rectangular; second cubital cell slanted

squarish; M+Cu forking greatly proximad relative to origin of 1Rs; 1M elongate, gently arching to meet 1Rs at distinct angle; 1Rs sloping proximally, separated from pterostigma by approximately length of pterostigmal base; r-rs elongate, about as long as pterostigma, 3Rs exceptionally short, about 2× vein width; 4Rs longer than r-rs; 5Rs not arching strongly to anterior wing margin, instead tapering slowly to marginal cell apex, with slightly curve in apical half; R extending along anterior wing margin well beyond marginal cell apex; 2Rs kinked medially; 2M exceptionally short, transverse; 3M and 4M forming comparatively straight line; distal abscissa of M terminating before wing margin; 1m-cu meeting second submarginal cell close to cells base; 1rs-m and 2rs-m comparatively straight, tubular, unpigmented; 1Cu shorter than 1cu-a; 1cu-a long, thus cubital cells comparatively broad; 2Cu longer than 3Cu; 2cu-a closing second cubital cell; elongate; 2m-cu straight, tubular, unpigmented; distal abscissa of Cu terminating prior to wing apex. Hind wing venation reduced to simple C+Sc+R; 3 distal

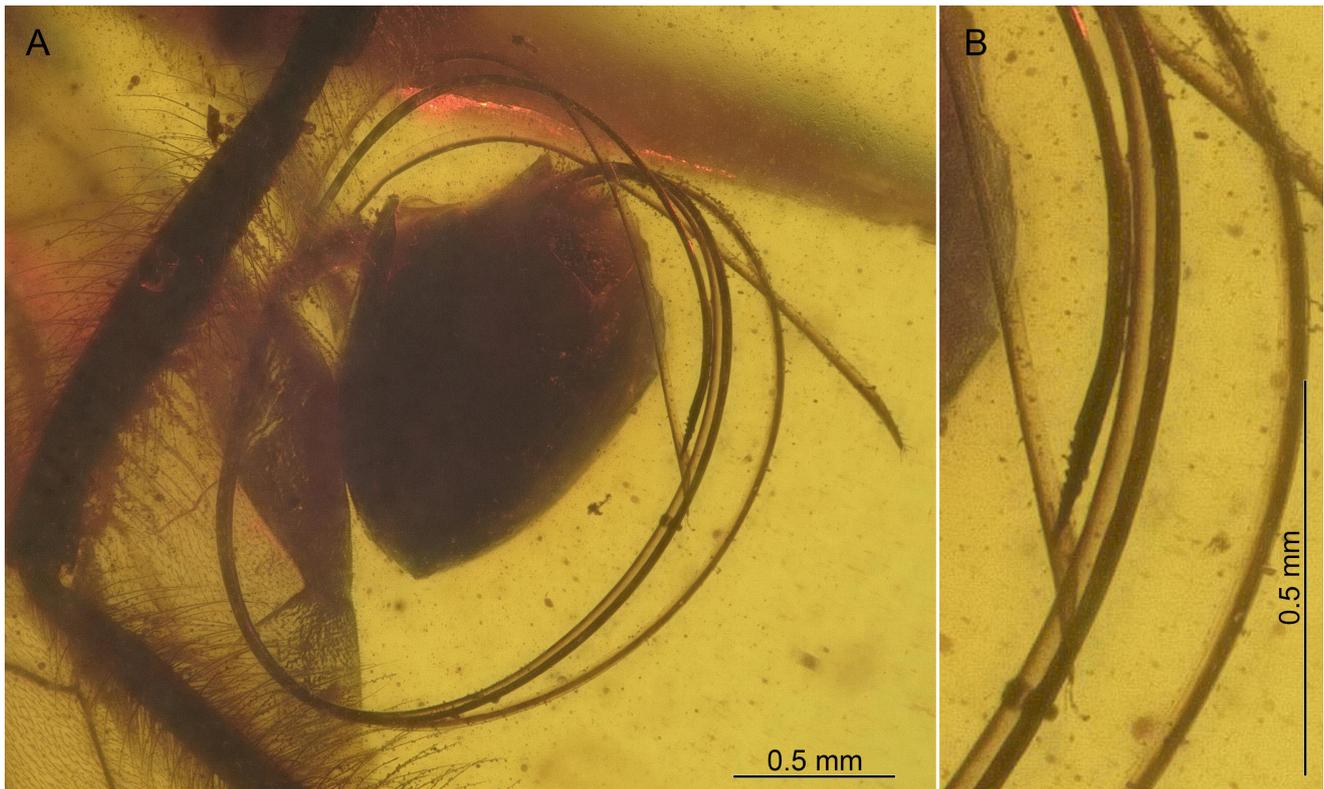


FIGURE 4. *Antevania hirsuta* sp. nov., holotype (PMF Ref-061356). **A.** Detail of metasoma with coiled ovipositor. **B.** Detail of ovipositor apex.

hamuli; jugal lobe deeply excised (partly bent forward and overlapping posterior of vannus as preserved).

Metasoma articulating on dorsal-facing surface of propodeum (Fig. 1) and more widely separated from metanotum than angle to posterior-facing surface of propodeum. Petiole elongate, slender (Fig. 2C), length 1.07 mm, width 0.12 mm, cylindrical, with faint transverse striations or rugae, more evident anteriorly and seemingly absent posteriorly, glabrous, tergum and sternum fused; gaster laterally compressed, slightly ovoid disk-shaped, length 0.97 mm, height 1.22 mm, largely smooth with sparsely scattered minute setae except terga IV and V with line of short, erect setae along midrib of disc and tergum VI with abundant discal setae, especially elongate along apical margins near ovipositor. Ovipositor and sheaths elongate, coiled once around gaster and then projecting posteriorly (Figs. 1, 4), ovipositor length 7.63 mm, apex undulate-serrate (Fig. 4B).

Pubescence appearing shaggy (Figs 1, 2B); face with abundant short, inclined setae nearly obscuring integument, such setae extending on to mandible and especially dorsal and lateral surfaces (Fig. 2A); such setae erect on vertex and slightly longer, gradually becoming sparser on posterior of head above occipital carina; gena nearly bare. Mesosoma with pubescence similar to that of vertex except sparser to nearly glabrous on

anterior-facing surface of pronotum and shorter setae on mesoscutum, mesoscutellum, and horizontal surface of propodeum, and sparser on upper portions of meso- and metapleura; longer setae of ventral portions of mesosomal pleura becoming elongate on lateral surface posteriorly and posterior surface of propodeum. Legs with abundant, mostly erect setae; procoxa to profemur with short to long shaggy setae, those setae on ventral surfaces of protrochanter and especially profemur longer relative to setae on opposing surfaces, protibia and tarsomeres with dense, minute, nearly decumbent setae, tarsomeres with apicolateral thicker, slightly longer setae; midleg similar to foreleg except mesotibia with some sparse, long, erect setae; metacoxa to metafemur with elongate, erect, shaggy setae like those of propodeal posterior surface, such setae on all surfaces, those of metafemur especially elongate, metatibia similar to metafemur except setae of dorsal surface shorter and more inclined apically, those of ventral surface like those of metafemur, metabasitarsus with short, inclined setae dorsally, longer, slightly thicker, inclined setae ventrally; petiole glabrous; gaster with sparsely scattered minute setae except terga IV and V with line of short, erect setae along midrib of disc and tergum VI with abundant discal setae, especially elongate along apical margins near ovipositor.

♂: *Latet.*

Discussion

The present fossil is readily assignable to Evanioidea by the articulation of the metasomal petiole on the dorsally facing surface of the propodeum, rather than on the posterior surface above and between the metacoxae (Crosskey, 1951; Mason, 1993). Within Evanioidea, *A. hirsuta* can be placed in Evaniiformes owing to its slender, cylindrical petiole, widely separated from the metanotal posterior margin, supporting a reduced, laterally compressed, disklike gaster, and the absence of hind wing venation (Jouault *et al.*, 2021). Historically, nearly all evaniiforms were treated as “Evaniidae” in a broad sense, but the considerable heterogeneity among stem groups rendered the traditional concept of the family increasingly confused (*e.g.*, Basibuyuk *et al.*, 2002). The discovery of *A. hirsuta* would only exacerbate this issue: its preaulacine-like forewing and ovipositor contrast with its evaniiform antennomere count (13 or fewer, with the sole exception of the likely misplaced *Mesevania*) and its deeply incised jugal lobe. Moreover, unlike most fossil evaniiforms, *A. hirsuta* possesses an elongate, gently arched forewing 1M, a feature characteristic of crown-group Evaniidae.

The new family Antevaniidae shares several notable traits with Evaniidae, including the aforementioned form of forewing 1M (as in Evaniinae, the clade of all extant Evaniidae), the presence of 13 antennomeres (at least in females), a robust mesosoma, and a deeply incised jugal lobe. In contrast, *A. hirsuta* exhibits a forewing with 10 closed cells—including 1rs-m, 2rs-m, and 2m-cu—more closely resembling the plesiomorphic venation of stem groups to Neoevanioidea (Engel, 2017; Jouault *et al.*, 2021). Indeed, the family is distinguished from all other Evaniiformes by its complete forewing venation and elongate, coiled ovipositor. Antevaniidae share the antennomere count of Evaniinae, *Grimaldivania* Basibuyuk, Fitton & Rasnitsyn, *Newjersevania* Basibuyuk, Quicke & Rasnitsyn, and *Protoparevania* Deans (Basibuyuk *et al.*, 2000b; Deans *et al.*, 2004), and share the presence of three submarginal cells with *Mesevania*, *Lebanevania*, and *Sinuevania* (Basibuyuk *et al.*, 2000a, 2002; Li *et al.*, 2018). These latter genera differ in antennomere number—12 in *Lebanevania*, 13 in *Sinuevania*, and more than 20 in *Mesevania*—and in the distinctive apically widened metatibia of *Mesevania* (Basibuyuk *et al.*, 2000a). Like *Mesevania* and *Sinuevania*, Antevaniidae possess a petiole with fused tergum and sternum, whereas these remain separate in *Lebanevania*, whose nontubular petiole suggests placement outside Evaniidae proper. *Sinuevania* is plesiomorphically most similar to *Antevania*, and one might be tempted to include the genus therein, but the absence of clear

synapomorphies precludes such a move. The elongate ovipositor of *Antevania* is also more plesiomorphic than that of *Sinuevania*, indicating they do not form a clade; their antennae likewise differ markedly (Li *et al.*, 2018). *Cretevania* Rasnitsyn, *Sorellevania* Engel, and Evaniinae all possess reduced wing venation and differ substantially from Antevaniidae in other characters as well (*e.g.*, the strongly triangular marginal cell in *Cretevania* and *Sorellevania*) (Engel, 2006; Pérez-de la Fuente *et al.*, 2012; Jouault, 2023; Li *et al.*, 2018). *Mesevania* is notably “preaulacid-like” and may represent a stem group to Evaniiformes, given its hind wing venation reduced to C+Sc+R and a stem of M+Cu combined with 20 antennomeres (Basibuyuk *et al.*, 2000a). Within a paraphyletic assemblage of preaulacids, this genus might be interpreted as a derived lineage approaching Evaniiformes owing to its thin tubular petiole, disklike gaster (described as “ovate”: Basibuyuk *et al.*, 2000a), and near-complete loss of hind-wing venation.

The possession of an ovipositor and sheaths exceeding body length suggests that the hosts of *A. hirsuta* were deeply concealed, and likely subcortical within living or decaying wood. It is therefore plausible that the species parasitized wood-boring beetle larvae, sharing this biology plesiomorphically with Aulacidae (and perhaps with “preaulacid” lineages). The serrate ovipositor apex further indicated that the valves were adapted for sawing through tough substrates, again consistent with hosts such as xylophagous beetles.

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