

A case of frozen behaviour: A flat wasp female with a beetle larva in its grasp in 100-million-year-old amber

Christine Kiesmüller¹, Joachim T. Haug^{2,3}, Patrick Müller⁴, Marie K. Hörnig¹

¹ University of Greifswald, Zoological Institute and Museum, Cytology and Evolutionary Biology, Soldmannstr. 23, 17489 Greifswald, Germany

² Ludwig-Maximilians-Universität München (LMU Munich), Biocenter, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany

³ GeoBio-Center der LMU München, Richard-Wagner-Str. 10, 80333 München, Germany

⁴ Kreuzbergstr. 90, 66482 Zweibrücken, Germany

<https://zoobank.org/D5DB0BBC-B925-40D3-8F67-56C69C54AC36>

Corresponding author: Christine Kiesmüller (christine.kiesmueller@palaeo-evo-devo.info)

Academic editor: Alexander Schmidt ♦ Received 18 February 2022 ♦ Accepted 25 August 2022 ♦ Published 16 September 2022

Abstract

Parasitism, a malignant form of symbiosis, wherein one partner, the parasite, derives benefits to the detriment of another, the host, is a widespread phenomenon. Parasitism *sensu lato* is understood here to include many phenomena, like parasitoidism, kleptoparasitism, phoresy and obligate parasitism. Insecta has many in-groups that have evolved a parasitic life-style; one of the largest in-groups of these is probably the group of Hymenoptera. Bethylidae, the group of flat wasps, is a smaller in-group of Aculeata, the group of hymenopterans with venom stings; representatives of Bethylidae are parasitic. They are more specifically larval ectoparasitoids, meaning that their immature stages are externally developing parasites that kill their host organism at pupation (end of interaction). They mostly parasitise immature representatives of Coleoptera and Lepidoptera. Female flat wasps search for a host for their progeny, paralyse it with their venom sting and then oviposit onto it.

Herein we describe one of the oldest findings of parasitic interactions of parasitoid wasps with their progenies' hosts, specifically a flat wasp female grasping and (potentially) stinging a beetle immature in Cretaceous Kachin (Myanmar) amber (ca. 100 million years old). This finding indicates that this type of parasitic interaction existed since the Cretaceous, temporally close to the earliest findings of representatives of Bethylidae.

Key Words

Bethylidae, Coleopteran larva, Kachin amber, parasitism, parasitoid wasp, syninclusion

Introduction

Reconstruction of behaviour of extinct organisms

Studying behaviour and trophic interactions of extinct animals can only be done indirectly amid demands for several different approaches (see below; Hörnig et al. 2022) and combinations of these. Spatially close fossilisations of several individuals of the same or different species (group fossilisation), e.g. as syninclusions in amber, are especially interesting in this context, as they can give valuable hints to biotic interactions. Group fossilisation of individuals of different species can indicate predator-prey

interactions and thus can help to reconstruct food-webs, but is rarely discussed in this context in the fossil record (examples below; see discussion in Hörnig et al. 2020; Haug JT et al. 2022). Some of these cases of group fossilisation can also fall into the category of the so-called 'frozen behaviour' (Boucot 1990; examples in e.g. Arillo 2007; Boucot and Poinar 2010; Hsieh and Plotnik 2020).

Frozen behaviour refers to "behaviorally critical specimens in which an organism(s) is preserved while actually doing something (such as two insects in copula)" (Boucot 1990, p. 3), which thus may provide insight into potential behavioural patterns. This 'best case scenario' is, however, not widely preserved in the fossil record. Within

euarthropods, especially cases of insects preserved in amber have been documented, e.g. during mating (Weitschat and Wichard 2002; Grimaldi and Engel 2005; Weitschat 2009; Boucot and Poinar 2010; Gröhn 2015; Fischer and Hörnig 2019), hatching (Weitschat 2009; Boucot and Poinar 2010; Gröhn 2015; Hörnig et al. 2019; Pérez-de la Fuente et al. 2019), feeding (Grimaldi 1996; Weitschat and Wichard 2002; Boucot and Poinar 2010; Gröhn 2015; Wang et al. 2016; Hörnig et al. 2020) and other behaviours (Boucot and Poinar 2010; Hsieh and Plotnik 2020).

There are also more indirect indications of behaviour or lifestyles that can be preserved in the fossil record. Trace fossils (ichnofossils; e.g. fossilised animal tracks) or feeding damage (on animals or plants) can be indicators for behaviour (compare e.g. Hsieh and Plotnik 2020 and references therein; but see e.g. Hasiotis 2003 for limitations of ichnofossils specifically). Functional morphology can also provide insight into potentially exhibited behaviours by comparison with extant organisms with similar morphologies to the fossilized organism (Reif 1983; Thomason 1997; Haug JT et al. 2012; Hörnig et al. 2016, 2018). Though if the fossil is e.g. only incompletely preserved and no inferences from functional morphology (or other indications mentioned above) can be made, the concept of the ‘extant phylogenetic bracket’ (Witmer 1995) can be used to estimate potentially exhibited behavioural patterns by comparing the fossilised organism with its closest extant relatives. The reliability of these approaches varies considerably for every case, however, and a combination of several approaches discussed thoroughly is useful for the reconstruction of behavioural aspects of extinct organisms (Hörnig et al. 2013, 2017, 2018, 2022; Zippel et al. 2021).

With regard to ancestral food webs, reliable reconstruction of predator-prey interactions based on cases of group fossilisation is challenging and often remains speculative. More obvious are examples where the individuals are in direct contact for extended time spans, as is often the case for parasites and their host(s).

Parasitism—a multitude of concepts

Finding clear characteristics of parasitism appears to be difficult (van der Wal and Haug JT 2019). There are many characterisations, “probably as many [...] as there are books on parasitism” (Price 1980, p. 4). Most of these characterisations have in common that parasitism *sensu lato* (s.l.) is an interaction between two organisms where in one (the parasite) derives benefits (mostly nutrients) and the other (the host) detriments from the interaction, including also that the parasite has certain morphological adaptations to such a lifestyle (e.g. Price 1980; Paracer and Ahmadjian 2000; Daintith and Martin 2010; Goater et al. 2014). Some authors also include the intimacy or dependency of the interaction into their characterisation (e.g. Olsen 1974).

These more general characterisations of parasitism have the consequence that they include phenomena that have been traditionally separate (e.g. herbivory) (as discussed in Poulin 2011; van der Wal and Haug JT 2019). Furthermore, parasitism is frequently seen as a trophic interaction (e.g. Grissell 1999; Lafferty and Kuris 2002; Goater et al. 2014). This may be true for most organisms that are called parasites (or derivatives of that), but some phenomena, especially within social (Wheeler 1928; Lucius et al. 2017) or behavioural (Poulin 2011) parasitism (e.g. kleptoparasitism or better kleptobiosis, but cf. Breed et al. 2012, brood parasitism (Litman 2019)) are not trophic interactions but interactions on the same trophic level (like e.g. competition; Nentwig et al. 2017).

There are many different approaches in how to differentiate between different types of parasites (s.l.). There are e.g. obligate versus facultative parasites, life-stage dependent parasites (larval versus adult parasites), temporary versus periodic versus permanent parasites (based on the length of interaction between parasite and host) or based on the cost of the parasitic interaction for the host (e.g. kleptobiosis, phoresy versus parasitic castrators, parasitoids) (compare e.g. Rothschild and Clay 1957). Parasitoids e.g. reduce their host’s fitness to zero by killing them at the end of their interaction and thus costing the host immensely.

A parasite can belong to multiple of these subdivisions at the same time; e.g. representatives of Strepsiptera (especially of Mengenillidae) are obligate, larval endoparasitic castrators (e.g. Kathirithamby 2009). There are a few works that tried to unite all these concepts into one (Lafferty and Kuris 2002; Poulin 2011), but these works have focused mainly on parasitism as a trophic interaction and thus excluded other forms that are associated with parasitism (Poulin 2011). Here, we understand parasitism s.l. in its widest characterisation, including phenomena such as social parasitism, parasitoidism, phoresy and, of course, parasitism *sensu stricto*, which includes (mostly) permanent and obligate parasites.

Flat wasps and their parasitoid immatures

Flat wasps (Bethyliidae) are rather small wasps of about 1–20 mm body length (Azevedo et al. 2018) that owe their common name to their dorso-ventrally flattened body. They are an in-group of Aculeata (wasps with venom sting), wherein they are part of Chrysidoidea. Together with their sister-group Chrysididae, flat wasps account for most species within Chrysidoidea today (Goulet and Huber 1993; but see e.g. Haug JT et al. 2016 for the logical incorrectness of this statement).

The oldest known flat wasp fossils are from the Lower Cretaceous (ca. 130 million years old), with at least twenty-two described species so far (amber only), half of which are from Myanmar amber (Azevedo et al. 2018; Engel 2019; Colombo et al. 2020; Jouault et al. 2020, 2021; Jouault and Brazidec 2021; see also Lepéco and Melo 2021

for taxonomic changes within fossil Bethyliidae). Beyond this, they have been also abundant in Cenozoic Lagerstätten (ca. 66 million years old) (e.g. Brues 1939).

Flat wasps are larval parasitoids of holometabolous insect immatures (mostly coleopteran and lepidopteran larvae) and their adults are mostly smaller than their future offspring's hosts (Gauld and Bolton 1988), which the females paralyse with their venom sting (Powell 1938; Finlayson 1950; Schaefer 1962; Evans 1964; Kühne and Becker 1974; Gordh and Medved 1986; Griffiths and Godfray 1988; Abraham et al. 1990; Howard et al. 1998). Since the host immatures often occur in more cryptic or concealed habitats, like soil, stems, wood or seeds (Evans 1964; Gauld and Bolton 1988; Howard and Flinn 1990), flat wasp adults may show additional adaptations for entering these habitats (Williams 1919; Gordh and Medved 1986), such as fossorial (digging, burrowing) forelegs and reduced wings (Evans 1964). Some flat wasps even exhibit subsocial behaviours (Evans 1964), additional (to parasitoidism) maternal care (Casale 1991; Hu et al. 2012; Yang et al. 2012; Tang et al. 2014) and many engage in prey carriage and some also in a sort of nest building (Finlayson 1950; Evans 1964; Rubink and Evans 1979; Howard et al. 1998; for review of prey carriage in wasps in general see e.g. Evans 1962). Yet, studies of behaviour and also their biology at large are mostly restricted to species of agricultural importance, as their immatures parasitise some crop and storage pests (Kühne and Becker 1974; Gordh and Hawkins 1981; Gordh 1998; Cheng et al. 2004; Gao et al. 2016; Jucker et al. 2020).

The immatures' host is often permanently paralysed (Finlayson 1950; Schaefer 1962; Lauzière et al. 2000; Amante et al. 2017; but there are exceptions: e.g. Kühne and Becker 1974; Gordh and Medved 1986; Witethom and Gordh 1994; Mayhew and Heitmans 2000); the flat wasp female then either carries them away to a sort of nest, where they can accumulate multiple potential host individuals for their progeny, or they oviposit onto them on site. The emerging immature(s) either attaches itself to its host or the mother bites the immatures' host to provide the immature easier access for feeding (e.g. Kühne and Becker 1974; Hu et al. 2012). The immature develops externally on its host as an ectoparasitoid and eventually kills it before it pupates (Powell 1938; Schaefer 1962; Kühne and Becker 1974; Gordh and Hawkins 1981; Abraham et al. 1990; Casale 1991; Cheng et al. 2004).

Here we report a flat wasp female that is supposedly in the process of stinging a coleopteran immature, as syninclusions in 100-million-year-old Kachin (Myanmar) amber.

Material and methods

Material

The study is based on one piece of amber from Kachin State (Myanmar) ("Burmese amber"), which is part of the State Natural History Museum, Braunschweig (Staatliches

Naturhistorisches Museum Braunschweig), stored under the accession number SNHM-6014. The piece was legally purchased by one of the authors (PM) in 2016.

The amber originates from the Noije Bum hill locality, in the Southwest corner of the Hukawng Valley in Kachin State, Northern Myanmar, South Asia. The amber locality was 'first' discovered (by Europeans) and intensively mined in the 19th and 20th century (Poinar 2019; Cruickshank and Ko 2003; Zherikhin and Ross 2000). It was assumed to be Eocene (33.9–56 million years old) (Chhibber 1934 in Grimaldi et al. 2002) to Miocene (3–23 million years old; Noetling 1893) in age, although Cockerell (1917a, 1917b) already questioned this, given numerous insect inclusions representing exclusively Mesozoic (66–252 million years old) groups (also discussed in Cruickshank and Ko 2003; Shi et al. 2012). In addition, an enclosed ammonite (Yu et al. 2019) as well as zircon dating (Shi et al. 2012) and the (potential) Cretaceous age of the embedding rock matrix (Cruickshank and Ko 2003) support the now widely accepted Cenomanian to Albian age (mid-Cretaceous; 94–113 million years old) of the amber.

The Hukawng Valley locality is a major Lagerstätte of Cretaceous amber in Southeastern Asia and contains a very diverse (palaeo-)biota (Grimaldi et al. 2002; Ross 2021). The palaeoenvironment of Kachin amber has been postulated to be subtropical to tropical (Grimaldi et al. 2002; Yu et al. 2019) consistent with its near equatorial (palaeo-)latitude (Grimaldi et al. 2002; Martínez-Delclòs et al. 2004), potentially nearshore, marine or lagoon (Cruickshank and Ko 2003; Yu et al. 2019) and potentially part of the past 'supercontinent' Gondwana (Poinar 2019).

Methods

The amber piece was photographed using a Keyence VHX-6000 light microscope (equipped with 20–2000 times magnification lenses). In order to reduce reflections and enhance the contrast, the specimens were photographed with a drop of distilled water and an above placed cover slip. Images were recorded in different focal planes (z-stacks) with different illuminations and then combined to a single image with extended field of depth in the microscope's accompanying software.

Additionally, it was photographed with a Canon EOS 70D reflex camera equipped with an MP-E 65 mm macro objective and a Macro Twin Lite MT-24 EX flash light for close-up images. The specimen was mounted and photographed as described above. The generated images (z-stacks) were stacked (fused) with CombineZP and stitched (xy-plane; merged) with Adobe Photoshop CS4 (compare e.g. Haug C et al. 2011).

In addition, the piece was documented with μ CT (XRadia MicroXCT-200, Carl Zeiss Microscopy GmbH, Jena, Germany). The tomography was performed with a 4 \times objective; the X-ray source settings were 40 kV, 200 μ A and 8.0 W. The exposure time was 2.5 s; the system-based pixel size is 5.0073 μ m, with an image size of 1015 \times 1015 px.

The tomographic images were reconstructed with XMReconstructor software (Carl Zeiss Microscopy GmbH, Jena, Germany), resulting in image stacks (TIFF format). Projections were recorded with Binning 2, tomographic images were reconstructed with Binning 1 (full resolution). Volume renderings were performed using Drishti (ver. 2.7) and Amira 6.1; surface reconstructions, as well as horizontal, vertical and longitudinal virtual sections were generated in Amira 6.1. All obtained images were optimised for colour balance, saturation and sharpness and arranged into figures using Adobe Photoshop CS2 and CS4.

Herein we used insect terminology with corresponding neutral euarthropod terminology in brackets, to ensure mutual understanding within the whole arthropod community. Also terminology of Crustacea sensu lato (CT) is pointed out where it differs from insect terminology (IT), as insects are an in-group of Crustacea sensu lato. Special hymenopteran (HY) (after Lanés et al. 2020) and coleopteran terminology (CO) (after Klausnitzer 1978; Crowson 1981) is also pointed out, where necessary and differing from insect terminology.

Results

Description of specimen SNHM-6014

There are two syninclusions in very close proximity in the amber piece: a hymenopteran adult and a coleopteran immature. The walking appendages of the hymenopteran adult appear to hold the coleopteran immature and its stinger is (seemingly) inserted within the coleopteran immature (compare Figs 1–4 for overview and details especially in Figs 5, 6).

Description of the hymenopteran adult

Hymenopteran adult well-preserved on one side (Figs 1, 2, 4), other side with parts of head, thorax and most of the appendages (including wings) not included in the amber piece (compare Fig. 4B,C); about 3 mm long; not depressed, body surface apparently smooth.

Head: Head (ocular segment and post-ocular segments 1–5) about 0.4 mm long and wide; square-shaped in ventral view and ovoid in lateral view; postero-lateral corners (IT: parts of gena) projecting slightly ventrally in lateral view (Fig. 1D); setae sparsely present. Large compound eyes (ocular segment); ovoid in lateral view; with numerous ommatidia (Fig. 1D). Antenna (appendage of post-ocular segment 1; CT: antennula) attached to head anterior to compound eye and very close to mouthparts (Figs 1D, 2A and 4D, turquoise); groove ventral to attachment area discernible; five elements discernible (probably not completely preserved), all elongated rectangular in lateral view; most proximal antenna element 1 (IT: scapus) about 3× wider than long; element 2 (IT: pedicellus) much shorter and about as wide as long; elements 3–5

(IT: flagellomeres 1–3) as wide as long, though slightly smaller than the pedicellus.

Mouth parts: labrum (sclerite of ocular segment) and appendages of post-ocular segments 3–5 attached and directed anteriorly (head prognathous (IT)); compare with Figs 1D, 2A, 4D):

Labrum (sclerite of ocular segment) not discernible. Clypeus (associated sclerite of labrum) triangular in frontal view (Fig. 4D), with potentially ridge (HY: median clypeal carina) medially.

Mandibles (appendages of post-ocular segment 3) (Fig. 4D, indigo blue) rectangular in frontal view with rounded corners; median edge with about 4 discernible protrusions (IT: teeth) medially, overlapping medially about one third its width; each mandible about 1.5× wider than long. Further associated structures (hypopharynx; CT: paragnaths) not discernible. Space between attachment of mandibles and compound eye (HY: malar space) short, less than half the proximal width of the mandible.

Of the maxilla (appendage of post-ocular segment 4; CT: maxillula) only distal part (IT: maxillary palp) discernible (Fig. 4D, bluish violet); 5 elements of maxillary palp discernible, all elongated rectangular in frontal view with rounded corners; element 1(?)–2 of maxillary palp about 2× longer than wide, but element 1(?) potentially not entirely discernible; elements 3–5(?) of maxillary palp all about 3× longer than wide; most distal element 5(?) of maxillary palp with rounded tip.

Of the labium (appendage of post-ocular segment 5; CT: maxilla) also only distal parts (IT: labial palps) discernible (Fig. 4D, reddish violet), median parts concealed underneath mandibles; at least 2 elements of labial palp discernible, also both rectangular with rounded corners in frontal view; element 1(?) of labial palp about 2× longer than wide, but potentially not entirely discernible; element 2(?) of labial palp about 3× longer than wide with rounded, but blunt tip.

Mesosoma (anterior trunk tagma): Post-ocular segments 6–9 (HY: mesosoma, IT: thorax and first abdomen segment) altogether ovoid with tapering, pronounced tips in lateral view (Figs 1, 2, 4); about 1 mm long and 0.4 mm wide at its widest; only sparsely setae present, where discernible; laterally on thorax with large structure discernible mostly in volume rendering of μ CT-images (Figs 4, 5C, 8) (probably artefact caused by leaked out body fluids during taphonomic processes; compare also with Fig. 1A), obscuring lateral thorax view.

Prothorax (post-ocular segment 6) dorsally apparently trapezoid with two right angles medially (as discernible); ventrally one half of the sclerite (HY: propleuron) also trapezoid with two right angles medially, sclerites conjoined medially; sternite (IT/HY: prosternum) not discernible medially.

First walking appendage (IT: foreleg) attached posteriorly to propleura; about 1.4 mm long; 5 major elements discernible; element 1 (IT: coxa) trapezoid with rounded corners, two right angles medially in anterior view, proximal edge about 2× longer than distal edge; element 2

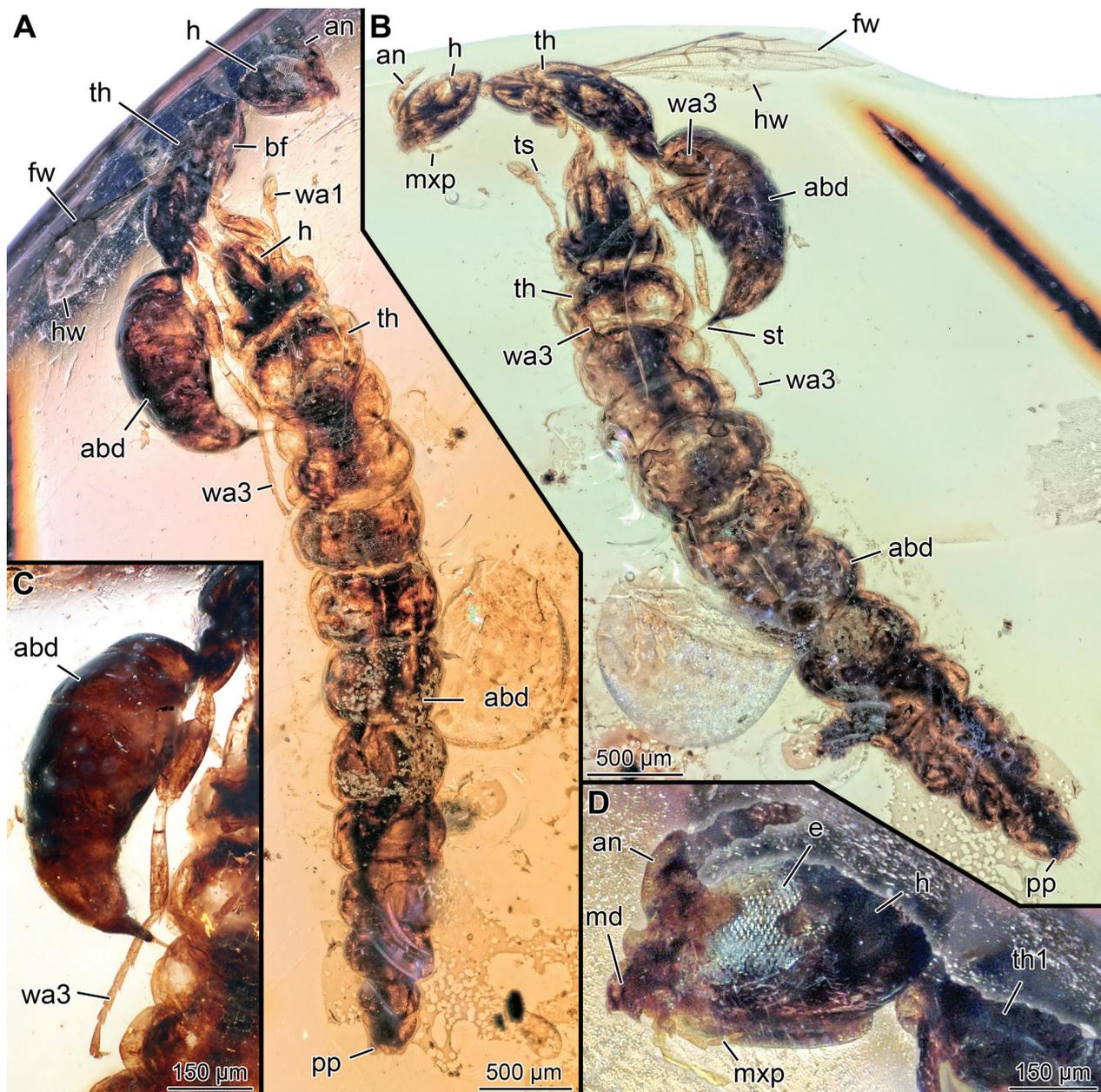


Figure 1. Photograph of amber piece SNHM-6014 with an adult hymenopteran and an immature coleopteran. **A.** Overview side 1 (coleopteran immature in dorsal, hymenopteran adult in lateral view); **B.** Overview side 2 (coleopteran immature in ventral, hymenopteran adult in lateral view); **C.** Detail of hymenopteran adult stinging coleopteran immature (side 1); **D.** Detail hymenopteran head (side 1), mirrored. **abd** – abdomen; **an** – antenna; **bf** – leaked body fluid; **e** – complex eye; **fw** – forewing; **h** – head; **hw** – hind wing; **pp** – pygopodium/postpedes; **th** – thorax; **ts** – tibial spur; **st** – sting (modified ovipositor of hymenopterans); **wa** – walking appendage.

(IT: trochanter) elongated ovoid in lateral view, widening distally to about 2× proximal width, about 4× longer than wide at its narrowest; element 3 (IT: femur) elongated ovoid in lateral view, more than 2× longer than wide at its widest; element 4 (IT: tibia) elongated rectangular with rounded corners in lateral view, more than 4× longer than wide, with one large spine (IT: tibial spur; HY: calcar, i.e. antenna cleaning apparatus) at its median distal corner and more distally a smaller spine with a quarter the length of the larger spine; element 5 (IT: tarsus) subdivided into 5 elements, all rectangular in lateral view; tarsus element 1 by far longest, with two setae at its most

distally and about 4× longer than wide; tarsus element 2 slightly longer than wide; tarsus elements 3–4 both as long as wide and thus more square-shaped; tarsus element 5 more trapezoid than rectangular in lateral view with a wider distal than proximal edge and more than 2× longer than wide, with distally two claws and rounded structure in between (IT: arolium), not discernible whether claws simple or with median protrusions (IT/HY: teeth); foreleg with sparse setae.

Mesothorax (post-ocular segment 7) dorsally rectangular (not entirely discernible due to preservation), potentially slightly longer than wide. Dorsally, forewings

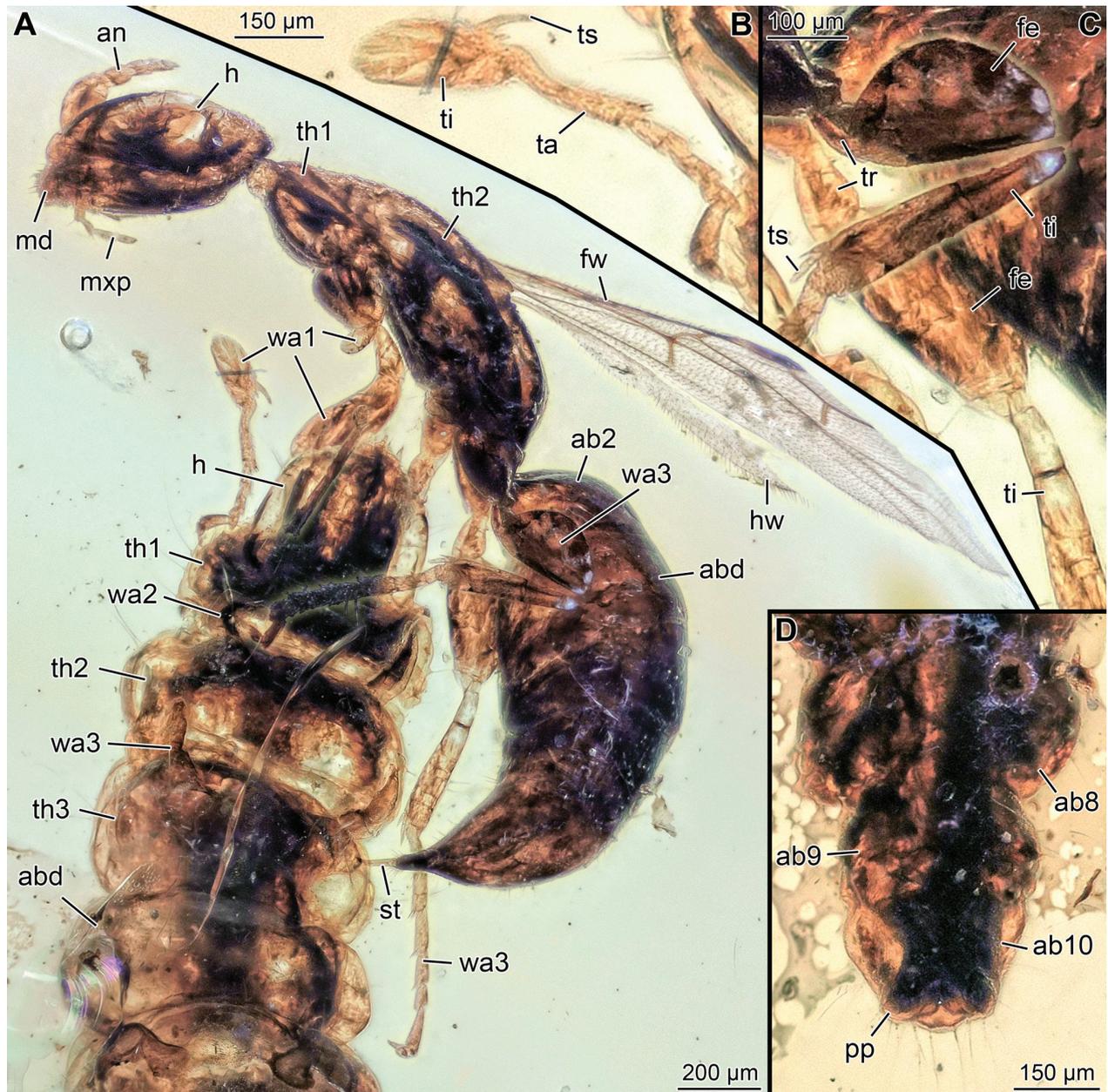


Figure 2. Detailed view on hymenopteran adult of Fig. 1 (side 2). **A.** Close-up overview of hymenopteran adult; **B.** Detailed view on distal part of first walking appendage shown in A; **C.** Detailed view on proximal part of third walking appendage of hymenopteran adult; **D.** Detailed view on posterior end of abdomen of the coleopteran immature. **ab** – abdomen segment; **abd** – abdomen; **an** – antenna; **fe** – femur; **fw** – forewing; **h** – head; **hw** – hind wing; **md** – mandible; **mxp** – maxillary palp; **pp** – pygopodium/postpedes; **th** – thorax; **ti** – tibia; **tr** – trochanter; **ts** – tibial spur; **st** – sting (modified ovipositor of hymenopterans); **wa** – walking appendage.

attaching at border between (possibly) artefactual structure and dorsal sclerite; one forewing preserved, but incomplete (distal part missing, including vein of post-stigmal abscissa of R_{1_2v}); anterior edge of wing straight (where preserved); vein C_{2v} not clearly visible; pterostigma (thickened and dark patch at the end of R_1) present distally on the anterior edge and elongate ovoid in lateral view; at least four closed cells (encased on all sites by veins) present (R_{2c} , $1R_{1_2c}$, $1M_{2c}$ and $1Cu_{2c}$); additionally cell C_{2c} potentially obscured, cell $2R_{1_2c}$ distally not preserved (but presumed closed); cell $2Cu_{2c}$ apparently open; cell $1R_{1_2c}$ pentagonal in dorsal view; all veins apparently

tubular (i.e. with distinctly apparent hollow interior), except potentially present vein M_{2v} (vein $Rs+M_{2v}$ distally apparently splitting in anterior Rs_{2v} vein and posteriorly into two M_{2v} veins (potentially reaching wing margin, though also potentially folding pattern)) and potentially also A_{2v} ; setae all over forewing; longer setae at the anterior and posterior edge.

Mesopectus (sclerite on ventral side of post-ocular segment 7) rectangular, probably 2× wider than long (incompletely preserved); second walking appendage (IT: midleg) attached latero-posteriorly to mesopectus, about 1.3 mm long; coxa circular in anterior view, about as wide

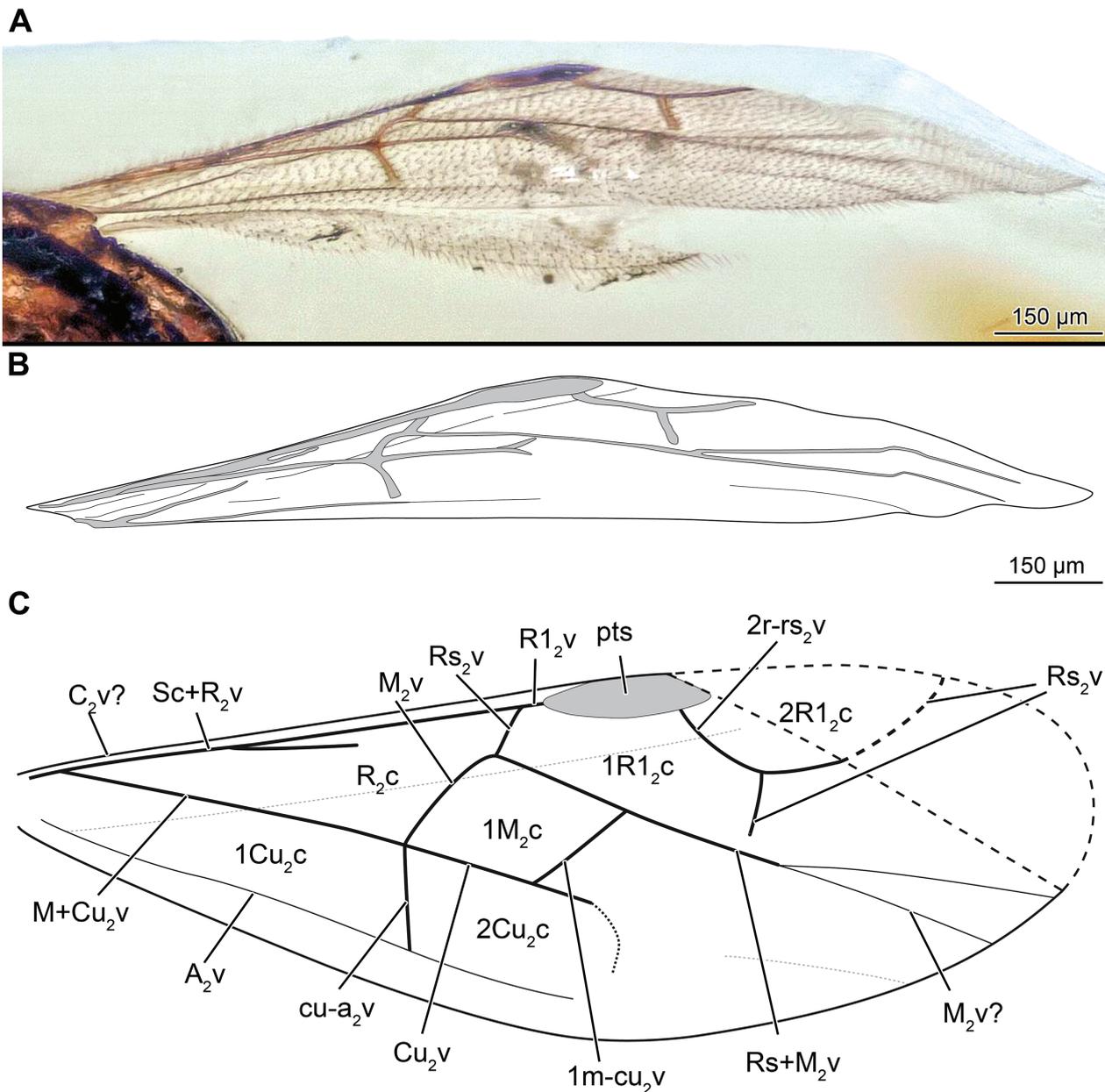


Figure 3. Forewing of hymenopteran adult. **A.** Photograph in dorso-posterior view on forewing; **B.** Drawing of A; **C.** Reconstruction of wing shown in A, B. **1Cu₂c** – First cubital cell; **1M₂c** – First medial cell; **1R₁c** – First radial cell 1; **2Cu₂c** – Second cubital cell; **2R₁c** – Second radial cell 1; **2r-rs₂v** – Second radial cross vein; **A₂v** – Anal vein; **C₂v** – Costal vein (note that it was not discernible in A); **Cu₂v** – Cubital vein; **cu-a₂v** – cubito-anal vein; **pts** – pterostigma; **M₂v** – Median vein; **1m-cu₂v** – medio-cubital vein; **M+Cu₂v** – Median+Cubital vein; **R₁v** – prestigmal abscissa of radial vein 1 (in this case); **R₂c** – Radial cell; **Rs₂v** – radial sector veins; **Rs+M₂v** – Radial sector + Median vein; **Sc+R₂v** – Subcostal + Radial vein.

as long; trochanter circular in median view, about one third as long as coxa; femur ovoid in lateral view, about 3× longer than wide; tibia elongated rectangular in lateral view, about 5.5× longer than wide and with no spines, spurs or setae discernible (possibly due to obstructed view in that area); tarsus with 5 elements, overall similar to tarsus of foreleg, setae present mostly at the median distal most corner of at least the three most proximal tarsus elements, further setae not discernible; tarsus element 2–3 about 2× longer than wide; tarsus element 5 similar to that of foreleg, but about 3× longer than wide.

Metathorax (post-ocular segment 8) dorsally rectangular, much wider than long; incompletely preserved laterally and partly covered by a similar artefact as mesothorax (see above). One hind wing present (but incomplete preserved); no wing venation discernible, except one possible vein at anterior edge of hind wing (compare Figs 2A, 3); potentially ‘fused’ vein of Costa+Subcosta+Radius; setae all over hind wing; longer setae at posterior(?) edge of the wing.

Circular sclerite on ventral metathorax (IT/HY: metasternum or metasternal plate) discernible in between midlegs; third walking appendage (IT: hindleg) attached

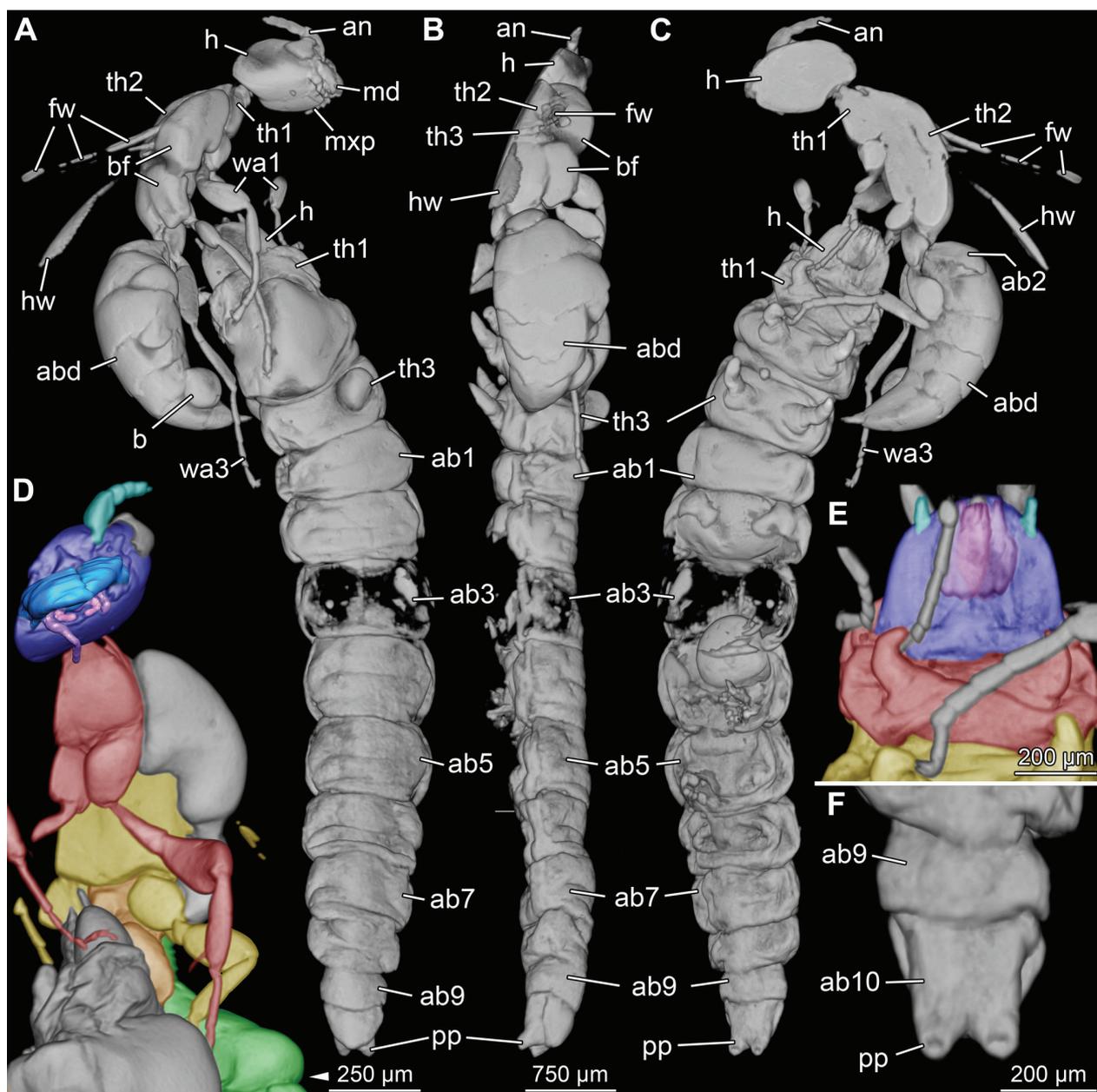


Figure 4. Volume rendering (mostly Drishti 2.7) of μ CT of amber piece SNHM-6014. **A–C.** Overview of hymenopteran adult and coleopteran immature; **A.** Dorsal view of coleopteran immature (side 1 of Fig. 1A); **B.** Dorsal view of hymenopteran adult; **C.** Ventral view of coleopteran immature (side 2 of Fig. 1B); **D.** Ventral view of mirrored, colour-marked anterior part of the hymenopteran adult; mouth parts 3D-reconstructed and image of volume rendering taken in Amira 6.1; **blue** – head; **turquoise** – antenna; **indigo blue** – mandible; **violet** – maxilla; **red** – prothorax; **yellow** – mesothorax; **orange** – metathorax; **green** – abdomen. **E.** Detailed colour-marked, ventral view of anterior part of coleopteran immature; same colour-coding as in D. **F.** Detailed, ventral view of mirrored, posterior part of coleopteran immature. **ab** – abdomen segment; **abd** – abdomen; **an** – antenna; **b** = artefact (possible air bubble or similar); **bf** – artefact (possible leaked body fluid or similar); **fw** – forewing; **h** – head; **hw** – hind wing; **md** – mandible; **mxp** – maxillary palp; **pp** – pygopodium/postpedes; **th** – thorax; **wa** – walking appendage.

latero-posteriorly to that ventral sclerite and about 1.6 mm long; coxa ovoid in anterior view, more than 2 \times longer than wide at its widest; trochanter trapezoid in lateral view with longer posterior edge, about 1.5 \times longer than wide at its widest; femur ovoid in lateral view, about 2.5 \times longer than wide at its widest; tibia elongated rectangular in lateral view, widening slightly distally, with two spines of different lengths at its median distal most corner; spine more distally (IT/HY: tibial spur) more than 2 \times longer

than shorter one, tibia about 6 \times longer than wide at its widest; tarsus with 5 elements, overall similar to tarsus of foreleg, tarsus elements 1–3 each with about two setae at median distal most corner, further setae not discernible, tarsus element 1 6 \times longer than wide and half as wide as the tibia, tarsus element 2 3 \times longer than wide, tarsus element 3 more than 3 \times longer than wide and tarsus element 4 about 2 \times longer than wide, tarsus element 5 4 \times longer than wide at its widest.

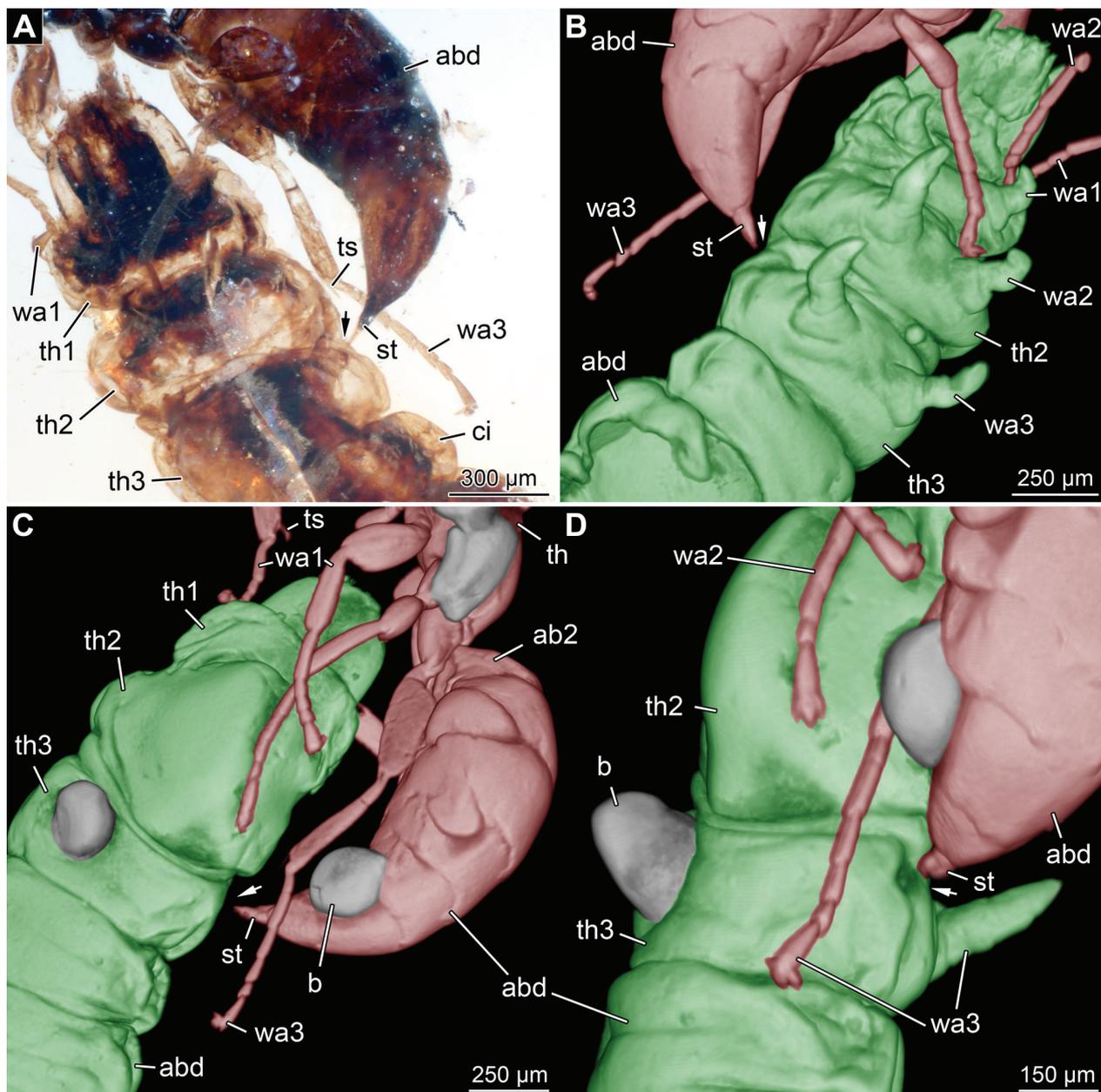


Figure 5. Detail of hymenopteran adult stinging coleopteran immature; arrows point to supposed puncture site. **A.** Photograph in same view as in Fig. 1B; **B–D.** Colour-marked, mirrored volume rendering of μ CT of amber piece SNHM-6014 (Drishti 2.7); in **green** coleopteran immature, in **red** hymenopteran adult; **B.** Ventral view of coleopteran immature; **C, D.** Dorsal view of coleopteran immature. **ab** – abdomen segment; **abd** – abdomen; **b** – artefact (possible air bubble or similar); **ci** – coleopteran immature; **st** – sting (modified ovipositor of hymenopterans); **th** – thorax; **ts** – tibial spur; **wa** – walking appendage.

Post-ocular segment 9 (HY: propodeum, IT: abdomen segment 1) only dorsally discernible (HY: metapectal-propodeal complex; note that it is a complex composed of the third thorax and first abdomen segment); rectangular shaped in dorsal view, about 1.5 \times longer than wide (but incompletely preserved); convexly curved in lateral view and smooth with no posterior spines.

Metasoma (posterior trunk tagma): Metasoma (post-ocular segments 10–19; HY: metasoma segment 1–10; IT: abdomen segments 2–11) attached anteriorly to the mesosoma very ventrally; about 1.6 mm long and 0.5 mm wide at its widest; overall ovoid in lateral view with a very pointy posterior end; curving ventrally,

especially posteriorly; only sparsely setae present, where discernible, mostly towards posterior.

Tergite of post-ocular segment 10 (HY: metasoma segment 1; IT: abdomen segment 2) half circular in dorsal view with a small anterior protrusion (petiolate structure; part of the ‘wasp waist’), about 0.2 mm long; sternite circular in ventral view with also small anterior protrusion (petiolate structure); no appendages.

Post-ocular segments 11–14 (HY: metasoma segments 2–5, IT: abdomen segment 3–6) dorsally all rectangular and wider than long; no appendages. Tergite of post-ocular segment 11 (HY: metasoma segment 2; IT: abdomen segment 3) 3 \times wider than long, 0.25 mm long; sternite of

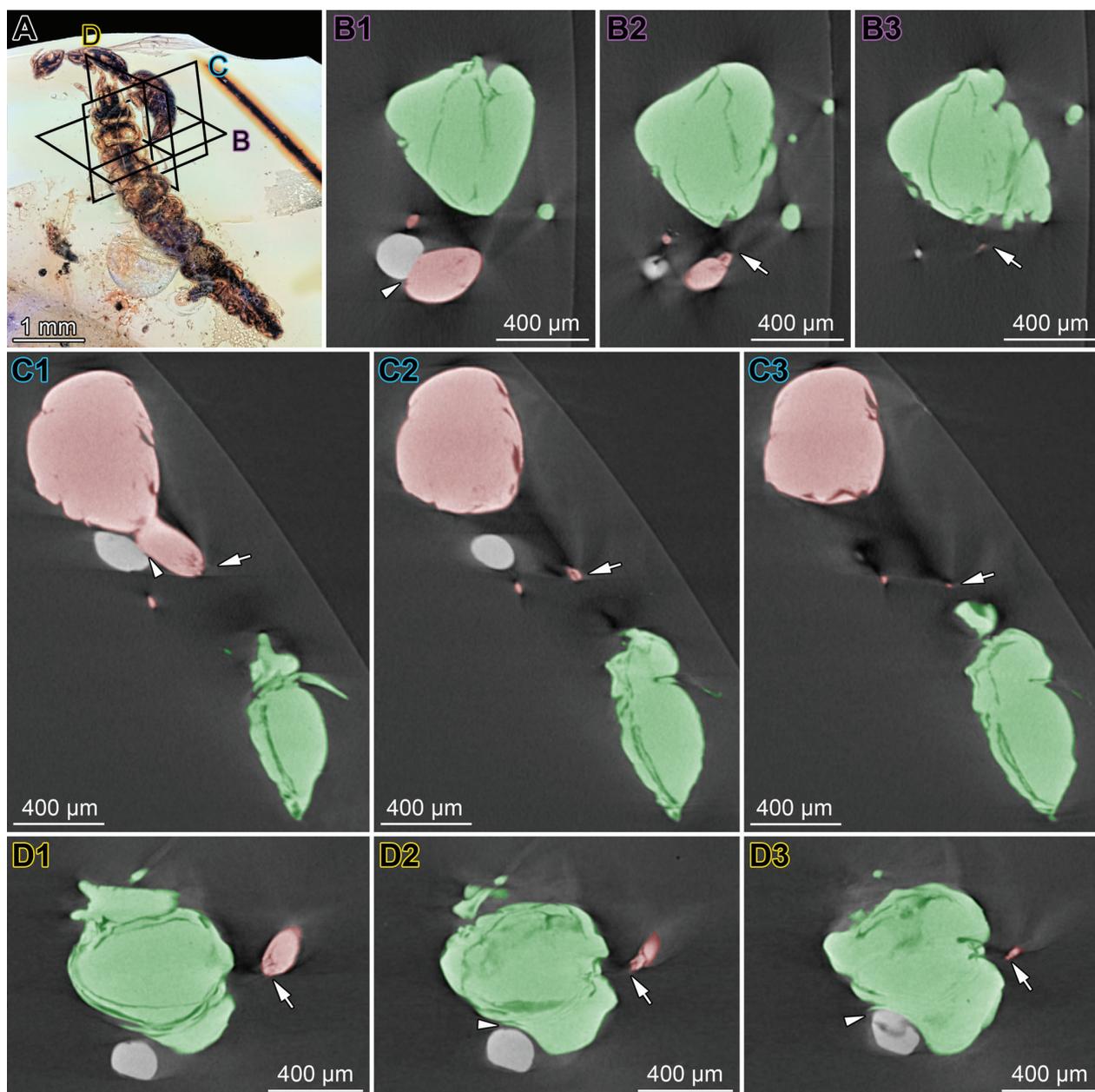


Figure 6. Details of supposed puncture site in the coleopteran immature by the sting of the hymenopteran adult. **A.** Overview photograph; lines within point out section planes of B–D; **B–D.** Colour-marked virtual sections based on μ CT of amber piece SNHM-6014 (Amira 6.1); in **green** coleopteran immature, in **red** hymenopteran adult; arrows point towards sting of hymenopteran adult; arrow-head pointing towards connection or disconnection between artefact (possible air bubble or leaked body fluid etc.) and each insect respectively; **B.** Transverse sections through coleopteran immature; 1–3 anterior to posterior sections; **C.** Frontal sections through coleopteran immature; 1–3 dorsal to ventral sections; **D.** Sagittal sections through coleopteran immature; 1–3 lateral to median sections.

post-ocular segment 11 pentagonal with a straight anterior edge and a pointed posterior edge, about as long as wide, tergite wider than sternite, also in subsequent three segments; tergite of post-ocular segment 12 (HY: metasoma segment 3; IT: abdomen segment 4) $2\times$ wider than long, about 0.3 mm long, sternite rectangular, about $3.3\times$ wider than long; tergites of post-ocular segments 13–14 (HY: metasoma segments 4–5; IT: abdomen segments 5–6) about $2.5\times$ wider than long each, metasoma tergite 4 about 0.2 mm long, metasoma tergite 5 about 0.1 mm long, sternites rectangular and $3\times$ wider than long.

Sclerites of post-ocular segments 15–16 (HY: metasoma segments 6–7, IT: abdomen segment 7–8) trapezoid in dorsal view with a longer anterior edge each; dorsal discernible sclerite of abdomen segment 7 slightly wider than long, about 0.2 mm long; dorsal discernible sclerite of abdomen segment 8 $1.5\times$ wider than long, 0.08 mm long, ventrally with no apparent segment border between these segments, trapezoid and posterior edge about one quarter width of anterior edge, also no apparent distinction into tergite and sternite; sting (modified ovipositor; appendages of abdomen segments 8 and 9 (post-ocular

segments 16–17; HY: metasoma segments 7–8)) elongated rectangular in lateral view, tapering distally, about 0.2 mm long; consisting of three discernible structures (IT: valvulae), anteriorly broadly connected with abdomen (IT: third valvulae) and posteriorly with distinct sclerotised structure (IT: first and second valvulae; HY: terebra), structure bipartite and side by side without gap, distal tip not discernible.

Description of the coleopteran immature

Coleopteran immature well preserved (compare Figs 1A, B, 2A, D, 4, 5); about 4.7 mm long; slightly dorso-ventral depressed; apparently smooth, but with many very small processes all over the tergites and sternites.

Head: Head (ocular segment and post-ocular segments 1–5) pentagonal in dorsal view with very rounded but pointed anterior edge (Figs 2A, 4E (blue)); about 0.4 mm long and 0.3 mm wide; dorsally potential moult lines discernible (IT/CO: epicranial frontal sutures), area anteriorly to that less than half the length of the head; lateral to ventral sclerite of head (IT: parietale) apparently ventrally not meeting medially, as additional sclerite (CO: gular plate (?)) present there (Figs 2A, 4E); that sclerite overall about trapezoid in ventral view, more than 2× wider than long.

Stemmata (ocular segment) very laterally discernible (but number of ocelli not discernible).

Antenna (appendage of post-ocular segment 1; CT: antennula) about 0.1 mm long; attached laterally on the anterior edge of head (Fig. 4E, turquoise); elongated rectangular in ventral view with 3 elements; antenna element 1 slightly longer than wide; antennal elements 2–3 about as wide as long each; antenna element 3 tapering into a pointed tip and laterally with one seta (CO: supplemental process).

Mouth parts: labrum (sclerite of ocular segment) and appendages of post-ocular segments 3–5 mostly discernible; attached ventrally and directed anteriorly (as is head: prognathous (IT)):

Labrum (sclerite of ocular segment) and mandibles (appendages of post-ocular segment 3) and associated structures not discernible; labrum potentially discernible at tip of head (Fig. 2A), mandibles potentially obscured by posterior mouthparts.

Maxilla (appendage of post-ocular segment 4; CT: maxillula) elongated rectangular in ventral view, with 2 elements; about two thirds the head length (Fig. 4E, bluish violet); proximal element of maxilla (IT: stipes) more than 2× longer than wide, wider than distal element; distal element tapering distally, forking into two tips (probably medially galea and lacinia (IT) and laterally maxillary palp (IT)); about 2× longer than wide at its widest; medially no further structures discernible.

Labium (appendage of post-ocular segment 5; CT: maxilla) elongated rectangular in ventral view (Fig. 4E, reddish violet); length about two thirds of the head length; 4 elements discernible: 2 proximal elements (submentum and mentum (?) (IT), anteriorly to gular plate

(?)), one medio-distal element (praementum (?) (IT)) and one distal element (the labial palps (?) (IT)); laterally on each side respectively); medio-distal element forking at its distal end into two tips; other details not discernible.

Thorax: Thorax (post-ocular segments 6–8; pro-, meso- and metathorax; Figs 4, 5); all thorax segments (mostly) rectangular with very rounded corners in dorsal view; much wider than long; overall about 0.9 mm long and about 0.6 mm wide at its widest.

Prothorax (post-ocular segment 6) more than 3× wider than long; first walking appendage (IT: foreleg) about 0.1 mm long, with 4 discernible elements: element 1 (IT: coxa) rectangular in posterior view, about 2.5× wider than long; element 2 (IT: trochanter) square-shaped in posterior view, about as long as wide; element 3 (IT: femur) trapezoid in posterior view with longer lateral than median edge, slightly wider than long; element 4 (IT/CO: tibio-tarsus(?)) triangular in posterior view with blunt tip, one claw (IT: praetarsus and claw (?)) discernible at its tip.

Mesothorax (post-ocular segment 7) pentagonal with very rounded corners in dorsal view, projecting slightly anteriorly dorsally; slightly wider than long in dorsal view and in ventral view more than 4× wider than long; convexly curved in lateral view; second walking appendage (IT: midleg) overall similar to foreleg, but about 0.2 mm long.

Metathorax (post-ocular segment 8) 3× wider than long in dorsal view and 2.3× wider than long in ventral view; third walking appendage (IT: hindleg) similar in appearance to midleg, but about 0.3 mm long.

Abdomen: Abdomen (post-ocular segments 9–19) overall very elongated rectangular, tapering distinctly posteriorly; about 3.4 mm long and 0.8 mm wide at its widest; segments all rectangular, wider than long; tergites and sternites not apparently different in form.

Tergites and sternites of abdomen segments 1–9 (post-ocular segment 9–17) all about 1.4–3× wider than long; no dorsal or posterior protrusions present on abdomen segment 9.

Tergite of trunk end (possible conjoined region of abdomen segments 10 and 11; post-ocular segments 18 and 19) slightly wider than long (at the widest point), with very rounded posterior edge, tapering posteriorly; posterior edge with at least 4 setae protruding posteriorly; more than 1.5× wider than long dorsally; two posterior directed protrusions (CO: pygopodia/postpedes(?)) ventrally with blunt end, making up about the last third of the ventral segment (Figs 2D, 4F).

Discussion

Phylogenetic position

The hymenopteran female clearly is a representative of Apocrita and can be assigned to its in-group Chrysoidea based on the following characteristics (after key in Goulet and Huber 1993): head not globular, but flat and

square-shaped (compare Figs 1D, 4A, 8A); head prognathous; malar space without depression; body hair (setation) sparse or short; forewing with three or more cells, pterostigma present and a tubular vein (C_2v or $C+R_2v$) on antero-basal part of wing (compare Fig. 3); coxa of hindleg strongly narrowed and tarsus cylindrical; metasoma very ventrally attached to mesosoma, without constriction between abdomen segments 2 and 3 and abdomen tergite 2 not longer than abdomen tergite 3.

Within Chrysoidea, it is a representative of the group Bethyloidea (flat wasps) due to the following characteristics (after key in Goulet and Huber 1993): sternum of prothorax small (often concealed; cf. Fig. 4D); trochanter of foreleg attached postero-laterally on the coxa and tibia of this leg slender; metasoma with seven externally discernible tergites. Additionally, also these characteristics can be seen (after Azevedo et al. 2018): head with well-developed compound eyes (Fig. 1D); dorsal pronotal area present (Fig. 4C) and metasternal plate large (Fig. 4D); forewing with no to seven closed cells (here: four discernible, but potentially six or even seven; compare Fig. 3) and hind wing with no closed cells (compare Fig. 3A; though hind wing incomplete); femur of foreleg swollen (in females; Figs 1A,B, 2) and foreleg with calcar (antenna cleaning apparatus; compare Fig. 2B); second abdomen segment anteriorly very narrow (“petiolar-shaped”) (Fig. 2A).

Within Bethyloidea, it is potentially a representative of Holopsenellinae Engel, Ortega & Azevedo, 2016 (Azevedo et al. 2018) due to the forewing with a tubular $Rs+M_2v$ vein and (potentially) seven closed cells. The forewing of the herein described hymenopteran female has at least four closed cells definitely discernible (R_2c , $1R_{1,2}c$, $1M_2c$ and $1Cu_2c$). The Costal cell (C_2c) is not discernible, but that is most likely because of the postero-dorsal view on the forewing (compare Fig. 3) and not an actual absence. The second Radial 1 cell ($1R_{2,c}$) is also only proximally discernible as the wing in its distal portion is cut off; but it is present and likely also closed. The second Cubital cell ($2Cu_2c$) is discernible, but apparently not closed. But in this area of the wing there is either a small stone or an air-bubble preserved which obstructs the view there (compare Figs 2A, 3A), so this cell ($2Cu_2c$) may potentially also be closed.

Within the Holopsenellinae, it seems to be most closely related to either *Cretabythus sibiricus* Evans, 1973 or *Holopsenelliscus pankowskiorum* Engel, 2019 (after key in Jouault et al. 2020). It shares the following characteristics with *C. sibiricus*: antenna elements slightly longer than wide; mandible with four teeth (apical one longest); reduced clypeus (with potential median clypeal carina); short malar space; coxae of fore- and hindleg on continuous line, coxae of midleg slightly separated from that; mesopleurae smooth; tibial spur formula also potentially matching (1-2-2, here: 1-?-2), longer spur of tibia of hindleg 0.4× length of distal element of same leg; forewing venation remarkable similar (except for the potential M_2v present in the new specimen), hind wing with strong anterior vein margin and without cells (as far as can be

seen in the new specimen); metanotum(?) discernible as thin band anterior to propodeum; metasoma slender and without unusual modifications (smooth integument). *C. sibiricus* is so far only known from one adult male from Taimyr amber (Evans 1973), is slightly smaller than the female described herein (2.5 mm of *C. sibiricus*, 3 mm of the new specimen) and features dentate claws which are lacking in the latter.

A comparison of the new specimen with *H. pankowskiorum* reveals the following shared characteristics: scapus distinctly enlarged compared with pedicellus and flagellum; clypeus not projected forward, anterior margin not emarginate (i.e. with indentation); genae broad; mandible short and thick (but *H. pankowskiorum* has only three teeth) and not obscured by the clypeus; femora distinctly swollen (particularly femur of foreleg); tibiae elongated (though more in the new specimen than in *H. pankowskiorum*), tibial spur formula also potentially matching (1-2-2, here: 1-?-2); proximal tarsus element slender, longer than wide and longest tarsus element; claws short, gently curved and simple (without teeth); forewing with closed $2R_{1,c}$ and pterostigma wider than long (but pterostigma in the new specimen longer than in *H. pankowskiorum*), other forewing venation remarkable similar (also potentially present M_2v); first metasomal tergite without ridge (transverse carina). *H. pankowskiorum* is also known from Kachin amber (Engel 2019). However, *H. pankowskiorum* differs from the new specimen in the following characteristics (Engel 2019): slightly longer (3.75 mm, new specimen just 3 mm); compound eyes circular (new specimen ovoid and shorter than in *H. pankowskiorum*); mandibles with three teeth (new specimen with four); shape of $1M_2c$ differs slightly, pterostigma length (longer in new specimen), M_2v not reaching wing margin (as it potentially does in new specimen); propodeum as wide as long (new specimen longer than wide); metasoma not petiolate (here distinctly so).

In summary, the herein described flat wasp cannot be confidently assigned to *C. sibiricus* or *H. pankowskiorum*, but neither can its inclusion in either of the two species or their genera be ruled out, as taxonomically relevant characters are only incompletely preserved. Owing to these uncertainties, we refrain from describing a new species or genus based on the new specimen.

The other individual can be unambiguously identified as a coleopteran (=beetle) immature due to its three well-articulated walking appendages and absence of other appendages posterior to the thorax (with the exception of the last externally discernible abdomen segment). Thorax appendages with four elements and a claw indicate that it is a representative of the group Polyphaga. Further identification of the immature is challenging; so far, the ample larval beetle fauna in Myanmar has not been treated in detail and the specimen lacks prominent features that would enable pinpointing of closer relationships to a specific in-group of Polyphaga. Especially the suboptimal structural resolution of the mouthparts proves detrimental in this context.

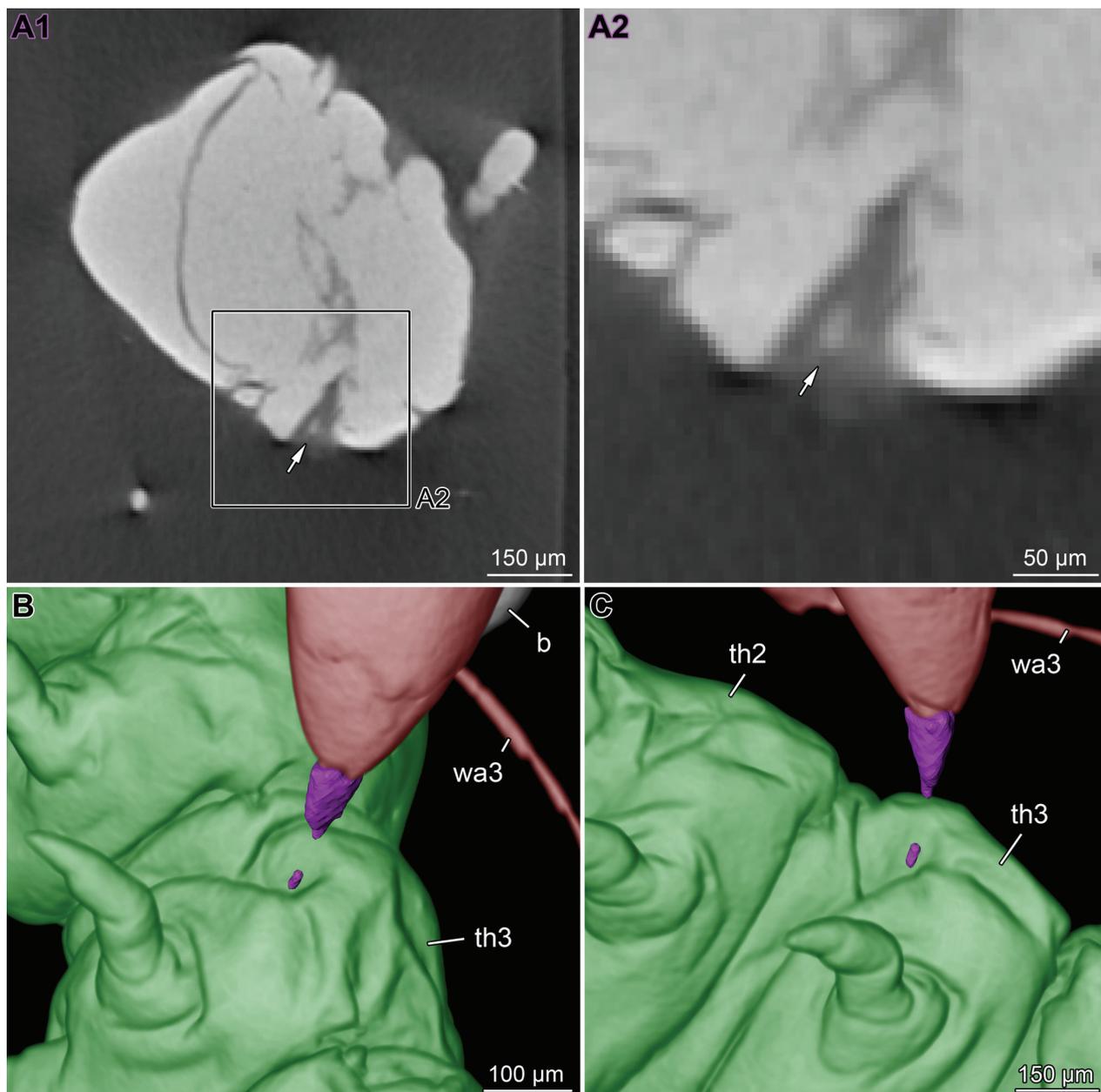


Figure 7. Details of supposed puncture site in the coleopteran immature by the sting of the hymenopteran adult (taken in Amira 6.1). **A.** Virtual section based on μ CT of amber piece SNHM-6014; transverse section through the coleopteran immature; arrow points toward supposed rest of the hymenopteran sting in the puncture site; **A1.** Overview image; **A2.** Detailed view of puncture site; **B, C.** Colour-marked volume rendering of μ CT of amber piece SNHM-6014 in slightly different views; in **green** coleopteran immature, in **red** hymenopteran adult, in **violet** the sting (3D reconstruction based on μ CT). **b** – artefact (possible air bubble or similar); **th** – thorax segment; **wa** – walking appendage.

Interpretation of the amber piece

The hymenopteran female and the coleopteran immature are in direct contact with each other. The hymenopteran's tarsi, especially the distal portion with the claws, are positioned in between segmental borders or in folds of the membranous area of the head and anterior thorax region of the coleopteran (Figs 1B, 2, 4C–E, 5A, B), possibly to facilitate better grasping of the immature. Extant females of Bethyilidae tend to grasp their progeny's coleopteran hosts during their initial attack with either both their mandibles

and their legs (Mertins 1980; Abraham et al. 1990; Howard et al. 1998), just the legs (Gordh and Medved 1986 [indirectly inferred]; Amante et al. 2017) or just the mandibles (Kühne and Becker 1974; Gordh and Hawkins 1981).

Additionally, the sting (modified ovipositor) of the wasp seems to be inserted into the metathorax of the coleopteran. This is clearly discernible in the macrophotographs (compare Figs 1, 2A, 5A), but less apparent in the μ CT data (compare Figs 4–6), which might be a result of too low contrast in X-ray due to preservation of this fine structure (as has been shown for other structures; see

Rühr and Lambertz 2019). However, there appears to be a small structure within the apparent puncture site that may belong to the sting (compare Fig. 7), being located where the tip of its sting (specifically the terebra) would be expected by extrapolation (Fig. 7B,C). Regardless of whether this small structure indeed represents the sting's tip or not, it appears that the sting of the wasp applied pressure onto the metathorax of the coleopteran and most likely also penetrated it, as a well-defined pressure site is present (esp. Figs 5D, 6B3, 7A, see also macrophotographs Figs 1, 2).

Notably, the amber displays no discernible layers around both insects, indicating that either the embedding in the resin was sudden and fast or that they did not move (much) during the process (incl. wriggling of the coleopteran immature as defensive behaviour; compare with Kühne and Becker 1974; Mertins 1980; Hu et al. 2012; Polaszek et al. 2019, S1 video). Together with the positioning of the wasp's sting and legs, this leaves two alternative explanations for the behaviour captured in the piece.

1) The wasp may have been caught in the process of paralysing the coleopteran. Since some extant representatives of Bethyridae sit and wait on the host until it is fully paralysed after the sting (Evans 1964; Kühne and Becker 1974; Abraham et al. 1990; Howard et al. 1998; Lauzière et al. 2000), a similar behaviour may explain the apparent lack of movement in the syninclusions studied here.

2) Other extant representatives of Bethyridae are motionless during oviposition, which may last several minutes (Gordh and Medved 1986; Abraham et al. 1990). Accordingly, it would be likewise possible that the wasp was in the process of ovipositing onto the coleopteran instead. As evidence against this, the body posture of the fossil wasp (compare Figs 1, 2A) lacks some of the characteristics typically observed in extant flat wasps during oviposition, such as the telescoped and arched metasomal segments, as well as a contorted hypopygium (last externally discernible abdomen segment) that permits egg extrusion (Gordh and Medved 1986). Furthermore, the sting is not always inserted into the host, but sometimes just closely pressed to it during oviposition (Gordh and Medved 1986). Thus, it is more probable that the herein described female wasp was preserved while stinging the coleopteran immature, rather than ovipositing onto it.

Parasitism/Parasitoidism in the fossil record

Direct interactions between parasites/parasitoids and their hosts in the fossil record are rare, but not completely unknown. Relatively well-documented examples of such interactions are e.g. nematode worms parasitizing different insects (endoparasitism), primarily representatives of Diptera (flies and mosquitoes), Formicidae (in-group of Hymenoptera; ants) and Hemiptera (true bugs) (e.g. Grimaldi 1996; Poinar 2003; Poinar and Buckley 2006; Arillo 2007; see also Boucot and Poinar 2010 and references

therein), with numerous cases of the nematodes emerging from their hosts preserved in amber. Similarly common are mites and ticks (ectoparasitism) as temporary parasites (see van der Wal and Haug JT 2019; Hörnig et al. 2020 for discussion of the term) especially on representatives of dipterans, moths (Lepidoptera) and scale insects (in-group of Hemiptera) (Arillo 2007; Boucot and Poinar 2010).

The majority of hymenopterans are parasitic, specifically parasitoid (e.g. Rasnitsyn 1980). In fact, parasitoidism is widely assumed to be the key innovation underlying the massive radiation within Hymenoptera (Gaston 1991; Davis et al. 2010; Huber 2017) which began in the Mesozoic (Rasnitsyn 1980; Rasnitsyn and Quicke 2002). Most likely, it evolved only once within the group Vespinina (Orussoidea+Apocrita; e.g. Rasnitsyn 1980; Gauld and Bolton 1988; Whitfield 2003) and some in-groups of Apocrita (specifically within the Aculeata) have secondarily lost it again (e.g. Snelling 1981; Anderson 1984; Gauld and Bolton 1988; Danforth 2002). Due to the early origin of parasitoidism within Hymenoptera, we should expect to find such parasitoid wasps regularly as fossils.

In line with this notion, the majority of the fossil hymenopterans hitherto described do indeed represent parasitoids. Beyond this, there are even some examples of direct interaction between the larval parasitoid or its parent and its host. There are two reports of wasps embedded during (supposed) oviposition: a representative of Stigmaphronidae (Arillo 2007; previously assigned to Megaspilidae by Alonso et al. 2000) ovipositing into/(onto?) a dipteran (Alonso et al. 2000, fig. 12-1) in Spanish amber (Álava) and a representative of Ichneumonidae ovipositing into a caterpillar (Wunderlich 1986 in Arillo 2007) in Baltic amber. Furthermore, there are other representatives of Ichneumonidae, which have also been found in direct interaction with their host, namely: an immature attached to a spider in Dominican amber (Poinar 1992 in Arillo 2007) and a cocoon adjacent to the seemingly depleted eggs of a spider in Baltic amber (Poinar 2004 in Arillo 2007; Boucot and Poinar 2010, fig. 60). An immature representative of the related group Braconidae has also been described emerging from an ant in Baltic amber (Poinar and Miller 2002).

Another well recorded group within amber is Dryinidae. The immatures of its extant representatives are ectoparasitic (and/or endoparasitic) on auchenorrhynchs (in-group of Hemiptera) (Goulet and Huber 1993; Olmi and Virla 2006; Guglielmino et al. 2013) and there are multiple syninclusions in Dominican amber that illustrate corresponding parasitism of immature representatives of Dryinidae on representatives of Fulgoroidea (in-group of Auchenorrhyncha; Poinar 1992, fig. 140, Poinar and Poinar 1999, fig. 140, and Ross 1998, fig. 73, in Arillo 2007; Poinar 2001; Grimaldi and Engel 2005, fig. 11.37; Boucot and Poinar 2010, fig. 56) and Cicadellidae (also in-group of Auchenorrhyncha; Grimaldi 1996, p. 97).

An unidentified hymenopteran immature is depicted in Boucot and Poinar (2010, fig. 58) emerging from an adult trichopteran (caddisfly) (also described in Poinar and Anderson 2005 in Boucot and Poinar 2010) in Baltic amber.

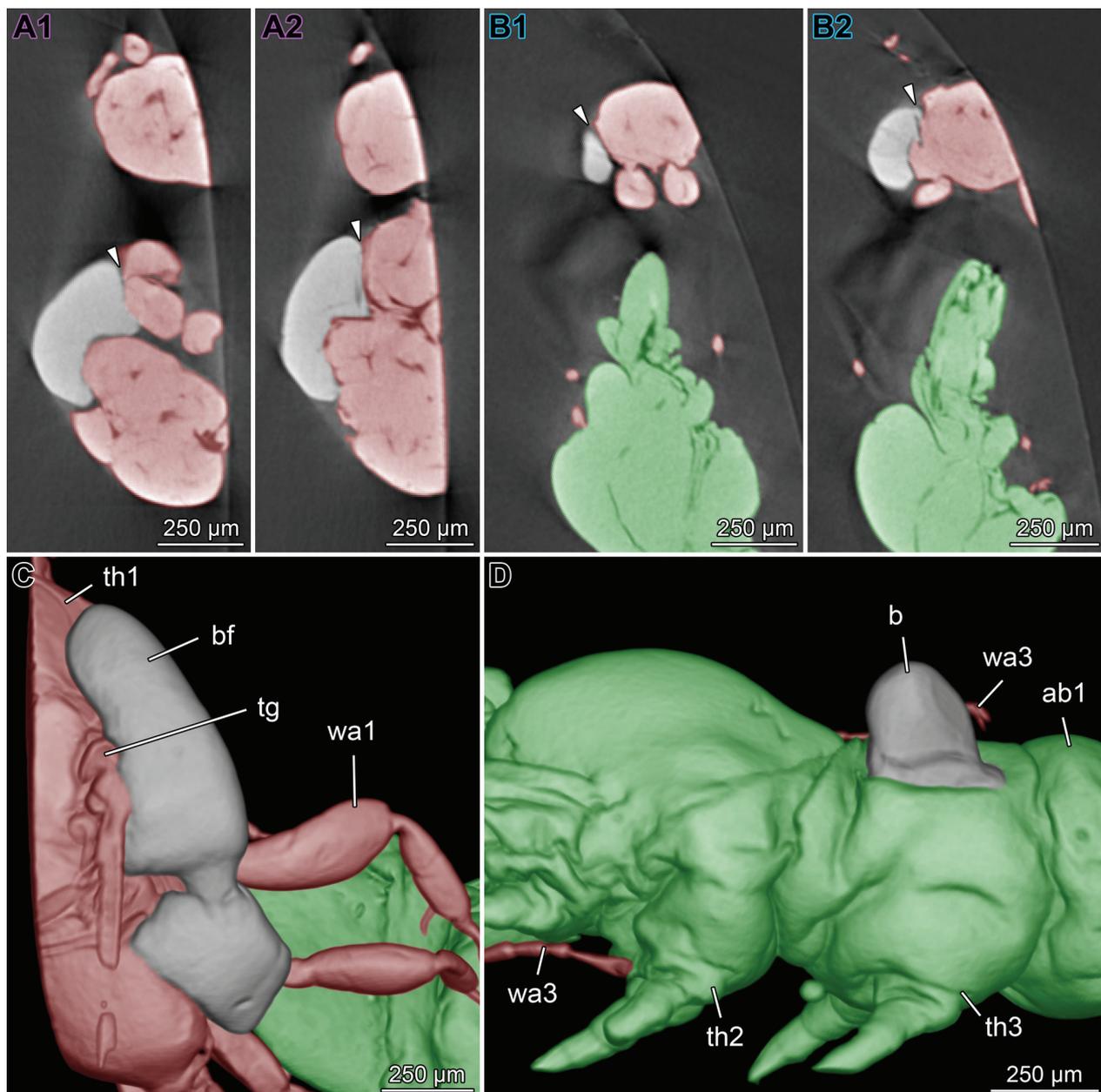


Figure 8. Details of artefacts on the hymenopteran adult and the coleopteran immature in amber piece SNHM-6014 (taken in Amira 6.1). **A, B.** Virtual section based on μ CT of amber piece SNHM-6014; in **green** coleopteran immature, in **red** hymenopteran adult; arrowhead pointing towards connection or disconnection between artefact (possible air bubble or leaked body fluid etc.) and the hymenopteran adult. **A.** Sagittal sections through hymenopteran adult; 1–2 ventral to dorsal sections; **B.** Transverse sections through hymenopteran adult; 1–2 anterior to posterior sections; **C, D.** Colour-marked volume rendering of μ CT of amber piece SNHM-6014; in **green** coleopteran immature, in **red** hymenopteran adult; **C.** Dorsal view on thorax of hymenopteran adult and artefacts there; **D.** Lateral view on mirrored thorax of coleopteran immature and artefacts there. **ab** – abdomen segment; **b** – artefact (possible air bubble or similar); **bf** – artefact (possible leaked body fluid or similar); **tg** – tegula (part of wing joint area); **th** – thorax segment; **wa** – walking appendage.

Conclusions

Examples of group fossilisation as cases of ‘frozen behaviour’ are of high value for the reconstruction of behavioural aspects and the evolution of lifestyles. Even if many species of fossil insects, and particularly hymenopterans (almost 2,500 fossil species; Aguiar et al. 2013), have been described, our knowledge about their way of life, including intra- and inter-specific interactions, is still very limited.

Adding further findings, such as the here represented specimen, will help to reach a better understanding of the food-web and therefore ecological impact of different arthropod groups in deep-time. This is especially important as the currently available data on food-webs of palaeo-ecosystems does not allow us to conclude a comprehensive view of interactions between extinct organism groups.

The specimen herein is, besides the representative of the Stigmaphronidae with a dipteran specimen in Spanish

amber (Alonso et al. 2000; Arillo 2007), one of the oldest examples of interaction of an adult hymenopteran with a putative host of their immatures and the oldest documentation of an interaction of flat wasps (Bethyridae) and coleopteran immatures. This indicates that the interaction between parasitoid flat wasp immatures and coleopteran immatures, as seen today, already existed at least about 100 million years ago.

Acknowledgments

CK is kindly funded by the Landesgraduiertenförderung MV. The Volkswagen Foundation kindly funds JTH with a Lichtenberg Professorship. Micro-computed tomography was performed at the Imaging Center of the Department of Biology, University of Greifswald (DFG INST 292/119-1 FUGG; DFG INST 292/120-1 FUGG). We thank C. Haug, Munich, and G. Brenneis, Greifswald, for their help and suggestions improving the manuscript. CK, JTH and MKH thank J. M. Starck, Munich, and S. Harzsch, Greifswald, for their continuous support. We would also like to thank an anonymous reviewer for helpful comments that helped improve the manuscript. We highly appreciate the effort of all people involved in providing open access, open source and low cost software.

References

- Abraham YJ, Moore D, Godwin G (1990) Rearing and aspects of biology of *Cephalonomia stephanoderis* and *Prorops nasuta* (Hymenoptera: Bethyridae) parasitoids of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* 80(2): 121–128. <https://doi.org/10.1017/S000748530001333X>
- Alonso J, Arillo A, Barrón E, Corral JC, Grimalt J, López JF, López R, Martínez-Delclós X, Ortuño V, Peñalver E, Trincão PR (2000) A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (Northern Spain, Basque-Cantabrian Basin). *Journal of Paleontology* 74(1): 158–178. <https://doi.org/10.1017/S0022336000031334>
- Amante M, Schöller M, Hardy ICW, Russo A (2017) Reproductive biology of *Holepyris sylvanidis* (Hymenoptera: Bethyridae). *Biological Control* 106: 1–8. <https://doi.org/10.1016/j.biocontrol.2016.12.004>
- Anderson M (1984) The evolution of eusociality. *Annual Review of Ecology and Systematics* 15: 165–189. <https://doi.org/10.1146/annurev.es.15.110184.001121>
- Aguiar AP, Deans AR, Engel MS, Forshage M, Huber JT, Jennings JT, Johnson NF, Lelej AS, Longino JT, Lohrmann V, Mikó I, Ohl M, Rasmussen C, Taeger A, Yu DSK (2013) Order Hymenoptera. In: Zhang Z-Q (Ed.) *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness* (Addenda 2013). *Zootaxa* 3703(1): 51–62. <https://doi.org/10.11646/zootaxa.3703.1.12>
- Arillo A (2007) Paleoethology: Fossilized behaviours in amber. *Geologica Acta* 5(2): 159–166. <https://doi.org/10.1344/105.000000301>
- Azevedo CO, Alencar IDCC, Ramos MS, Barbosa DN, Colombo WD, Vargas JMR, Lim J (2018) Global guide of the flat wasps (Hymenoptera, Bethyridae). *Zootaxa* 4489(1): 1–294. <https://doi.org/10.11646/zootaxa.4489.1.1>
- Boucot AJ (1990) *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier Science Publishers B.V., Amsterdam (Netherlands), 725 pp.
- Boucot AJ, Poinar Jr GO (2010) *Fossil Behavior Compendium*. 1st Edn. CRC Press, Boca Raton (Florida, USA), 324 pp. <https://doi.org/10.1201/9781439810590>
- Breed MD, Cook C, Krasnec MO (2012) Cleptobiosis in social insects. *Psyche: A Journal of Entomology* 2012(Special Issue): e484765. <https://doi.org/10.1155/2012/484765>
- Brues CT (1939) New Oligocene Braconidae and Bethyridae from Baltic Amber. *Annals of the Entomological Society of America* 32(2): 251–263. <https://doi.org/10.1093/aesa/32.2.251>
- Casale A (1991) Some notes on the parental and parasocial behaviour of *Scleroderma domesticus* Latreille (Hymenoptera Bethyridae). *Ethology Ecology & Evolution* 3(sup1): 34–38. <https://doi.org/10.1080/03949370.1991.10721905>
- Cheng LL, Howard RW, Campbell JF, Charlton RE, Nechols JR, Ramaswamy SB (2004) Mating behavior of *Cephalonomia tarsalis* (Ashmead) (Hymenoptera: Bethyridae) and the effect of female mating frequency on offspring production. *Journal of Insect Behavior* 17(2): 227–245. <https://doi.org/10.1023/B:JOIR.0000028572.76021.d9>
- Cockerell TDA (1917a) Arthropods in Burmese amber. *Psyche: A Journal of Entomology* 24: 40–45. <https://doi.org/10.1155/1917/83242>
- Cockerell TDA (1917b) Arthropods in Burmese amber. *American Journal of Science* s4-44(263): 360–368. <https://doi.org/10.2475/ajs.s4-44.263.360>
- Colombo WD, Gobbi FT, Perkovsky EE, Azevedo CO (2020) Synopsis of the fossil *Pristocerinae* (Hymenoptera, Bethyridae), with description of two new genera and six species from Burmese, Taimyr, Baltic and Rovno ambers. *Historical Biology* 33(9): 1736–1752. <https://doi.org/10.1080/08912963.2020.1733551>
- Crowson RA (1981) *The Biology of the Coleoptera*. Academic Press, London (UK), 802 pp. <https://doi.org/10.1016/C2013-0-07304-5>
- Cruikshank RD, Ko K (2003) Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* 21: 441–455. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- Daintith J, Martin EA (2010) *A Dictionary of Science* (Oxford Paperback Reference). 6th Edn. Oxford University Press, Oxford (UK), 900 pp.
- Danforth BN (2002) Evolution of sociality in a primitively eusocial lineage of bees. *Proceedings of the National Academy of Sciences of the United States of America* (PNAS) 99(1): 286–290. <https://doi.org/10.1073/pnas.012387999>
- Davis RB, Baldauf SL, Mayhew PJ (2010) The origins of species richness in the Hymenoptera: Insights from a family-level supertree. *BioMed Central (BMC) Evolutionary Biology* 10(1): e109. <https://doi.org/10.1186/1471-2148-10-109>
- Engel MS (2019) A holopsenelline wasp in mid-Cretaceous amber from Myanmar (Hymenoptera: Bethyridae). *Palaeoentomology* 002(2): 199–204. <https://doi.org/10.11646/palaeoentomology.2.2.10>
- Evans HE (1962) The evolution of prey-carrying mechanisms in wasps. *Evolution* 16(4): 468–483. <https://doi.org/10.2307/2406179>
- Evans HE (1964) A synopsis of the American Bethyridae (Hymenoptera, Aculeata). *Bulletin of the Museum of Comparative Zoology, Harvard University* 132(1): 1–222. <https://www.biodiversitylibrary.org/item/25435#page/11/mode/1up>
- Evans HE (1973) Cretaceous aculeate wasps from Taimyr, Siberia (Hymenoptera). *Psyche: A Journal of Entomology* 80: 166–178. <https://doi.org/10.1155/1973/16876>

- Finlayson LH (1950) The Biology of *Cephalonomia waterstoni* Gahan (Hym., Bethyilidae), a Parasite of *Laemophloeus* (Col., Cucujidae). Bulletin of Entomological Research 41(1): 79–97. <https://doi.org/10.1017/S0007485300027498>
- Fischer TC, Hörnig MK (2019) Mating moths (Tineidae, Ditrysiinae, Lepidoptera) preserved as frozen behavior inclusion in Baltic Amber (Eocene). Palaeontologia Electronica 22.1.7: 1–10. <https://doi.org/10.26879/829>
- Gao SK, Wei K, Tang YL, Wang XY, Yang ZQ (2016) Effect of parasitoid density on the timing of parasitism and development duration of progeny in *Scleroderma pupariae* (Hymenoptera: Bethyilidae). Biological Control 97: 57–62. <https://doi.org/10.1016/j.biocontrol.2016.03.003>
- Gaston KJ (1991) The Magnitude of Global Insect Species Richness. Conservation Biology 5(3): 283–296. <https://doi.org/10.1111/j.1523-1739.1991.tb00140.x>
- Gauld I, Bolton B [Eds] (1988) The Hymenoptera. British Museum (Natural History) Oxford University Press, New York (USA), 332 pp.
- Goater TM, Goater CP, Esch GW (2014) Parasitism. The diversity and ecology of the animal parasites. 2nd Edn. Cambridge University Press, Cambridge (UK), 498 pp. <https://doi.org/10.1017/CBO9781139047876>
- Gordh G (1998) A New Species of *Sierola* Parasitic on Moth Larvae in Western Australia (Hymenoptera: Bethyilidae). Proceedings of the Hawaiian Entomological Society 33: 83–88. <http://hdl.handle.net/10125/16306>
- Gordh G, Hawkins B (1981) *Goniozus emigratus* (Rohwer), a primary external parasite of *Paramyelois transitella* (Walker), and comments on bethylids attacking Lepidoptera (Hymenoptera: Bethyilidae; Lepidoptera: Pyralidae). Journal of the Kansas Entomological Society 54(4): 787–803. <https://www.jstor.org/stable/25084238>
- Gordh G, Medved RE (1986) Biological notes on *Goniozus pakmanus* Gordh (Hymenoptera: Bethyilidae), a parasite of pink bollworm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae). Journal of the Kansas Entomological Society 59(4): 723–734. <https://www.jstor.org/stable/25084850>
- Goulet H, Huber JT [Eds] (1993) Hymenoptera of the world: An identification guide to families. Canada Communication Group Publishing, Ottawa (Canada), 668 pp. <https://cfs.nrcan.gc.ca/publications?id=35617>
- Griffiths NT, Godfray HCJ (1988) Local mate competition, sex ratio and clutch size in bethylid wasps. Behavioral Ecology and Sociobiology 22(3): 211–217. <https://doi.org/10.1007/BF00300571>
- Grimaldi DA (1996) Amber: Window to the Past. Harry N. Abrams/American Museum of Natural History, New York (USA), 216 pp.
- Grimaldi DA, Engel MS (2005) Evolution of the Insects. Cambridge University Press, New York (USA), 755 pp.
- Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous Amber from Myanmar (Burma): Its Rediscovery, Biotic Diversity, and Paleontological Significance. American Museum Novitates 2002(3361): 1–71. [https://doi.org/10.1206/0003-0082\(2002\)361%3C0001:FCAFMB%3E2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)361%3C0001:FCAFMB%3E2.0.CO;2)
- Grissell EE (1999) Hymenopteran biodiversity: some alien notions. American Entomologist 45(4): 235–244. <https://doi.org/10.1093/ae/45.4.235>
- Gröhn C (2015) Einschlüsse in Baltischem Bernstein. 1st Edn. Wacholtz Verlag/Murmann Publishers, Kiel/Hamburg (Germany), 424 pp. [in German]
- Guglielmino A, Olmi M, Bückle C (2013) An updated host-parasite catalogue of world Dryinidae (Hymenoptera: Chrysoidea). Zootaxa 3740(1): 1–113. <https://doi.org/10.11646/zootaxa.3740.1.1>
- Hasiotis ST (2003) Complex ichnofossils of solitary and social soil organisms: Understanding their evolution and roles in terrestrial paleoecosystems. Palaeogeography, Palaeoclimatology, Palaeoecology 192(1–4): 259–320. [https://doi.org/10.1016/S0031-0182\(02\)00689-2](https://doi.org/10.1016/S0031-0182(02)00689-2)
- Haug C, Mayer G, Kutschera V, Waloszek D, Maas A, Haug JT (2011) Imaging and documenting gammarideans. International Journal of Zoology 2011: e380829. [9 pp] <https://doi.org/10.1155/2011/380829>
- Haug JT, Haug C, Garwood RJ (2016) Evolution of insect wings and development—new details from Palaeozoic nymphs. Biological Reviews 91(1): 53–69. <https://doi.org/10.1111/brv.12159>
- Haug JT, Waloszek D, Maas A, Liu Y, Haug C (2012) Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. Palaeontology 55: 369–399. <https://doi.org/10.1111/j.1475-4983.2011.01124.x>
- Haug JT, Kiesmüller C, Haug GT, Haug C, Hörnig MK (2022) A fossil aphidion preserved together with its prey in 40 million-year-old Baltic amber. Palaeobiodiversity and Palaeoenvironments: 1–9. <https://doi.org/10.1007/s12549-021-00521-z>
- Hörnig MK, Haug JT, Haug C (2013) New details of *Santanmantis axelrodi* and the evolution of the mantodean morphotype. Palaeodiversity 6: 157–168.
- Hörnig MK, Haug JT, Haug C (2017) An exceptionally preserved 110 million years old praying mantis provides new insights into the predatory behaviour of early mantodeans. PeerJ Life & Environment 5: e3605. <https://doi.org/10.7717/peerj.3605>
- Hörnig MK, Fischer TC, Haug JT (2019) Caught in the act of hatching—a group of heteropteran nymphs escaping from their eggs preserved in Dominican amber. Palaeodiversity 12(1): 123–134. <https://doi.org/10.18476/pale.v12.a12>
- Hörnig MK, Haug C, Schneider JW, Haug JT (2018) Evolution of reproductive strategies in dictyopteran insects—clues from ovipositor morphology of extinct roachoids. Acta Palaeontologica Polonica 63(1): 1–24. <https://doi.org/10.4202/app.00324.2016>
- Hörnig MK, Haug C, Müller P, Haug JT (2022) Not quite social—possible cases of gregarious behaviour of immatures of various lineages of Insecta in 100-million-year-old amber. Bulletin of Geoscience 97(1): 69–87. <https://doi.org/10.3140/bull.geosci.1818>
- Hörnig MK, Sombke A, Haug C, Harzsch S, Haug JT (2016) What nymphal morphology can tell us about parental investment—a group of cockroach hatchlings in Baltic Amber documented by a multi-method approach. Palaeontologia Electronica 19.1.6A: 1–20. <https://doi.org/10.26879/571>
- Hörnig MK, Kiesmüller C, Müller P, Haug C, Haug JT (2020) A new glimpse on trophic interactions of 100-million-year old lacewing larvae. Acta Palaeontologica Polonica 65(4): 777–786. <https://doi.org/10.4202/app.00677.2019>
- Howard RW, Flinn PW (1990) Larval trails of *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) as kairomonal host-finding cues for the parasitoid *Cephalonomia waterstoni* (Hymenoptera: Bethyilidae). Annals of the Entomological Society of America 83(2): 239–245. <https://doi.org/10.1093/aesa/83.2.239>
- Howard RW, Charlton M, Charlton RE (1998) Host-finding, host-recognition, and host-acceptance behavior of *Cephalonomia tarsalis* (Hymenoptera: Bethyilidae). Annals of the Entomological Society of America 91(6): 879–889. <https://doi.org/10.1093/aesa/91.6.879>
- Hsieh S, Plotnick RE (2020) The representation of animal behaviour in the fossil record. Animal Behaviour 169: 65–80. <https://doi.org/10.1016/j.anbehav.2020.09.010>

- Hu Z, Zhao X, Li Y, Liu X, Zhang Q (2012) Maternal Care in the Parasitoid *Sclerodermus harmandi* (Hymenoptera: Bethylinidae). *PLoS ONE* 7(12): e51246. <https://doi.org/10.1371/journal.pone.0051246>
- Huber JT (2017) Biodiversity of Hymenoptera. In: Fottitt RG, Adler PH (Eds) *Insect Biodiversity: Science and Society*. Vol. I, 2nd Edn. John Wiley & Sons Ltd., West Sussex (UK), 419–461. <https://doi.org/10.1002/9781444308211.ch12>
- Jouault C, Brazidec M (2021) A new protopristocerine wasp (Hymenoptera: Bethylinidae) from the mid-Cretaceous Burmese amber. *Annales de Paléontologie* 107(4): 102522. <https://doi.org/10.1016/j.annpal.2021.102522>
- Jouault C, Perrichot V, Nel A (2021) New flat wasps from mid-Cretaceous Burmese amber deposits highlight the bethylin antiquity and paleobiogeography (Hymenoptera: Chrysidoidea). *Cretaceous Research* 123(21): 104772. <https://doi.org/10.1016/j.cretres.2021.104772>
- Jouault C, Ngô-Muller V, Pouillon J-M, Nel A (2020) New Burmese amber fossils clarify the evolution of bethylin wasps (Hymenoptera: Chrysidoidea). *Zoological Journal of the Linnean Society* 191(4): 1044–1058. <https://doi.org/10.1093/zoolinnean/zlaa078>
- Jucker C, Hardy IC, Malabusini S, de Milato S, Zen G, Savoldelli S, Lupi D (2020) Factors affecting the reproduction and mass-rearing of *Sclerodermus brevicornis* (Hymenoptera: Bethylinidae), a natural enemy of exotic flat-faced longhorn beetles (Coleoptera: Cerambycidae: Lamiinae). *Insects* 11(10): e657. [22 pp] <https://doi.org/10.3390/insects11100657>
- Kathirithamby J (2009) Host-Parasitoid Associations in Strepsiptera. *Annual Review of Entomology* 54(1): 227–249. <https://doi.org/10.1146/annurev.ento.54.110807.090525>
- Klausnitzer B (1978) *Ordnung Coleoptera (Larven)*. Springer-Science+Business Media, B.V., Dordrecht (Netherlands), 378 pp. <https://doi.org/10.1007/978-94-009-9975-6> [in German]
- Kühne H, Becker G (1974) Zur Biologie und Ökologie von *Scleroderma domesticum* Latreille (Bethylinidae, Hymenoptera), einem Parasiten holzzerstörender Insektenlarven. *Zeitschrift für Angewandte Entomologie* 76: 278–303. <https://doi.org/10.1111/j.1439-0418.1974.tb01888.x> [in German]
- Lafferty KD, Kuris AM (2002) Trophic strategies, animal diversity and body size. *Trends in Ecology and Evolution* 17(11): 507–513. [https://doi.org/10.1016/S0169-5347\(02\)02615-0](https://doi.org/10.1016/S0169-5347(02)02615-0)
- Lanes GO, Kawada R, Azevedo CO, Brothers DJ (2020) Revisited morphology applied for Systematics of flat wasps (Hymenoptera, Bethylinidae). *Zootaxa* 4752(1): 1–127. <https://doi.org/10.11646/zootaxa.4752.1.1>
- Lauzière I, Pérez-Lachaud G, Brodeur J (2000) Behavior and Activity Pattern of *Cephalonomia stephanoderis* (Hymenoptera: Bethylinidae) Attacking the Coffee Berry Borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Journal of Insect Behavior* 13(3): 375–395. <https://doi.org/10.1023/A:1007762202679>
- Lepecho A, Melo GAR (2021) The wasp genus †*Holopsenella* in mid-Cretaceous Burmese amber (Hymenoptera: †Holopsenellidae stat. nov.). *Cretaceous Research* 131: 105089. <https://doi.org/10.1016/j.cretres.2021.105089>
- Litman JR (2019) Under the radar: Detection avoidance in brood parasitic bees. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374: 20180196. <https://doi.org/10.1098/rstb.2018.0196>
- Lucius R, Loos-Frank B, Lane RP, Poulin R, Roberts CW, Grens RK (2017) *The Biology of Parasites*. Wiley-VCH Verlag GmbH & Co. KGaA, Weinheim (Germany), 452 pp.
- Martínez-Delclòs X, Briggs DEG, Peñalver (2004) Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203(1–2): 19–64. [https://doi.org/10.1016/S0031-0182\(03\)00643-6](https://doi.org/10.1016/S0031-0182(03)00643-6)
- Mayhew PJ, Heitmans WRB (2000) Life history correlates and reproductive biology of *Laelius pedatus* (Hymenoptera: Bethylinidae) in The Netherlands. *European Journal of Entomology* 97(3): 313–322. <https://doi.org/10.14411/eje.2000.048>
- Mertins JW (1980) Life history and behavior of *Laelius pedatus*, a gregarious bethylin ectoparasitoid of *Anthrenus verbasci*. *Annals of the Entomological Society of America* 73(6): 686–693. <https://doi.org/10.1093/aesa/73.6.686>
- Nentwig W, Bacher S, Brandl R (2017) *Ökologie kompakt*. 4th Edn. Springer Spektrum, Berlin/Heidelberg (Germany), 369 pp. <https://doi.org/10.1007/978-3-662-54352-8> [in German]
- Noetling F (1893) On the Occurrence of Burmite, a new Fossil Resin from Upper Burma. *Records of the Geological Survey of India* 26(1): 31–40.
- Olmi M, Virla E (2006) Familia Dryinidae. In: Fernández F, Sharkey MJ (Eds) *Introducción a los Hymenoptera de la Región Neotropical*. Serie Entomología Colombiana. Sociedad Colombiana de Entomología y Universidad Nacional de Colombia, Bogotá D. C. (Columbia), 401–418. <https://repository.agrosavia.co/handle/20.500.12324/34432> [in Spanish]
- Olsen OW (1974) *Animal parasites. Their Life Cycles and Ecology*. 3rd Edn. Dover Publications Inc., New York (USA), 562 pp.
- Paracer S, Ahmadjian V (2000) *Symbiosis. An Introduction to Biological Associations*. 2nd Edn. Oxford University Press, Inc., New York (USA), 291 pp.
- Pérez de la Fuente R, Engel MS, Azar D, Peñalver E (2019) The hatching mechanism of 130-million-year-old insects: an association of neonates, egg shells and egg bursters in Lebanese amber. *Palaeontology* 62(4): 547–559. <https://doi.org/10.1111/pala.12414>
- Poinar Jr GO (2001) Dominican amber. In: Briggs DEG, Crowther PR (Eds) *Paleobiology II*. Blackwell Science Ltd., Oxford (UK), 362–364. <https://doi.org/10.1002/9780470999295.ch86>
- Poinar Jr GO (2003) Trends in the evolution of insect parasitism by nematodes as inferred from fossil evidence. *Journal of Nematology* 35(2): 129–132. <https://www.ncbi.nlm.nih.gov/pubmed/19265986>
- Poinar Jr GO (2019) Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Historical Biology* 31(10): 1304–1309. <https://doi.org/10.1080/08912963.2018.1446531>
- Poinar Jr GO, Miller JC (2002) First fossil record of endoparasitism of adult ants (Formicidae: Hymenoptera) by Braconidae (Hymenoptera). *Annals of the Entomological Society of America* 95(1): 42–43. [https://doi.org/10.1603/0013-8746\(2002\)095\[0041:FFROEJ\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2002)095[0041:FFROEJ]2.0.CO;2)
- Poinar Jr GO, Buckley R (2006) Nematode (Nematoda: Mermithidae) and hairworm (Nematomorpha: Chordodidae) parasites in Early Cretaceous amber. *Journal of Invertebrate Pathology* 93(1): 36–41. <https://doi.org/10.1016/j.jip.2006.04.006>
- Polaszek A, Almandhari T, Fusu L, Al-Khatiri SAH, Al Naabi S, Al Shidi RH, Hardy ICW (2019) *Goniozus omanensis* (Hymenoptera: Bethylinidae) an important parasitoid of the lesser date moth *Batrachedra amydraula* Meyrick (Lepidoptera: Batrachedridae) in Oman. *PLoS ONE* 14(12): e0223761. <https://doi.org/10.1371/journal.pone.0223761>
- Poulin R (2011) Chapter 1—The many roads to parasitism. A tale of convergence. In: Rollinson D, Hay SI (Eds) *Advances in*

- Parasitology. 1st Edn., Vol. 74, Iss. C. Elsevier Ltd., Oxford (UK), 1–40. <https://doi.org/10.1016/B978-0-12-385897-9.00001-X>
- Powell D (1938) The Biology of *Cephalonomia tarsalis* (Ash.), a Vespid Wasp (Bethyridae: Hymenoptera) Parasitic on the Sawtoothed Grain Beetle. *Annals of the Entomological Society of America* 31(1): 44–49. <https://doi.org/10.1093/aesa/31.1.44>
- Price PW (1980) *Evolutionary Biology of Parasites*. Monographs in Population Biology Vol. 15. Princeton University Press, Princeton (New Jersey, USA), 256 pp.
- Rasnitsyn AP (1980) Proizhozhdenie i evoliutia pereponchatokrilih nasekomih [= The Origin and Evolution of the Hymenopterous Insects]. Akademia Nauk SSSR, Trudi Paleontologicheskogo Instituta, Tom 174 [= Transactions of the Paleontological Institute, Academy of Sciences of the USSR, Vol. 174]. Izdatelstvo “Nauka” [= “Science” Publishing House], Moscow (Russia), 192 pp. [in Russian]
- Rasnitsyn AP, Quicke DL (2002) *History of insects*. Kluwer Academic Publishers, Dordrecht (Netherlands), 517 pp. <https://doi.org/10.1007/0-306-47577-4>
- Reif W-E (1983) Functional morphology and evolutionary biology. *Paläontologische Zeitschrift* 57(3–4): 255–266. <https://doi.org/10.1007/BF02990316>
- Ross AJ (2021) Burmese (Myanmar) amber taxa. on-line supplement v.2021.1, 27 pp. <http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/>
- Rothschild M, Clay T (1957) *Fleas, Flukes & Cuckoos. A Study of Bird Parasites*. The Macmillan Company, New York (USA), 305 pp. <https://www.biodiversitylibrary.org/item/28804#page/7/mode/1up>
- Rubink WL, Evans HE (1979) Notes on the nesting behavior of the Bethyrid wasp, *Epyris eriogoni* Kieffer, in Southern Texas. *Psyche: A Journal of Entomology* 86(4): 313–319. <https://doi.org/10.1155/1979/58308>
- Rühr PT, Lambertz M (2019) Surface contrast enhancement of integumentary structures in X-ray tomography. *Journal of Anatomy* 235(2): 379–385. <https://doi.org/10.1111/joa.13008>
- Schaefer CH (1962) Life History of *Conophthorus radiatae* (Coleoptera: Scolytidae) and its Principal Parasite, *Cephalonomia utahensis* (Hymenoptera: Bethyridae). *Annals of the Entomological Society of America* 55(5): 569–577. <https://doi.org/10.1093/aesa/55.5.569>
- Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang M, Lei W, Li Q, Li X (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163. <https://doi.org/10.1016/j.cretres.2012.03.014>
- Snelling RR (1981) Systematics of social Hymenoptera. In: Hermann HR (Ed.) *Social insects*. Vol. II, 2nd Edn. Academic Press Inc., New York (USA), 369–453. <https://doi.org/10.1016/B978-0-12-342202-6.50012-5>
- Tang X, Meng L, Kapranas A, Xu F, Hardy ICW, Li B (2014) Mutually beneficial host exploitation and ultra-biased sex ratios in quasi-social parasitoids. *Nature Communications* 5: e4942. <https://doi.org/10.1038/ncomms5942>
- Thomason J [Ed.] (1997) *Functional Morphology in Vertebrate Paleontology*. 1st Paperback Edn. Cambridge University Press, New York (USA), 277 pp.
- van der Wal S, Haug JT (2019) Letter to the editor referencing “The apparent kleptoparasitism in fish-parasitic gnathiid isopods”. *Parasitology Research* 118(5): 1679–1682. <https://doi.org/10.1007/s00436-019-06281-2>
- Wang B, Xia F, Engel MS, Perrichot V, Shi G, Zhang H, Chen J, Jarzembowski EA, Wappler T, Rust J (2016) Debris-carrying camouflage among diverse lineages of Cretaceous insects. *Science Advances* 2(6): e1501918. <https://doi.org/10.1126/sciadv.1501918>
- Weitschat W (2009) Jäger, Gejagte, Parasiten und Blinde Passagiere—Momentaufnahmen aus dem Bernsteinwald. *Denisia 26/Kataloge der oberösterreichischen Landesmuseen Neue Serie* 86(2009): 243–256. [in German]
- Weitschat W, Wichard W (2002) *Atlas of Plants and Animals in Baltic Amber*. Verlag Dr. Friedrich Pfeil, München (Germany), 256 pp.
- Wheeler WM (1928) *The Social Insects. Their Origin and Evolution*. Kegan Paul, Trench, Trubner & Co. Ltd./Harcourt, Brace and Company, London (UK)/New York (USA), 378 pp. <https://www.biodiversitylibrary.org/item/238968#page/7/mode/1up>
- Whitfield JB (2003) Phylogenetic insights into the evolution of parasitism in Hymenoptera. In: *Advances in Parasitology*. Vol. 54. Elsevier Ltd., Oxford (UK), 69–101. [https://doi.org/10.1016/S0065-308X\(03\)54002-7](https://doi.org/10.1016/S0065-308X(03)54002-7)
- Williams FX (1919) *Epyris extraneus* Bridwell (Bethyridae), a Fossorial Wasp That Preys on the Larva of the Tenebrionid Beetle, *Gonocephalum seriatum* (Boisduval). *Proceedings of the Hawaiian Entomological Society* 4(1): 55–63. <http://hdl.handle.net/10125/15656>
- Witthom B, Gordh G (1994) Development and Life Table of *Gonozus thallandensis* Gordh & Witthom (Hymenoptera: Bethyridae), A Gregarious Ectoparasitoid Of A Phycitine Fruit Borer (Lepidoptera: Pyralidae). *Journal of the Science Society of Thailand* 20: 101–114. <https://doi.org/10.2306/scienceasia1513-1874.1994.20.101>
- Witmer LM (1995) The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils. In: Thomason J (Ed.) *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge (UK), 19–33.
- Yang Z-Q, Wang X-Y, Yao Y-X, Gould JR, Cao L-M (2012) A New Species of *Sclerodermus* (Hymenoptera: Bethyridae) Parasitizing *Agrilus planipennis* (Coleoptera: Buprestidae) From China, With a Key to Chinese Species in the Genus. *Annals of the Entomological Society of America* 105(5): 619–627. <https://doi.org/10.1603/AN12017>
- Yu T, Thomson U, Mu L, Ross R, Kennedy J, Broly P, Xia F, Zhang H, Wang B, Dilcher D (2019) An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences* 116(23): 11345–11350. <https://doi.org/10.1073/pnas.1821292116>
- Zherikhin VV, Ross AJ (2000) A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum, London (Geology Series)* 56(1): 3–10. <https://www.biodiversitylibrary.org/page/40537672#page/5/mode/1up>
- Zippel A, Kiesmüller C, Haug GT, Müller P, Weiterschan T, Haug C, Hörnig MK, Haug JT (2021) Long-headed predators in Cretaceous amber—fossil findings of an unusual type of lacewing larva. *Palaeoentomology* 004(5): 475–498. <https://doi.org/10.11646/palaeoentomology.4.5.14>