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A new genus of the extinct family †Holopsenellidae (Hymenoptera, Aculeata) from the mid-Cretaceous Burmese amber

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Abstract

Aculeata is a clade including all ants, bees, and a large array of stinging wasps. In recent years, the systematics of these groups has been changed substantially by molecular phylogenetics, directly impacting our understanding about their evolution. Regardless, the paleontology of Aculeata still imposes many challenges, including enigmatic groups that cannot be confidently linked to any extant lineage. One of these lineages corresponds to the family †Holopsenellidae, which represents one of the earliest representatives of Aculeata in the fossil record. The single known genus, †*Holopsenella*, was first described from Early Cretaceous Lebanese amber, being also recorded in the younger Burmese amber. In the present work, we describe †*Typhopsenella obscura* **gen. et sp. nov.**, based on an inclusion from Burmese amber, representing the second genus known for the family. This wasp is remarkable for its size, being far larger than †*Holopsenella* and also in relation to the overall size of wasps described from amber inclusions. Further evidence supporting the removal of †Holopsenellidae from Chrysidoidea is raised. Novel records of the family may turn out to be imperative for understanding its phylogenetic affinities among other stinging wasps.

Keywords: fossils, Mesozoic, sting, taxonomy, wasp

Introduction

Stinging wasps (Aculeata) form a diverse group, which comprise all hymenopterans that have modified their ovipositor to deliver venom rather than egg laying (Brothers, 1975). Accordingly, the group includes the ants, the bees, and a large array of predatory and parasitoid wasps exhibiting different behaviors. Aculeata was traditionally split into three superfamilies based on cladistic analyses of morphology: Chrysidoidea, Vespoidea, and Apoidea, with the latter two forming a clade called the Aculeata *s. str.* (Brothers, 1975, 2011; Brothers & Carpenter, 1993). More recently, results from molecular analyses showed that Chrysidoidea and Vespoidea were paraphyletic groups, being split into several smaller superfamilies (Pilgrim *et al.*, 2008; Wilson *et al.*, 2013; Branstetter *et al.*, 2017; Peters *et al.*, 2017; Blaimer *et al.*, 2023). The earliest diverging branches of the Aculeata tree of life are composed of mostly small ectoparasitoid wasps with reduced wing venation, forming the Dryinoidea (*i.e.*, the clade comprising Dryinidae, Embolemidae, and Sclerogibbidae) and the Chrysidoidea *s. str.* (Branstetter *et al.*, 2017; Tang *et al.*, 2019; Pauli *et al.*, 2021; Zhang *et al.*, 2024). Wasp families included originally in the Vespoidea form a grade towards bees and apoid wasps, with the ants (Formicoidea) being the sister group of Apoidea (Johnson *et al.*, 2013; Branstetter *et al.*, 2017; Camacho *et al.*, 2019; Rosa & Melo, 2023).

Regardless of recent improvements brought to our understanding about the evolutionary relationships among stinging wasp families, mainly through molecular phylogenetics, the paleontology of Aculeata still imposes many challenges. The diversification of stinging wasps likely occurred between the Lower Jurassic (Peters *et al.*, 2017; Tang *et al.*, 2019) and the Lower Cretaceous (Blaimer *et al.*, 2023), with fossil stem-lineages recorded as early as the Upper Jurassic (Rasnitsyn, 1988). Cretaceous deposits revealed the earliest known members of extant families, also representing the first records of crown Aculeata (Grimaldi & Engel, 2005; Zhang *et al.*, 2024). One of the most relevant sources of fossil Aculeata is Burmese amber, where many families with uncertain evolutionary affinities have been found (see Zhang *et*

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al., 2018a; Rasnitsyn *et al*., 2020; Lepeco *et al*., 2022). Deposits in Myanmar have been dated between 110 and 99 Ma (Shi *et al*., 2012; Xing & Qiu, 2020), revealing a rich diversity of extinct and extant families of aculeate wasps that coexisted during this specific time-slice in the Burma terrane (Zhang *et al*., 2018b).

One of the most enigmatic groups of stinging wasps found in Burmese amber is the fossil family †Holopsenellidae, which was first described from Lebanese amber (Engel *et al*., 2016). Fossil deposits from Lebanon are an important source of evidence for the earliest evolution of Hymenoptera, since they include some of the earliest records of crown Aculeata (Álvarez-Parra & Azar, 2024; Zhang *et al*., 2024). The Dryinoidea (Dryinidae and Sclerogibbidae) and Chrysidoidea *s. str*. (Bethylidae and Scolebythidae), both representing early diverging lineages among Aculeata, are also recorded in Lebanese amber (Prentice *et al*., 1996; Olmi, 2000; Engel & Grimaldi, 2006, 2007; Azevedo & Azar, 2012). Additionally, there are records of the presence of Ampulicidae in Lebanese amber, even though those putative specimens remain unnamed (Prentice, 1993, 1994; Rosa & Melo, 2023). Therefore, †Holopsenellidae are an important group for understanding the initial diversification of Aculeata, since they represent the earliest definitive record of Aculeata *s. str*. available.

The †Holopsenellidae are currently represented by a single genus, †*Holopsenella*. The genus was originally placed in its own subfamily within the chrysidoid family Bethylidae (Engel *et al*., 2016). Altogether with other bethylid fossils, the genus was considered as an early branching lineage among the flat wasps (Azevedo *et al*., 2018; Engel, 2019; Colombo *et al*., 2020; Jouault *et al*., 2021). However, discovery of new material from Burmese amber revealed that †*Holopsenella* does not belong in Bethylidae, rather being related to Aculeata *s. str*. lineages (Lepeco & Melo, 2022). This positioning is based on the presence of a relatively complete hind wing venation, possession of 10 flagellomeres on the female antenna, reduced number of exposed metasomal segments, among other characteristics that are unusual among Chrysidoidea. Due to the lack of obvious morphological synapomorphies supporting affinities with other clades of Aculeata *s. str*., the precise positioning of the family is still uncertain. These wasps also do not exhibit clear evolutionary affinity to any extant clade within Aculeata *s. str*., possessing the widespread anatomy of parasitoid aculeate wasps attacking insect larvae living in concealed conditions. In the present study, we describe a second genus of †Holopsenellidae, and discuss its implications for our understanding on the identity of the family and about their putative behavior.

Material and methods

The holotype specimen described herein is deposited in the fossil collection at the Department of Zoology of the Universidade Federal do Paraná (DZUP), Curitiba, Brazil, under the care of the second author. The surface of the amber piece was manually trimmed with a goldsmith's saw and ground with wet emery paper (grit sizes between 800 and 3000) by hand. A sanding sponge pad with grit size of 5000 was used for final polishing of the piece. Direct examination of the specimen was performed with a Leica M125 stereomicroscope, and photographs were taken using a Leica DFC295 camera attached to the stereomicroscope. Multiple photographs were taken in different focus levels and the final images were generated by stacking of the photographs in Zerene Stacker 1.4. Illustrations and plate preparations were made in GIMP. Terminology for morphological structures follows Hubber & Sharkey (1993) with amendments introduced in Lepeco & Melo (2022). The flagellomeres of the antenna are indicated as F1, F2, *etc*. Terga and sterna, respectively, are indicated as T1, T2, *etc*., and S1, S2, *etc*.

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Family †Holopsenellidae Engel, Ortega-Blanco & Azevedo, 2016

Genus †*Typhopsenella* gen. nov.
http://zoobank.org/urn:lsid:zoobank.org:act:564EF92B-4891-44FF-806E-3948AA80CB6A

Type species. †*Typhopsenella obscura* **sp. nov.**

Species included. type species only.

Etymology. The name is a combination of "*Typhon*", the name of a monstrous giant creature of Greek mythology and the diminutive form of the Greek word "*psen*", meaning wasp. It is a reference to the relatively large size of the type species in comparison to other wasps included in the family. Gender feminine.

Diagnosis. The new genus exhibits the characteristic morphology of the family (Fig. 1) including the clypeus with a medial reentrance delimiting a pair of lateral lobes; frons projecting dorsally over antennal foramina; propodeum with ventrolateral prominences on its posterior surface; T1 anteriorly crossed by a transverse carina (Fig. 1); among other features indicated in the family diagnosis by Lepeco & Melo (2022). It can be differentiated from the nominal genus of the family by the head globular in lateral view (somewhat triangular in †*Holopsenella*); clypeal lobes not projecting over mandibles (distinctly projecting over mandibles in †*Holopsenella*); hind femur longer and less incrassate, its posteroventral concave surface shallower; posterior margin of S5 slightly incurved medially (strongly incurved in †*Holopsenella*); and S6 entire, not divided into two halves as in †*Holopsenella*. The only specimen known for the genus is also remarkable for its large size in comparison to other specimens recognized in the family.

Description. *Head.* Hypognathous, globular in lateral view (Fig. 2B). Head wider than long. Mandible robust, curved; with a well-marked longitudinal sulcus near dorsal margin (Fig. 3B); distal margin with broad cutting edge bearing four teeth, ventral tooth the sharpest; ventral ridge well developed. Maxillary palp with six palpomeres (Fig. 3A). Labial palp with four palpomeres. Clypeus shortened laterally; surface strongly depressed ventral to antennal foramen; medial portion deeply incurved, with projecting lateral lobe (Fig. 3). Frons produced as a small tab over antennal foramen. Antennal foramina directed ventrad; distanced medially from each other; ventral margin almost confluent with dorsal clypeal margin. Eye rounded, occupying about half of the head length in lateral view (Fig. 2B). Posterior surface of gena gently deepening towards hypostoma (Fig. 2C). Hypostomal bridge well-developed (Figs 2C, 3A). Occipital carina present, complete, halves meeting on posterior region of head (Fig. 2C). Scape nearly cylindrical. Antenna remarkably long, its length nearly reaching posterior region of mesosoma when extended.

Mesosoma. Transition between anterior and dorsal surfaces of pronotum not marked by a carina (Fig. 4A). Propleura with a posterior transverse carina seem from ventral view, posterior region slanting towards articulation with forecoxa (Figs 3A, 5D). Prosternum small, not produced between forecoxae (Figs 3A, 5D). Mesoscutum with well-marked anterior depression on region of contact with pronotum (Figs 1B, 4A). Notauli well developed as sulci; strongly converging posteriorly (Figs 1, 4A). Scutellum with an arched anterior fovea medially; dorsal surface mostly triangular (Fig. 4B). Metanotum not covered by scutellum medially, its length homogeneous throughout. Dorsal surface of propodeum delimited posteriorly by arched carina, lateral corner projected posterad (Fig. 4B), forming a concave posterior surface. Ventral portion of metepisternum not produced between metacoxae (Figs 3A, 5C). Proximal tarsomeres with acutely produced distal corners. Arolia well developed. Coxae and femora robust (Figs 4C, 5C), tibiae and tarsi slender in comparison. Mesocoxae separated by a narrow distance medially (Fig. 3A); articulation with mesepisternum not exposed ventrally (Fig. 5C). Mesotibia with two distal spurs, the anterior slightly shorter than the posterior. Metacoxae separated by a narrow distance medially. Metafemur somewhat swollen, bearing a shallow posteroventral concave surface to receive metatibia. Tegula relatively small. Jugal lobe present on hind wing.

Metasoma. Six exposed segments, each with exposed tergum and sternum. Sulcus on T1 reaching posterior margin of sclerite laterally (Fig. 1). Posterior surface of S1 slanting, separated from the anterior surface by a transverse carina. T2 longer than remaining terga, anterior surface depressed on articulation with T1; lateral surface with a longitudinal sulcus near ventrolateral margin of sclerite. Posterior terga progressively shorter. Anterior surface of S2 depressed on its articulation with S1. Posterior margin of S3 to S4 nearly straight. Posterior margin of S5 arched, without medial cleft. S6 not divided medially (Fig. 5B); posterior margin entire, arched anterad. Sting well-developed, shaft with no apparent curvature.

†*Typhopsenella obscura* sp. nov.

(Figs 1–5)
http://zoobank.org/urn:lsid:zoobank.org:act:EBE906AC-82D4-4256-858F-73866965F53A

Type material. Holotype female, in amber piece DZUP Bur-1642a (Burmese amber).

Preservation: The specimen is almost completely articulated, lacking only some parts of appendages. The right antenna was sanded off distad of the F1. The distal tarsomeres of the right fore and hind legs were sanded off. The tarsus of the left hind leg is detached and could not be found in the piece. The distal portion of the right hind wing was sanded off. The T4 is disarticulated from the T3, even though both sclerites are complete. A small portion of T5 is damaged dorsally. When first examined, the inclusion had an overall dark metallic blue coloration, which deteriorated after the piece was polished and converted to a silvery luster, obfuscating the underlying color. Debris covers various parts of the specimen. Syninclusions: three Acari, as well as a large amount of wood debris.

Etymology. The specific epithet is derived from the Latin, meaning “dark”. The name is an allusion to the color of the specimen and its obfuscation by syninclusions.

Diagnosis. As for the genus.

Locality and horizon. Mid-Cretaceous amber from Hukawng Valley, Kachin State, in northern Myanmar. For references about the age of the putative deposits see Shi *et al*. (2012).

Description. Female holotype. *Measurements*. Approximate body length: 9.8 mm; forewing length: 5.0 mm; medial head length: 1.1 mm; maximum head width: 1.4 mm; intertegular distance: 1.5 mm.

Color. Integument, where preserved, mostly black. Palpi light brown. Antenna dark brown. Legs mostly dark brown, with tibiae and tarsi lighter than preceding articles. Tegula light brown. Wings homogeneously brownish tanned, without distinctly darkened areas; venation and pterostigma dark brown.

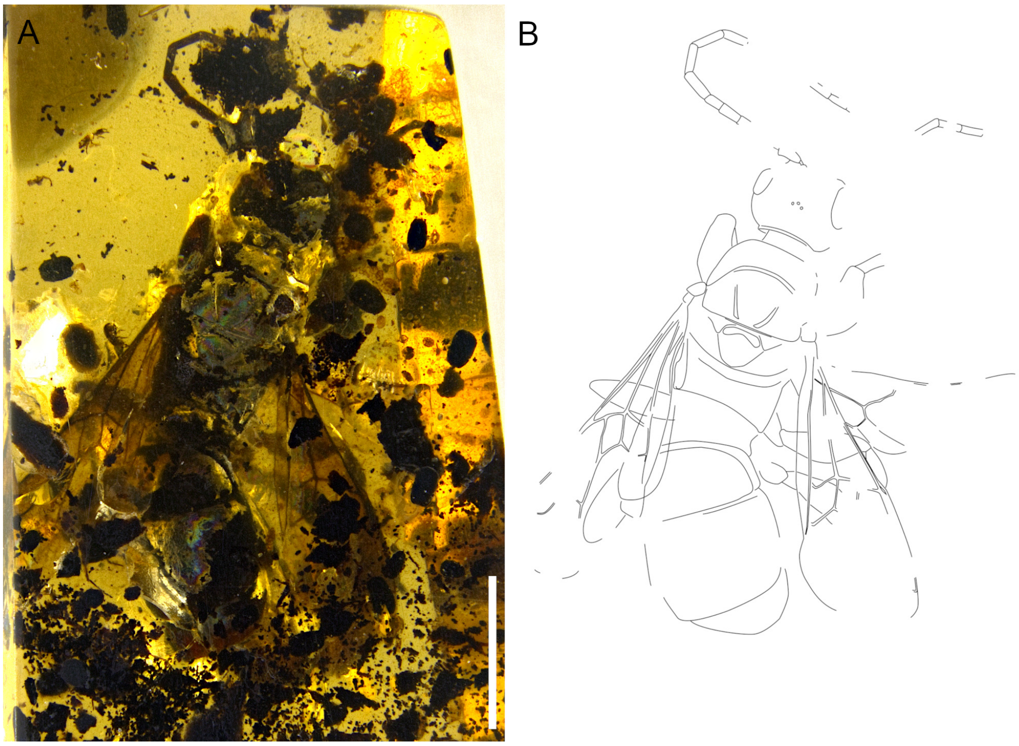

FIGURE 1. Holotype of †*Typhopsenella obscura* **sp. nov.** (DZUP Bur-1642a). **A**, Dorsal habitus. **B**, Line drawing at the same view. Scale bar = 2 mm.

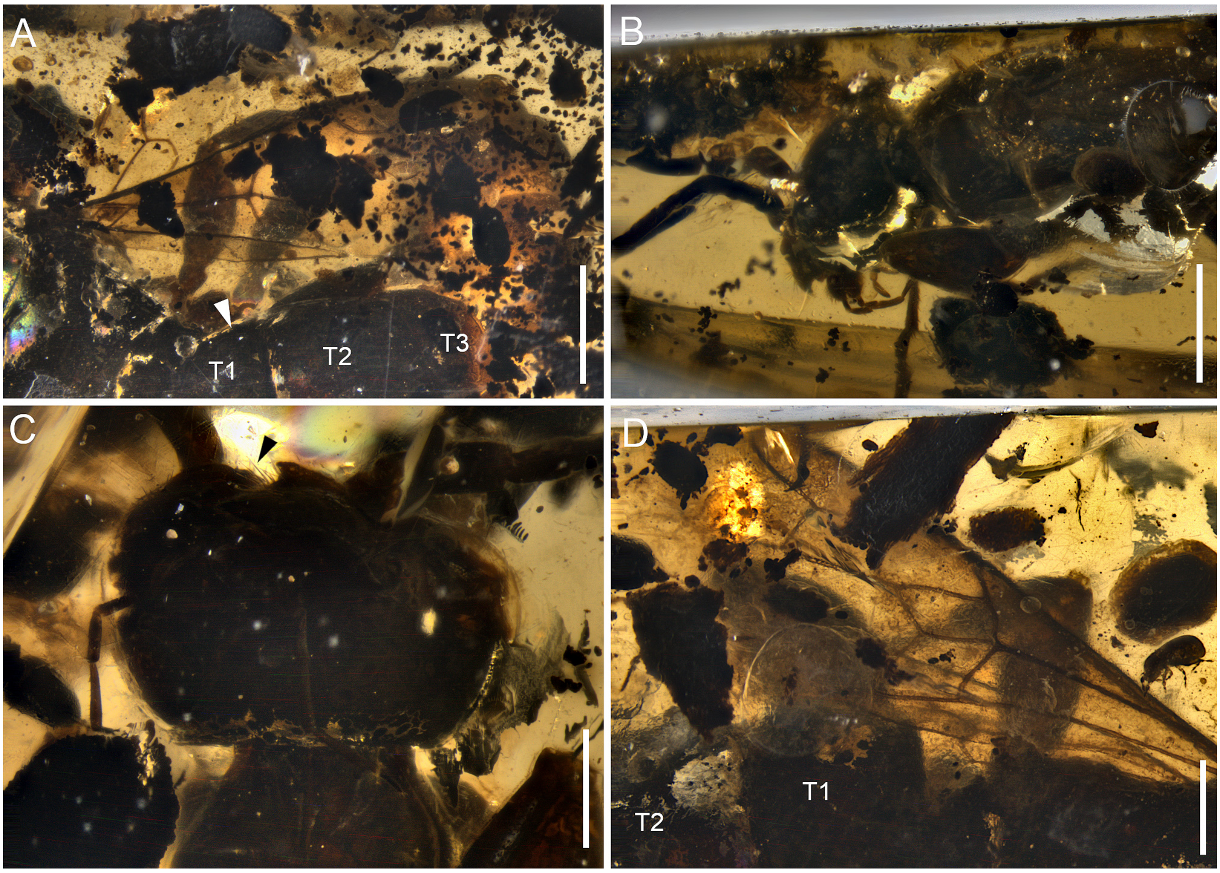

FIGURE 2. Holotype of †*Typhopsenella obscura* **sp. nov.** (DZUP Bur-1642a). **A**, Wings of the right side, the white arrowhead indicates the position of the anterior carina on T1. **B**, Lateral view of head and mesosoma. **C**, Ventral view of head, the black arrowhead indicates the deeply incurved clypeus. **D**, Left forewing. Scale bars = 1 mm (**A**, **B**); 0.5 mm (**C**, **D**).

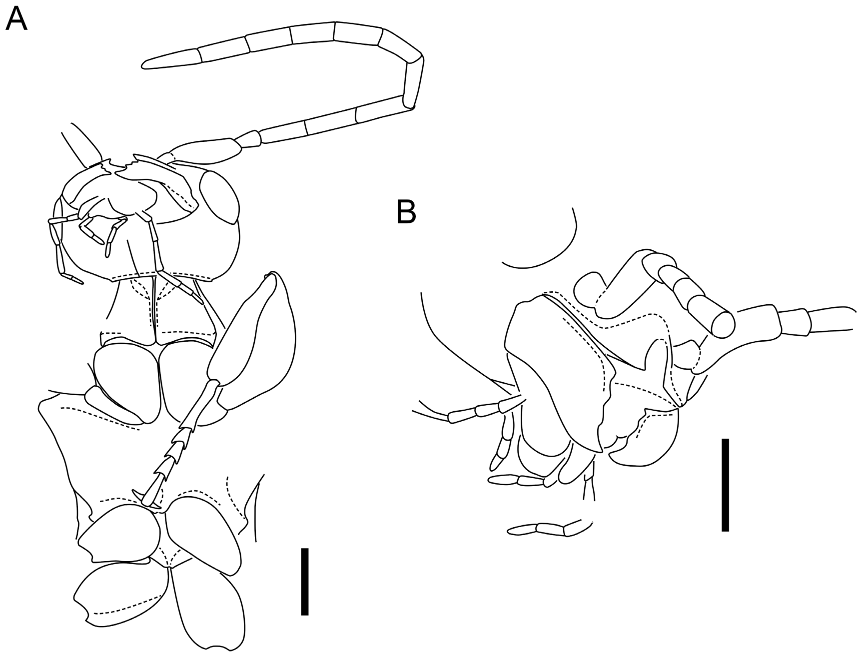

FIGURE 3. Line drawings of †*Typhopsenella obscura* **sp. nov.** (DZUP Bur-1642a). **A**, Ventral view of head and mesosoma. **B**, Anterolateral view of head, showing the structure of clypeus and mouthparts. Scale bars = 0.5 mm.

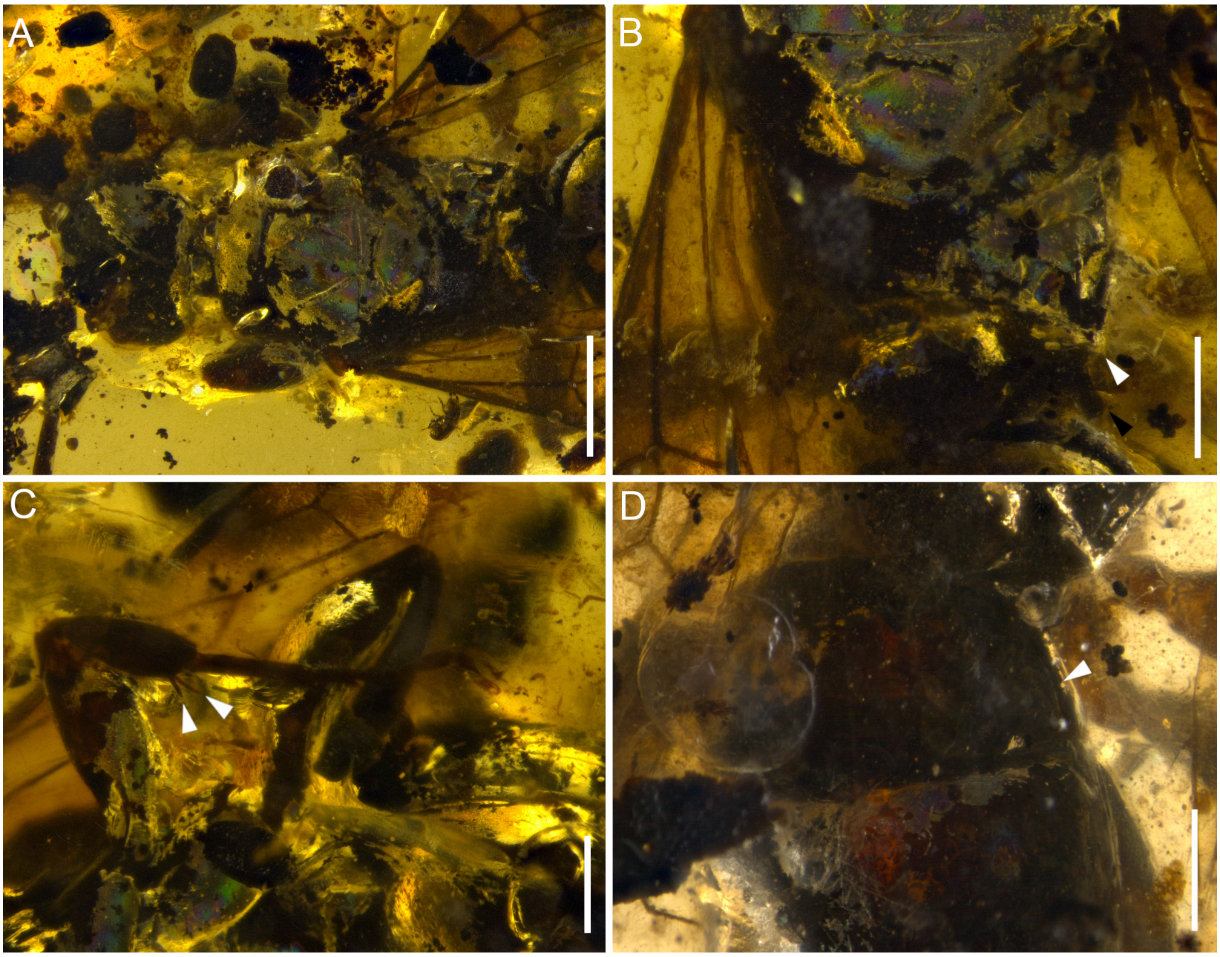

FIGURE 4. Holotype of †*Typhopsenella obscura* **sp. nov.** (DZUP Bur-1642a). **A**, Dorsal view of head and mesosoma. **B**, Dorsal view of scutellum and propodeum, the white arrowhead indicates the posterodorsal angle of the propodeum, while the black arrowhead indicates the ventrolateral prominence. **C**, Right mid and hind legs, the white arrowheads indicate the two mesotibial spurs. **D**, Dorsal view of anterior portion of metasoma, the white arrowhead indicates the position of the anterior carina on T1. Scale bars = 1 mm (**A**); 0.5 mm (**B**, **C**, **D**).

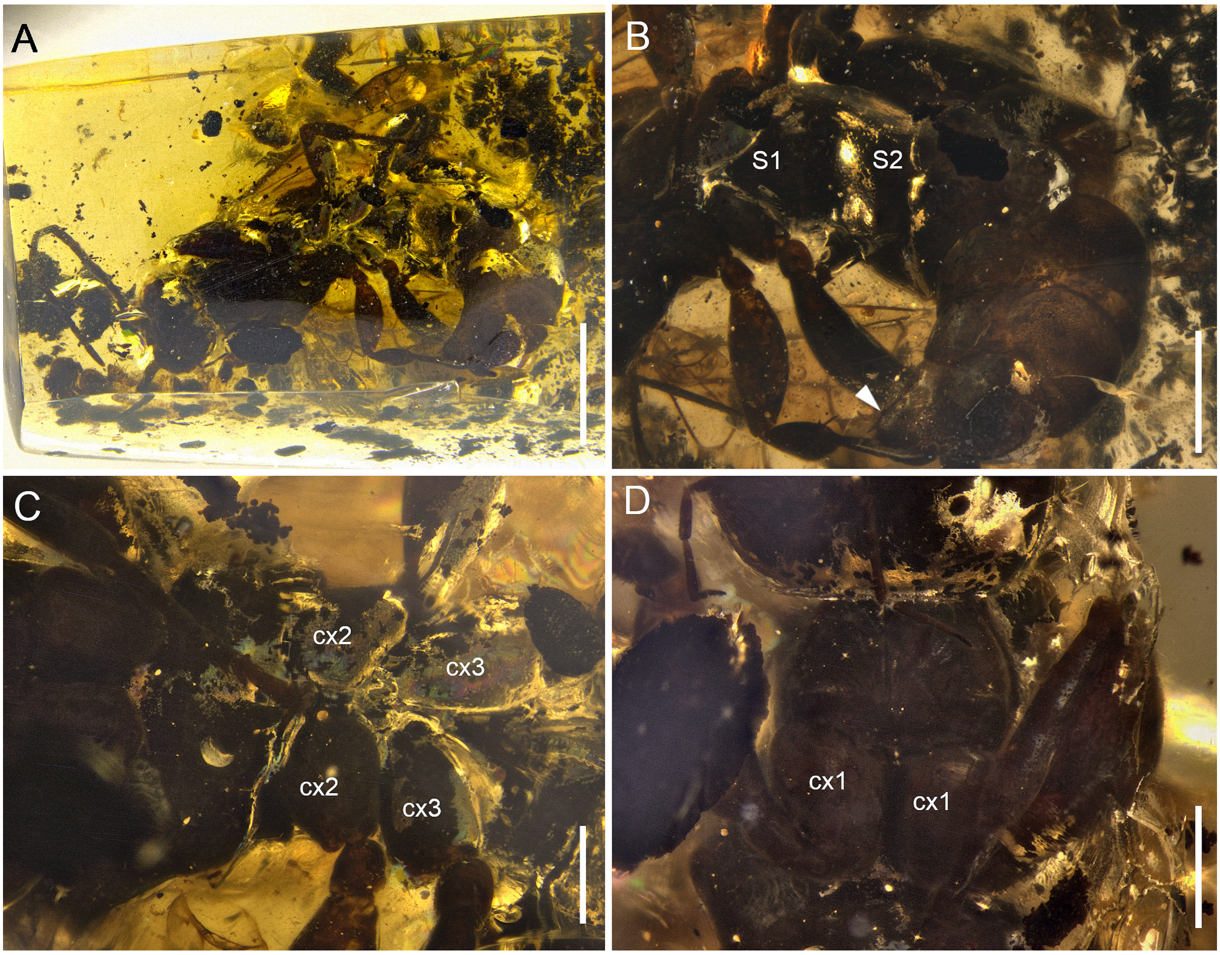

FIGURE 5. Holotype of †*Typhopsenella obscura* **sp. nov.** (DZUP Bur-1642a). **A**, Ventral habitus. **B**, Lateral view of metasoma, the white arrowhead indicates the limit of the medial cleft on S6. **C**, ventral view of posterior portion of mesosoma, head to the left, showing meso- (cx2) and metacoxae (cx3). **D**, Ventral view of anterior portion of mesosoma, showing procoxae (cx1), head to the top. Scale bars = 2 mm (**A**); 1 mm (**B**); 0.5 mm (**C**, **D**).

Pubescence. Setae with black color overall. Mandibles covered with long fine setae about 1.2 times as long as diameter of antennal foramen. Clypeus with sparse erect setae about 0.3 times as long as diameter of antennal foramen. Legs mostly covered with short, stiff bristles. Tarsal claws covered with fine short setae. Sterna with scattered fine erect setae on medio-posterior surface. Remaining regions nearly glabrous.

Sculpture. Mostly not preserved. Some parts of head and mesosoma exhibiting smooth to loosely microreticulate integument. Punctures, where preserved, small and sparse. Dorsal surface of propodeum filled with strong longitudinal carinae which apparently delimit wide foveae. Metasomal sclerites with smooth integument.

Structure. Mandibles apparently overlapping each other medially when closed; about 4 times as long as proximal width. Maxillary palp relatively long, nearly reaching procoxa at rest. Antennal foramina separated by about 2.7 times their diameter. Malar space about as long as antennal foramen width. Ocelli separated by about anterior ocellus diameter. Hypostomal bridge about 2.3 times as long as diameter of antennal foramen. Scape 2.7 times as long as maximum width. Pedicel twice as long as maximum width. F1 2.1 times as long as wide. Proportion between first three flagellomeres 4:5:5; remaining flagellomeres about as long as F3, except F10, slightly longer. Dorsal surface of pronotum about 3.4 times as wide as medial length; postero-dorsal margin widely arched anterad. Mesoscutum twice as long as dorsal surface of pronotum; about 0.5 times as long as wide. Scutellum about 0.7 times as long as mesoscutum; anterior sulcus broad, with arched shape. Propodeum mostly flat in lateral view, posterolateral corner not produced; dorsal surface about 2.3 times as wide as medial length. Mesofemur 2.8 times longer than broad. Pterostigma 2.9 times as long as maximum width. Marginal cell 3.2 times as long as its maximum width; its apex contiguous to the wing margin, not appendiculate. Medial cell of forewing 1.8 times as long as wide. Vein Rs distad vein 2rs-m broadly curved towards distal margin of forewing. Vein cu-a on forewing not forming a spur near distal portion of vein A. Hind wing with vein Rs not strongly curving at juncture with vein rs-m. Dorsal surface of T1 slightly wider than long.

Discussion

The preservation of a wasp with nearly 10 mm in length is unusual, since the nature of amber favors the preservation of tiny insects as inclusions (Martínez-Delclòs *et al.*, 2004). In addition, †*Typhopsenella obscura* **sp. nov.** adds to the taxonomic and morphological diversity of †Holopsenellidae, even though its general morphology is mostly reminiscent of other species known in the family. Assuming the monophyly of †*Holopsenella* as currently known, we can conclude that its evolutionary split from †*Typhopsenella* **gen. nov.** occurred prior to the Barremian, when the family is first recorded (Engel *et al.*, 2016). Given its relatively large size, novel records of †*T. obscura* **sp. nov.** in amber should be considered unlikely. This observation can be expanded to the genus, if other species exhibited comparable body sizes. However, future findings of the family as rock impressions (*e.g.*, in Mesozoic deposits of Brazil, China, and Russia, which often include aculeate wasps with larger sizes) have considerable potential to positively improve our understanding of the biogeographic affinities of the Burmese amber fauna.

The large size of *T. obscura* **sp. nov.** can be interpreted as representing an additional point arguing against a close relationship between †Holopsenellidae and Bethylidae. Even though some species of Bethylidae can reach 30 mm in body size (Azevedo *et al.*, 2018), most of the known diversity of the Chrysidoidea and Dryinoidea is composed of small wasps (< 1 cm). This pattern is even more conspicuous for chrysidoids in Burmese amber, which rarely surpass a few millimeters in length. The reduced hind wing venation of most Chrysidoidea is likely a reflection of the putative small size of their ancestors, given that small insects tend to exhibit wing vein reduction throughout their evolution (Danforth, 1989). The ancestor of †Holopsenellidae may have been large enough to preserve the hind wing venation, as in most Aculeata *s. str*. and in the unusual chrysidoid families Plumariidae and †Plumalexiidae.

Species attributed to †Holopsenellidae also exhibit a set of derived characteristics which place them as a singular branch in the evolutionary tree of Aculeata. The peculiar clypeus projecting as a large lobe with a medial semicircular incision (Fig. 3B) is not common, and may have served a particular role in their behavior. Another feature not documented for any other Chrysidoidea, including Bethylidae, is the well-marked transverse carina on the T1 (Fig. 1), which is present in all members of †Holopsenellidae (Engel *et al*., 2016, Lepeco & Melo, 2022). Judging by the morphology of Cretaceous bethylids, in particular the Barremian *Lancepyris opertus* Azevedo & Azar, 2012, the body-plan of the flat wasps was already well-established by the Early Cretaceous. In general, the similarity between †*Holopsenella* and Bethylidae is restricted to their overall appearance, likely linked to the use of hosts living in concealed conditions (Lepeco & Melo, 2022). Even though the forewing venation of †Holopsenellidae (Fig. 2A, D) resembles that of some Cretaceous bethylids, such as †*Holopsenelliscus pankowskiorum* Engel, 2019 and †*Cretabythus sibiricus* Evans, 1973, the venation of the hind wing reveals that this similarity is convergent. Currently, Cretaceous bethylids with developed forewing venations are placed in their own subfamily, †Cretabythinae, including wasps remarkably different from †Holopsenellidae (Brazidec *et al*., 2023).

In contrast to all known species of †*Holopsenella*, the new genus lacks the cleft on the last exposed metasomal sternum (Lepeco & Melo, 2022). This cleft should have been used by †*Holopsenella* to increase the mobility of the sting, which could be further curled anterad (in relation to the wasp body) to reach the host. This anatomical adaptation could have been useful to access hosts living in enclosed conditions, such as tight burrows in the wood. The lack of the sternal cleft in †*Typhopsenella* **gen. nov.** may also indicate behavioral differences and/or host preferences between both genera. Nevertheless, as mentioned in Lepeco & Melo (2022) and highlighted by the amount of wooden material entombed together with these wasps (Figs 1A, 5A), the best evidence points to the use of wood-boring beetle larvae by females of †Holopsenellidae. In this context, the robust legs and the hypognathous head with developed mandibles could have been used to grab the larva prior to stinging, as is observed in morphologically similar groups of Mutilloidea (used here to encompass the families Sierolomorphidae, Tiphiidae *s.l.*, Sapygidae, Mutillidae and Pompilidae; see Melo & DalMolin, 2024: 514), as well as in Scoliidae, Bethylidae, and Scolebythidae (Melo *et al*., 2011).

The existence of a remarkably distinct taxon in Burmese amber indicates that †Holopsenellidae exhibited a larger diversity in the Cretaceous than previously thought. However, the four species known from two genera do not provide definitive evidence on their phylogenetic affinities among superfamilies of Aculeata *s. str.* As previously discussed by Lepeco & Melo (2022), †Holopsenellidae lack main synapomorphies of Apoidea (Rosa & Melo, 2023) and Formicoidea (Boudinot *et al*., 2020). Their overall appearance indicates a close affinity with Mutilloidea. However, a closer relationship with crown Scolioidea or a position as a stem lineage of other superfamilies cannot be disregarded. Continuous efforts towards understanding the aculeate wasps preserved in Cretaceous deposits may reveal novel species belonging to the family. These findings may turn out to be imperative to properly link this enigmatic group to the evolutionary history of extant lineages of Aculeata.

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