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Research Article

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Amber Syninclusions Represent Fossil Environment with Coexistence and Interaction Between Organisms - Guidance for Studies of Fossil Amber Inclusions

***(Running title:** Guidance for studies of fossil amber inclusions)*

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Abstract
Amber syninclusions are common and represent the fossil environment with coexistence and interactions between organisms. Amber syninclusions are mostly a random process reflecting the coexistence of these fossils trapped together, but some represent interactions between different organisms. To face the challenge of supporting interactions between organisms in amber, in this study we used three pieces from Burmese Cretaceous ca. 99 million years ago (Mya) and one piece from Baltic Eocene ca. 40-50 Mya amber to study fossil syninclusions. The results support the presence of fossil amber syninclusions representing ancient environment with coexistence and rare interactions between fossil organisms. The paleoproteomics analysis in some amber pieces would advance research to support coexistence with possible interactions between these organisms.

***Keywords:** Amber; Arthropod; Baltic; Burmite; Fossil; Predation; Syninclusion.*

1. Introduction

The objective of this study is to provide guidance for the analysis of amber syninclusions to evaluate coexistence and interactions between organisms in fossil environment.

From authors perspective, arthropod syninclusions in amber are common and represent the fossil environment (de la Fuente and Estrada-Peña 2026a, de la Fuente 2026a). However, some organisms such as ticks are rarer inclusions in amber and thus unique for the study of fossils with evolutionary implications (de la Fuente 2003, de la Fuente et al. 2026a, 2026b). Fossil stories are represented in amber, limestones and bone beds and although with trusted origin, depending on preservation quality sometimes it is difficult to approach taphonomic biases for classification (de la Fuente 2026b).

As approach in this study, although some amber arthropod inclusions are rare and with known interactions (e.g., de la Fuente et al. 2026c, de la Fuente and Estrada-Peña 2026b), syninclusions are mostly a random process reflecting the coexistence of these fossil organisms trapped together (e.g., de la Fuente and Estrada-Peña 2026a, de la Fuente et al. 2026c) (Figs. 1A-1D and 2A-2D). However, Arachnida spider and Insecta wasp syninclusions are likely not a random process but evidence of interactions between these organisms that evolved at least since Cretaceous period, ca. 99 million years ago (Mya) (Figs. 3A-3E). In Baltic amber (ca. Eocene, ca. 40-50 Mya), syninclusions of Insecta (long-legged fly and barklice nymph), Arachnida mite and plant moss are probably also a representation of Eocene environment with interactions between multiple organisms (Figs. 4A-4D and 5A-5B).

2. Materials and methods

Four amber pieces were used in this study. Amber origins were from Myanmar (formerly Burma) for Burmese amber (also known as Burmite), Cretaceous, ca 99 Mya (Figs. 1A-1D, 2A-2D, and 3A-3E) and Baltic amber from Kaliningrad region, amber mine Yantarny, Lithuania (Figs. 4A-4D and 5A-5B), Eocene, ca. 40-50 Mya.

As described in previous studies (e.g., de la Fuente et al. 2026c), amber pieces were polished under natural conditions and were certified by tests with UV light, saltwater floating, sinks in fresh water, acetone resistant, and heat-smell of pine resin. Amber pieces originated from author's J. de la Fuente KGJ Collection (Ciudad Real, Spain) and ensures that "Amber provider knows that in line with the laws and regulations in his country it is allowed to sell/export these objects". Images of amber pieces were captured using a Leica (L`Hospitalet de Llobregat, Barcelona, Spain) M80 routine stereomicroscope with a 1X PLAN objective and a 2X-6X zoom (https://www.leica-microsystems.com/products/light-microscopes/stereo-microscopes/p/leica-m80/) and a Carl Zeiss stereomicroscope (SteREO Discovery V12, Munich, Germany) using the ZEN 2 pro software. Microscope images were analyzed using Image J program (https://imagej.net/ij/) and interpretative camera drawings were generated with the Befunky application (https://www.befunky.com/features/photo-to-sketch/) or composed with ColorifyAI (https://colorifyai.art/photo-to-sketch/). For classification of fossil organism inclusions, morphology references by Fossil Identifier (https://www.identifyrock.net/tools/fossil-identifier), experts' opinion and published literature were used. When relevant and possible, large resolution images are disclosed in Supplementary Information.

3. Results

3.1. Braconid wasp and gnat bug in Burmese amber inclusions

Braconid wasp and gnat bug syninclusions were identified in Burmese amber (Fig. 1A). For braconid wasp, the specimen displays the characteristic petiole, "wasp waist" abdomen, long filiform antennae, and the distinct venation pattern of the forewing typical of the family Braconidae preserved in amber (Álvarez-Parra et al. 2022) (Fig. 1B). The elongated hind legs and robust thorax are consistent with the morphology seen in many Cretaceous-aged parasitic wasps preserved in Burmese amber. The drawing shows a distinct pterostigma in the marginal cell of the forewing, which is the defining diagnostic characteristic for the family Braconidae. The venation pattern depicted, specifically the reduction of cross-veins in the distal portion of the wing and the thickened anterior margin, is consistent with the standard wing architecture seen in fossil specimens of this group preserved in Cretaceous Burmese amber. The Braconidae are a family of parasitoid wasps. After the closely related Ichneumonidae, braconids make up the second-largest family in the order Hymenoptera, with about 17,000 recognized species and many thousands more undescribed (Jones et al. 2009, Wikipedia contributors 2025).

The gnat bug is not well preserved, but the specimen displays the distinctive elongated, slender head and raptorial forelegs characteristic of unique-headed bugs (Fig. 1C). The specialized structure of the legs, designed for grasping prey, combined with the general body plan visible within the amber, aligns with the morphology of these predatory hemipterans. **Enicocephalidae**, commonly known as unique-headed bugs or gnat bugs, are a fascinating family of predatory true bugs Hemiptera known for hunting other soft-bodied arthropods, such as springtails and symphylans. They are active hunters that operate primarily under leaf litter, stones, and loose bark, and sometimes hunt at night (Fernandes and Weirauch 2015).

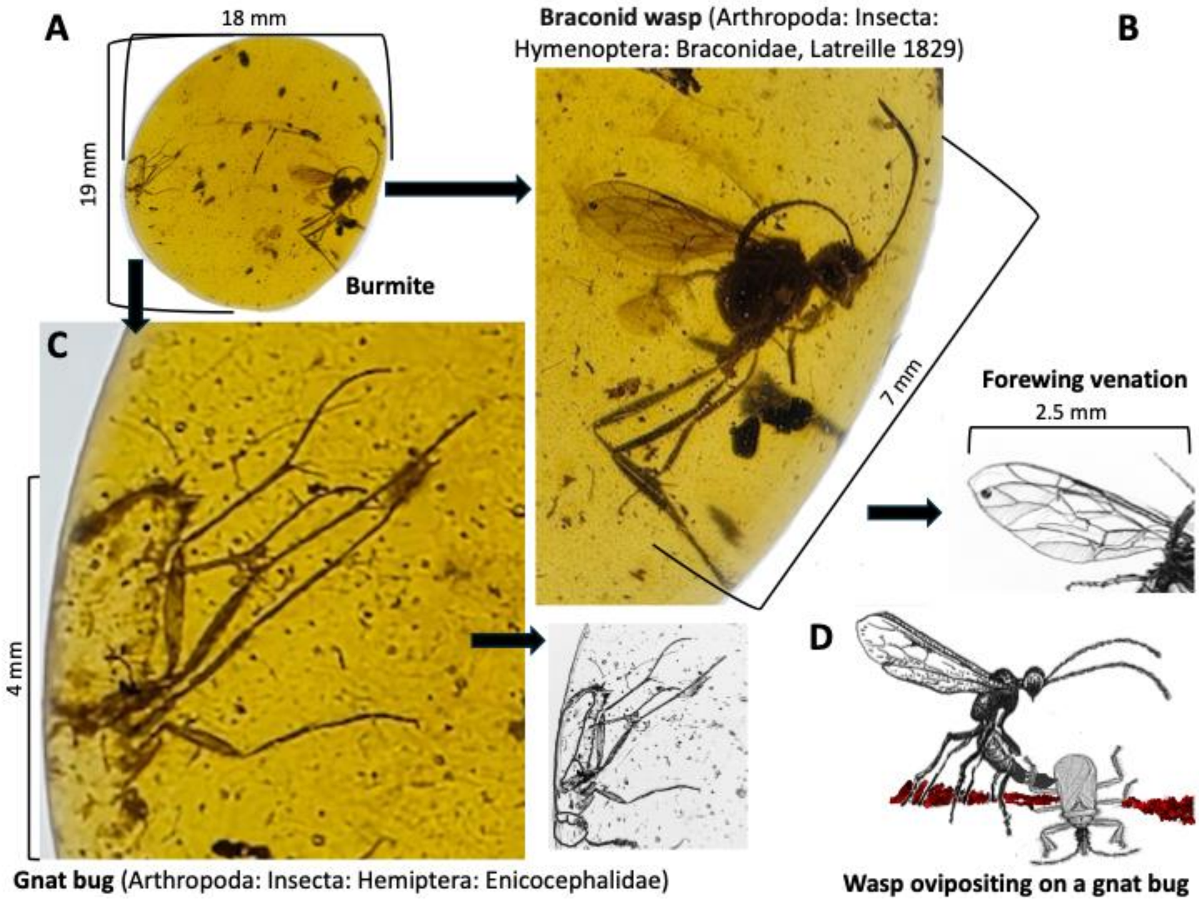


Figure 1. Insect syninclusions in Burmese amber. (A) Burmite (ca. 99 Mya). (B) Braconid wasp. (C) Gnat bug. (D) Representation of interactions by wasp oviposition on gnats.

Some braconid wasps parasitize mainly caterpillars, but some species within the family *Braconidae* use true bugs (Hemiptera) as hosts for their oviposition (Moore et al. 2024, Folly et al. 2025) (Fig. 1D). Once hatched, the wasp larva consumes the internal organs of the true bug. The bug continues to live and feed while the larva grows, eventually dying when the fully developed larva chews its way out to pupate. Because they control populations of both true bugs and caterpillars, these wasps are considered highly beneficial insects in agriculture and garden pest management (Lavoipierre 2026).

3.2. Lacewing larva, springtail and wasp in Burmese amber inclusions

Lacewing larva, springtail and wasp syninclusions were identified in Burmese amber (Fig. 2A, Supplementary Information – Appendix 1). For Osmylidae lacewing larva, the specimen exhibits characteristic morphological features of an aquatic or semi-aquatic lacewing larva, specifically a long, cylindrical, multi-segmented body with prominent, elongated, sickle-shaped mouthparts with mandibular-maxillary stylets directed forward, which is diagnostic of the order Neuroptera (Winterton et al. 2017) (Fig. 2B). The distinct lateral projections scoli on the abdominal segments and the terminal hooks are hallmarks of the larval stage of the family Osmylidae giant lacewings (Pérez-de la Fuente et al. 2020, Mao et al. 2024). Based on the size, larva is likely in the third instar final developmental stage before pupating. Other neuropteran larvae such as Chrysopidae or Hemerobiidae lack the specific elongated body proportions and the distinct specialized terminal structures seen here, while coleopteran larvae like Elateridae or Carabidae would possess more robust, sclerotized, or differently articulated biting mouthparts rather than the suctorial, needle-like piercing mouthparts typical of Neuroptera.

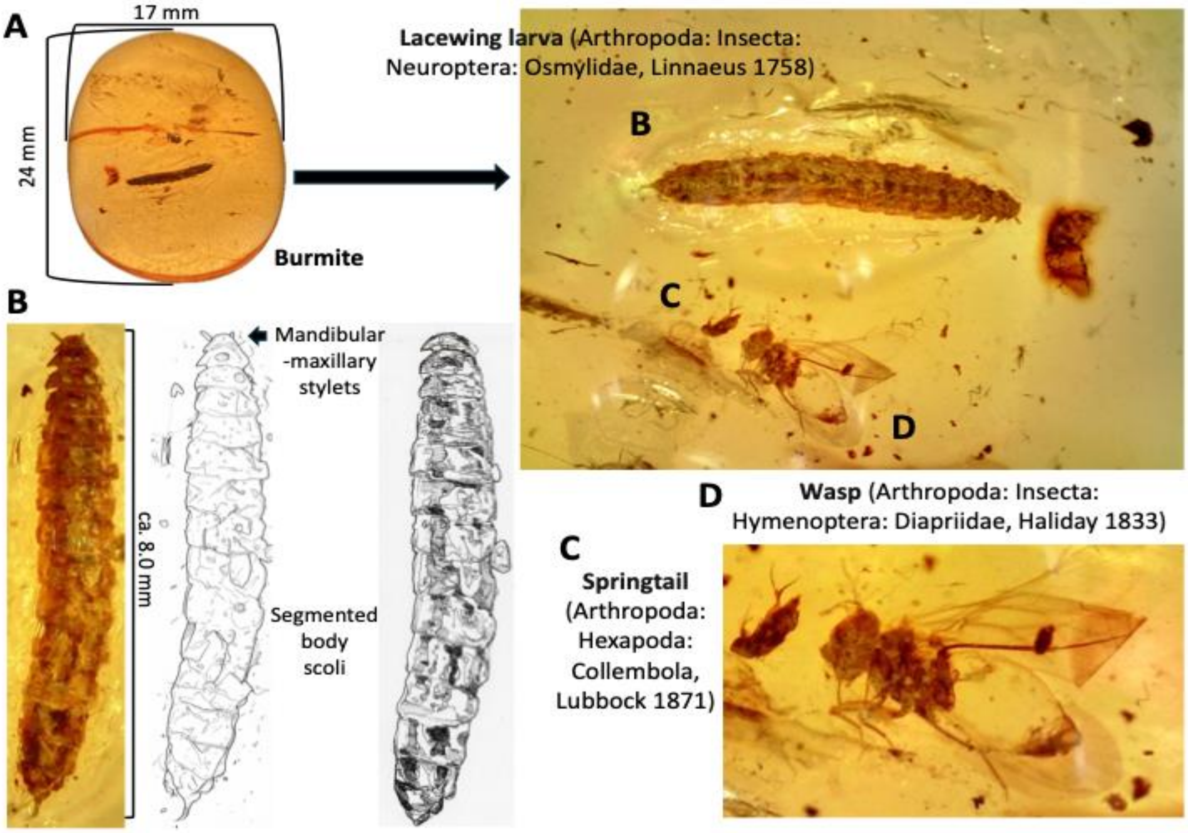


Figure 2. Hexapod syninclusions in Burmese amber. (A) Burmite (ca. 99 Mya). (B) Lacewing larva. (C) Springtail. (D) Wasp.

The springtail was classified with low resolution based on the elongated shape of an entomobryomorpha springtail, showing clear evidence of a furcula, the forked jumping organ, extending from the posterior ventral side and visible antennae, which are body characteristics of Collembola body (Fig. 2C).

The wasp specimen exhibits a distinct petiolate abdomen attached to the dorsal surface of the propodeum with the characteristic highly reduced wing venation and elongate distinctively clavate antennae typical of Diapriidae wasp family (Fig. 2D).

3.3. Spider, wasp and caddisfly larvae in Burmese amber inclusions

Spider, wasp and putative caddisfly larvae were identified in Burmese amber (Fig. 3A). The wasp in contact with a spider specimen exhibits a compact, robust body typical of small parasitoid wasps (Apocrita) characterized by a distinct "wasp waist" (petiole) connecting the mesosoma and metasoma (Fig. 3B). The presence of elongated slender legs and visible antennal structures embedded in the Burmese amber matrix aligns with the morphology of parasitoid wasps commonly found in Cretaceous deposits (Lepeco et al. 2022). Phorid flies or small beetles are plausible alternatives, but they lack the characteristic constricted waist and the specific ovipositor structure often seen in this group. Distinguishing features include the number of antennal segments, wing venation patterns, and the tarsal claw structure, which are distinct in Hymenoptera compared to Diptera or Coleoptera.

A caddisfly larva case was putatively identified with the characteristic tubular or barrel-shaped architecture created by caddisfly larvae (order *Trichoptera*) using silk and fine organic debris (Baranov et al. 2023). The protruding structural elements at both ends are consistent with the "portable cases" these aquatic insects construct for protection using silk and materials like sand, gravel, and twigs, which can be preserved in amber when resin flows into riparian or stagnant aquatic environments (Chen 2024). One plausible alternative is a piece of terrestrial detritus or a plant seed pod. However, these lack the distinct, symmetrical woven structure typical of larval cases.

The identified spider (Araneomorphae "true spiders") exhibits characteristic soft-body morphology including a distinct cephalothorax and abdomen, eight legs, and specialized anterior appendages (pedipalps) visible in the amber (Fig. 3D). The long, slender legs and general body plan are consistent with various families of wandering or web-building spiders commonly preserved in Cretaceous Burmese amber (Coddington 2005). Based on spider classifications (Coddington 2005, Magalhaes et al. 2020), alternative classifications include families like Linyphiidae or Theridiidae, which share similar leg proportions and general habitus. Distinguishing between these spiders requires high-magnification observation of the tarsal claws, trichobothria patterns on the legs, and the specific shape of the pedipalp bulb to determine taxonomic family or genus.

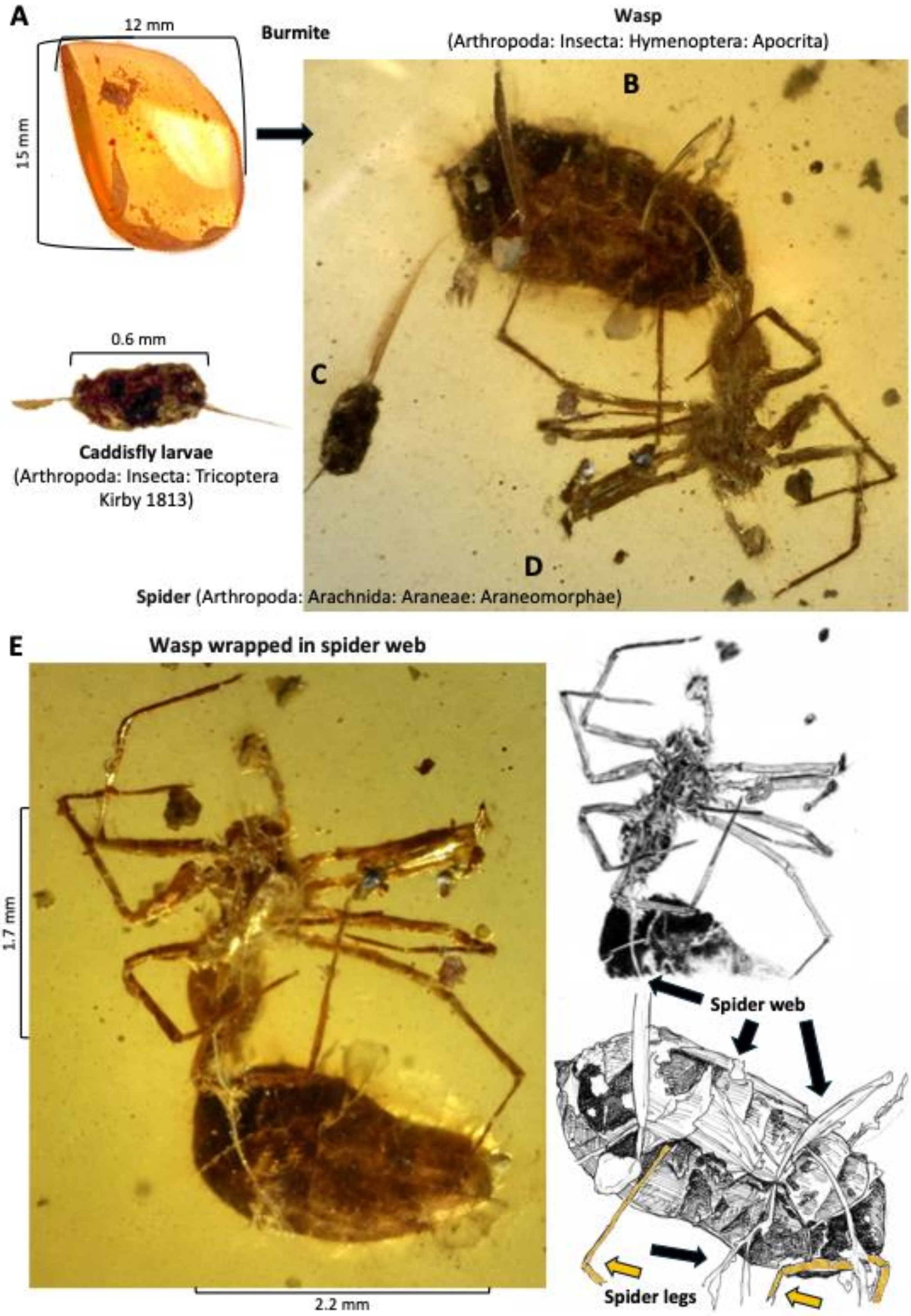
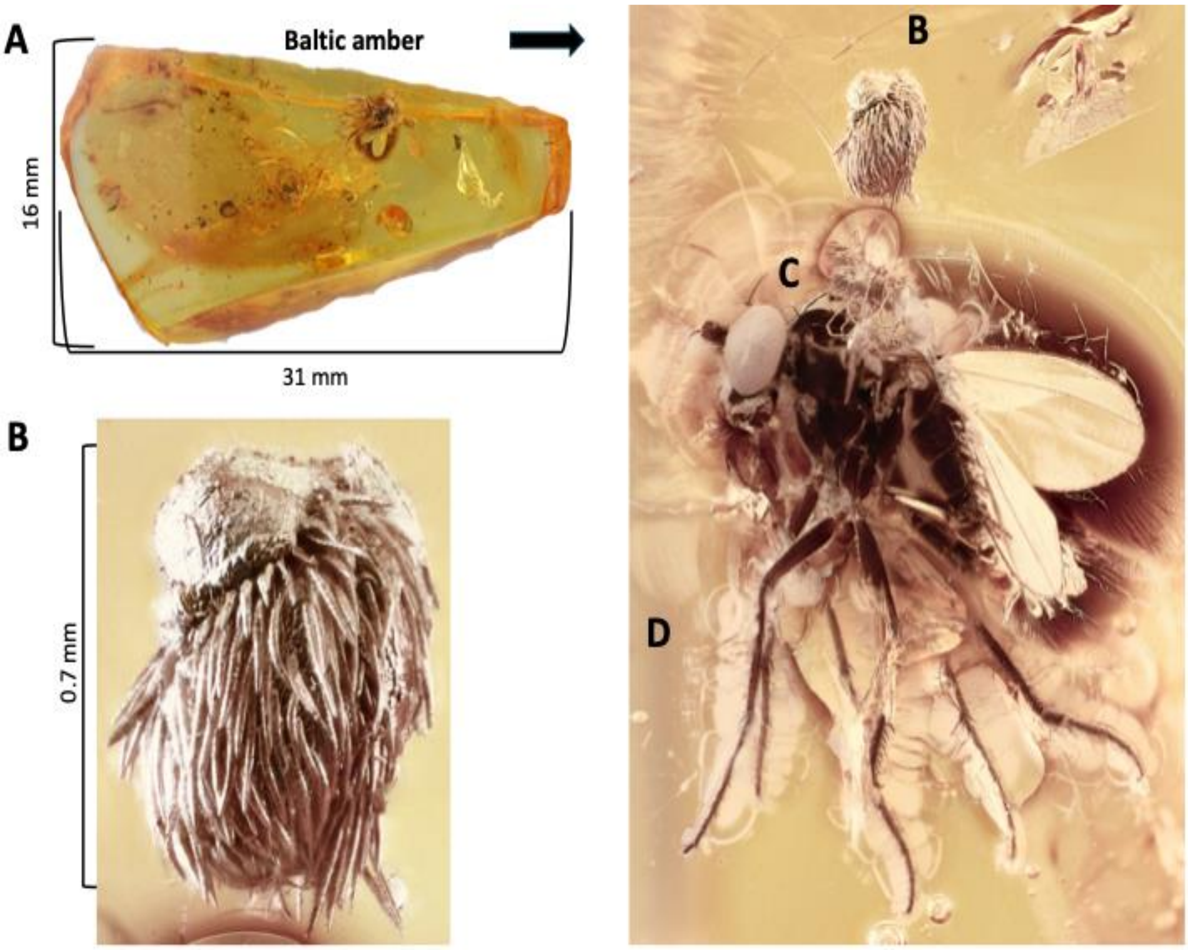


Figure 3. Spider-wasp syninclusions in Burmese amber. (A) Burmite (ca. 99 Mya). (B) Wasp. (C) Caddisfly larvae. (D) Spider. (E) Arachnida spider-Insecta wasp interactions. Spider legs and web are shown in contact with the wrapped wasp.

3.4. Long-legged fly, barklouse nymph, mite and plant moss in Balic amber inclusions

Long-legged fly, barklouse nymph, mite and plant moss were identified in Baltic amber (Fig. 4A, Supplementary Information – Appendix 2).



Moss (Plantae: Embryophytes: Bryophyta *sensu lato*)

C: Barklouse nymph and Mite
D: Long-legged fly

Figure 4. Insect-mite-plant syninclusions in Baltic amber. (A) Baltic amber (ca. 40-50 Mya). The piece was mined in Kaliningrad region, amber mine Yantarny, Lithuania. (B) Plant moss. (C) Barklouse nymph and mite. (C) Long-legged fly. Barklouse nymph-mite-fly interactions are described in Figures 5A and 5B.

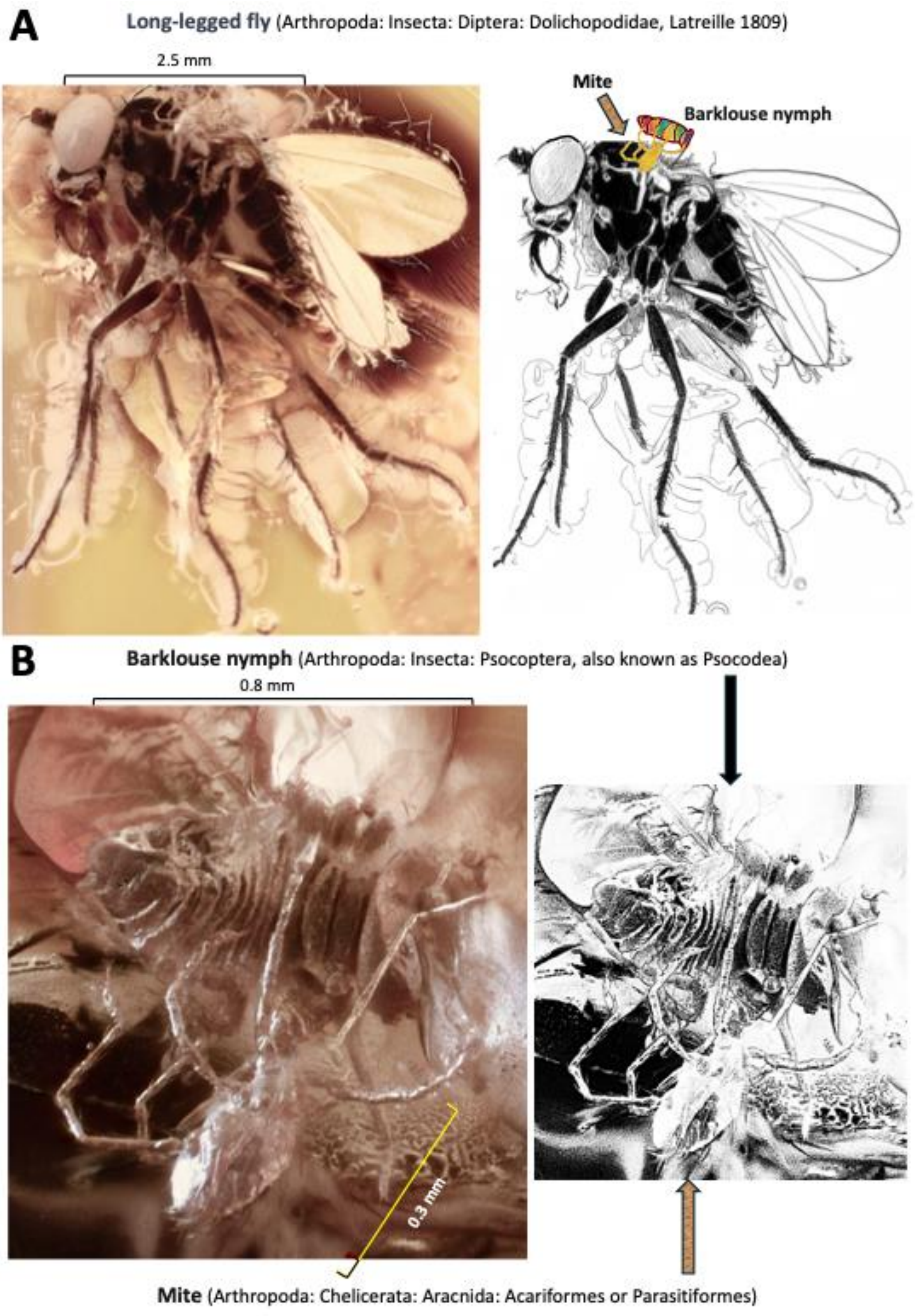


Figure 5. Long-legged fly interactions with mite and lice nymph. (A) Long-legged fly and contact position with mite and barklouse nymph. (B) Interaction between barklouse nymph and mite.

The Bryophyta moss presents numerous small, narrow, lanceolate leaves arranged in a dense, overlapping cluster typical of mosses (Fig. 4B). The preservation in Baltic amber is a common medium for finding such delicate plant structures, and the overall morphology matches the growth habit of bryophyte gametophores (Hedges 2002). Although Bryophyta *sensu lato* contains three groups of non-vascular land plants, liverworts, hornworts, and mosses, the division Bryophyta consists of the mosses only (Hedges 2002). Barklouse nymph (Psocoptera, also known as Psocodea) and mite were identified in close contact (Figs. 4C, 5A and 5B) and near a long-legged fly (Figs. 4D and 5A). **Barklouse nymphs** are the immature life stages of the insect order Psocodea, a paraphyletic group of insects that are commonly known as booklice, barklouse or barkfly (Cao and Liu 2025) (Fig. 5B).

The mite shows small, eight-legged arachnid with size, leg structure and rounded body attached to the exoskeleton of a long-legged fly with possible phoretic behavior of clinging to a host for transport, which are diagnostic of mite's characteristics (Michalska et al. 2025) (Figs. 5A and 5B).

The fly (Dolichopodidae) displays the characteristic morphology of a long-legged fly, including the slender body, elongated legs with distinct bristling, and a specific wing venation pattern (Fig. 5A). Its preservation in Baltic amber is consistent with known fossils of this family from the Eocene epoch (e.g., Słomczyński and Soszynska 2023).

4. Discussion

In the study of fossil amber syninclusions, to differentiate between interaction or just coexistence between organisms is a challenge (e.g., de la Fuente et al. 2026a, 2026c, de la Fuente and Estrada-Peña, 2026b). As approached in this study, some organisms may have interactions but fossil syninclusions do not represent these interactions but coexistence in ancient periods. However, in some unique fossils, syninclusions do represent the interactions between different organisms preserved in amber.

4.1. Representation of fossil environment with organisms' coexistence

For example, although some braconid wasps parasitize mainly caterpillars, some species within the family *Braconidae* use true bugs (Hemiptera) as hosts for their oviposition (Moore et al. 2024, Folly et al. 2025). Nevertheless, the identification of a braconid wasp and gnat bug in Burmite (Figs. 1A-1D), likely does not reflect the interaction between these organisms but the coexistence in the Cretaceous environment.

In another Burmite, a lacewing (Neuroptera) larva, springtail and wasp syninclusions were identified (Figs. 2A-2D). Braconidae wasps have been described in amber with syninclusions of silvanid beetle larva (Kiesmüller et al. 2026). The Osmylidae larva are generalist predators on small insects and other invertebrates using their elongated lance-like jaws to impale their prey (Winterton et al. 2017), and a recent study in Baltic amber syninclusions proposed wingless aphids as possible preys of a lacewing larva (Haug et al. 2023). However, as described in Figures 1A-1D with amber insect inclusions, the Cretaceous amber syninclusions of lacewing larva with other arthropods likely does not reflect interaction between these organisms but the coexistence in the fossil environment.

4.2. Representation of fossil environment with predator-prey interactions

Parasitic evidences preserved in fossils are rare like the fossil record of parasitoid wasps next to their hosts (De Baets and Littlewood 2015, Nagler and Haug 2015, van de Kamp et al. 2018), and predator-predator-prey interactions described in amber syninclusions from Chiapas, Mexico (García-Villafuerte and Carbot-Chanona 2024).

The soft-bodied spider inclusions range from solitary spiders to specimens with preserved mid-attack on prey, or even beside fossilized strands of ancient silk (e.g., Dunlop et al. 2018, de la Fuente et al. 2024, de la Fuente, J. 2026a). Parasitoid wasps like Apocrita parasitize other insects (Jackson and Nelson 2012, Burke and Sharanowski 2024) including Hymenoptera (Wikimedia Commons 2023) as preserved in Burmite (Figs. 3A-3E). However, the wasp trapped in spider web and legs is likely a representation of fossil predator spider-prey wasp interactions (Fig. 3E).

Although less likely, considering the alternative for caddisfly larvae as terrestrial detritus or plant seed pod (Fig. 3C), spiders occasionally interact with specific pathogenic fungi like *Gibellula* or *Cordyceps* in a **parasitic predator-prey relationship (**Nyffeler and Hywel-Jones 2024**)**. The fungal spores land on the spider, germinate, and consume the host from the inside, often manipulating the spider's behavior before emerging as fruiting bodies to spread more spores.

How fossil amber syninclusions of long-legged fly, mite and barklouse nymph got trapped together in contact?
The interaction between mite and long-legged fly represents a phoretic behavior of clinging to a host for transport rather than feeding on them directly (Michalska et al. 2025) (Fig. 5A). The contact between mite and barklouse may represent predator behavior or most likely, **saprophagous behavior by** feeding on decomposing material **(**OConnor 2009**) (Fig. 5B).**

Mite fossil associations (Michalska et al. 2025) observed in Baltic amber (Figs. 4A-4D, 5A and 5B) can by summarized as:

a) Phoretic mites (phoresy). These mites (often Astigmata deutonymphs or Prostigmata larvae) attach to the barklouse nymph to hitchhike to a more suitable, less crowded, or less moldy environment. They are common in damp, sheltered areas where barkfly aggregate.

b) Location on nymph. Mites frequently attach to the membranous, soft areas of the barklouse nymph, such as the wing buds or joints, as these areas provide a secure anchor point.

c) **Parasitic appearance.** While some larval Prostigmata (e.g., Erythraeidae or Trombidiidae) can feed on the host, many are relatively harmless and transient, using the host for both food and transport. Nevertheless, considering the mite legs size and structure, a predatory behavior cannot be discarded.

d) **Environment.** Barklouse, which include booklouse, are non-parasitic scavengers feeding on algae, lichens, and fungi on tree bark. Mites are often found on them because both organisms thrive in high-humidity, mold-friendly environments.

In conclusion, these findings support the presence of amber syninclusions representing ancient environment with coexistence and interactions between fossil organisms. As previously approached (de la Fuente et al. 2026d), paleoproteomics analysis in some amber pieces would advance research to support coexistence with possible interactions between these organisms.

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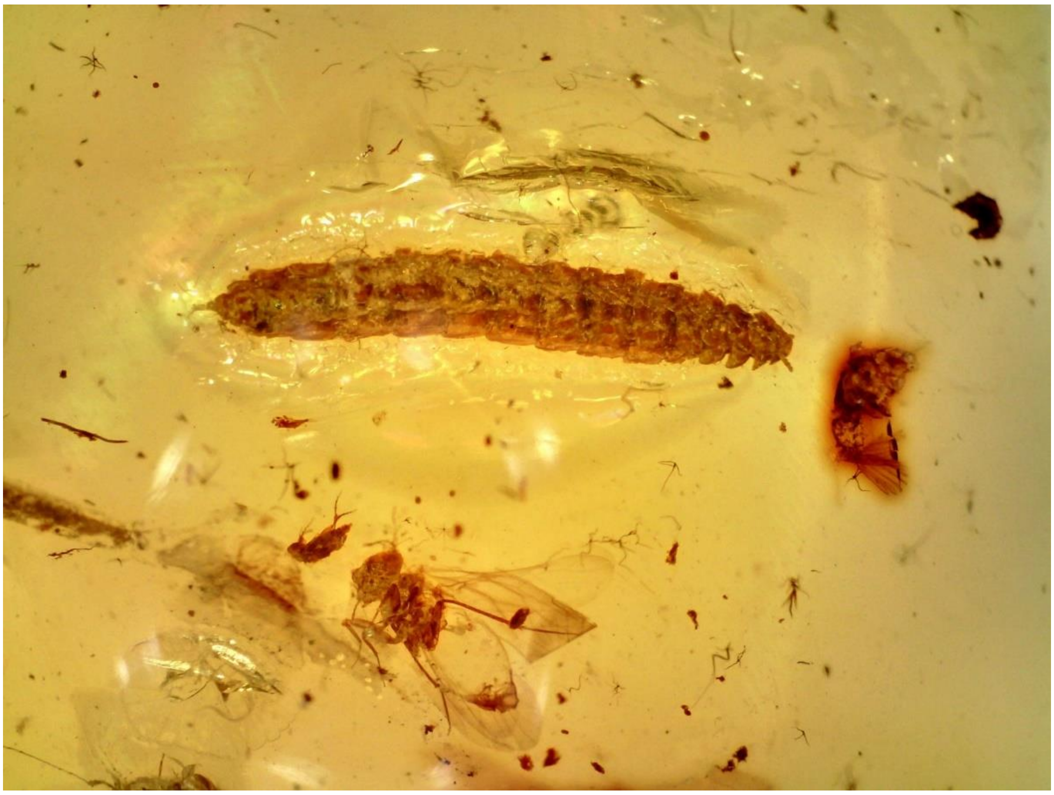
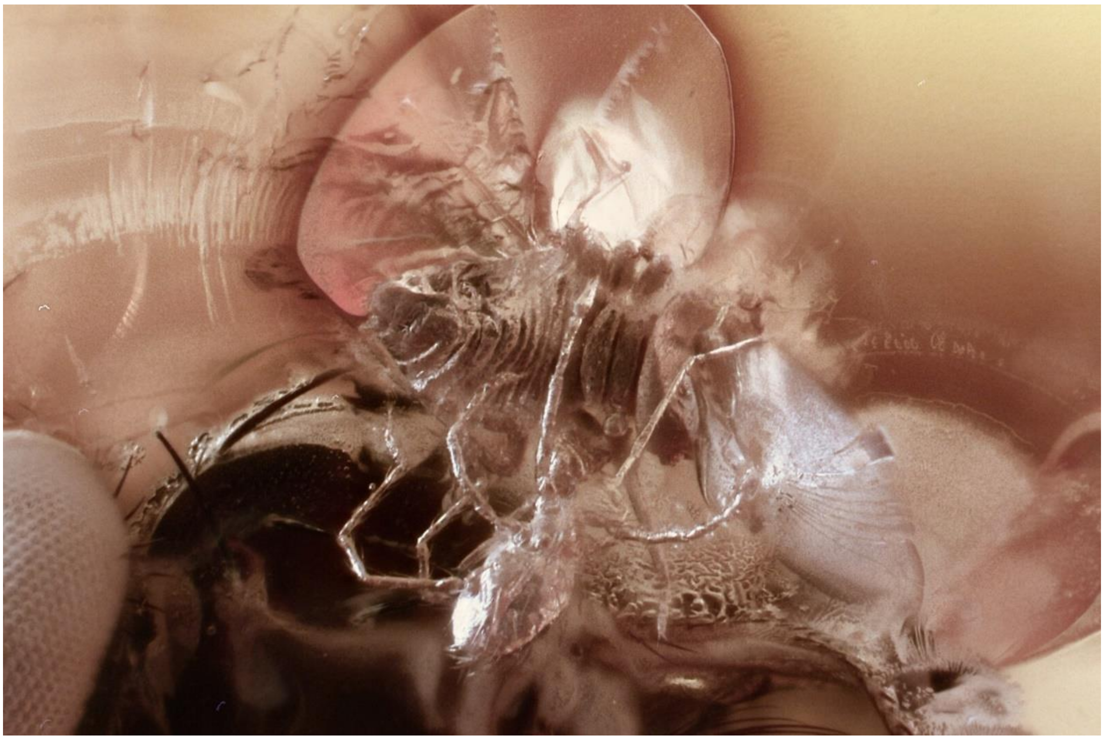
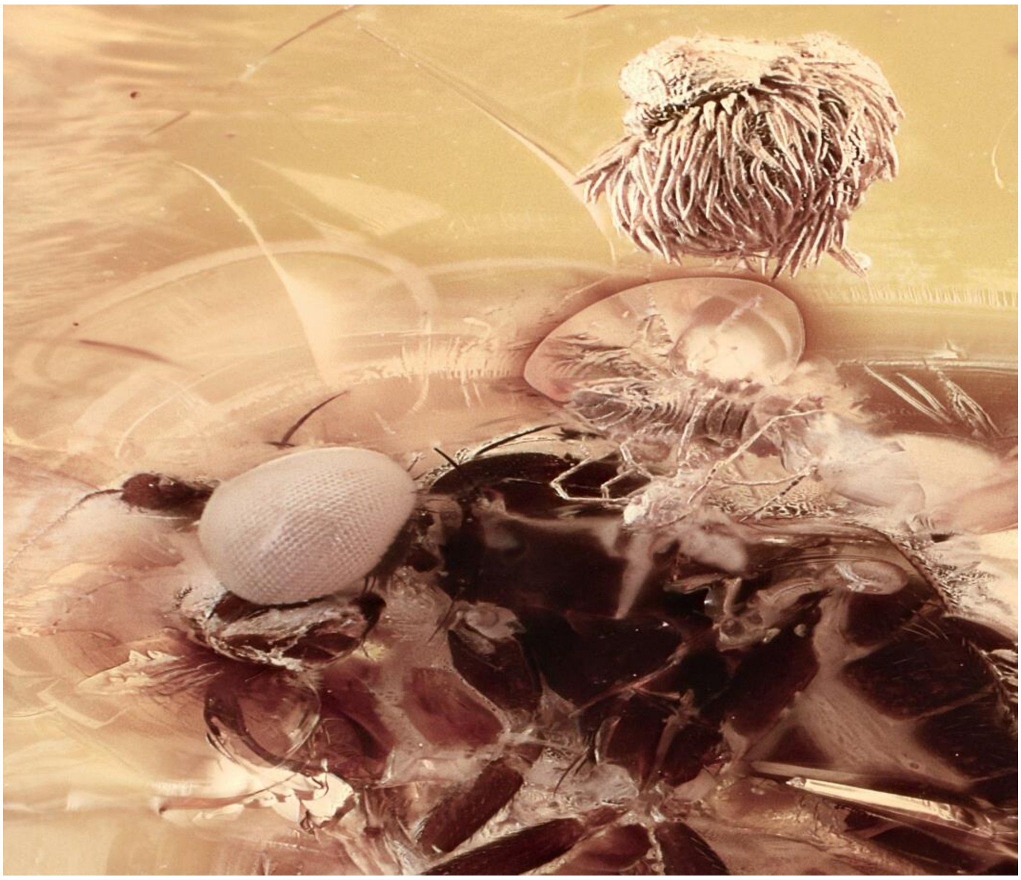
Supplementary Information

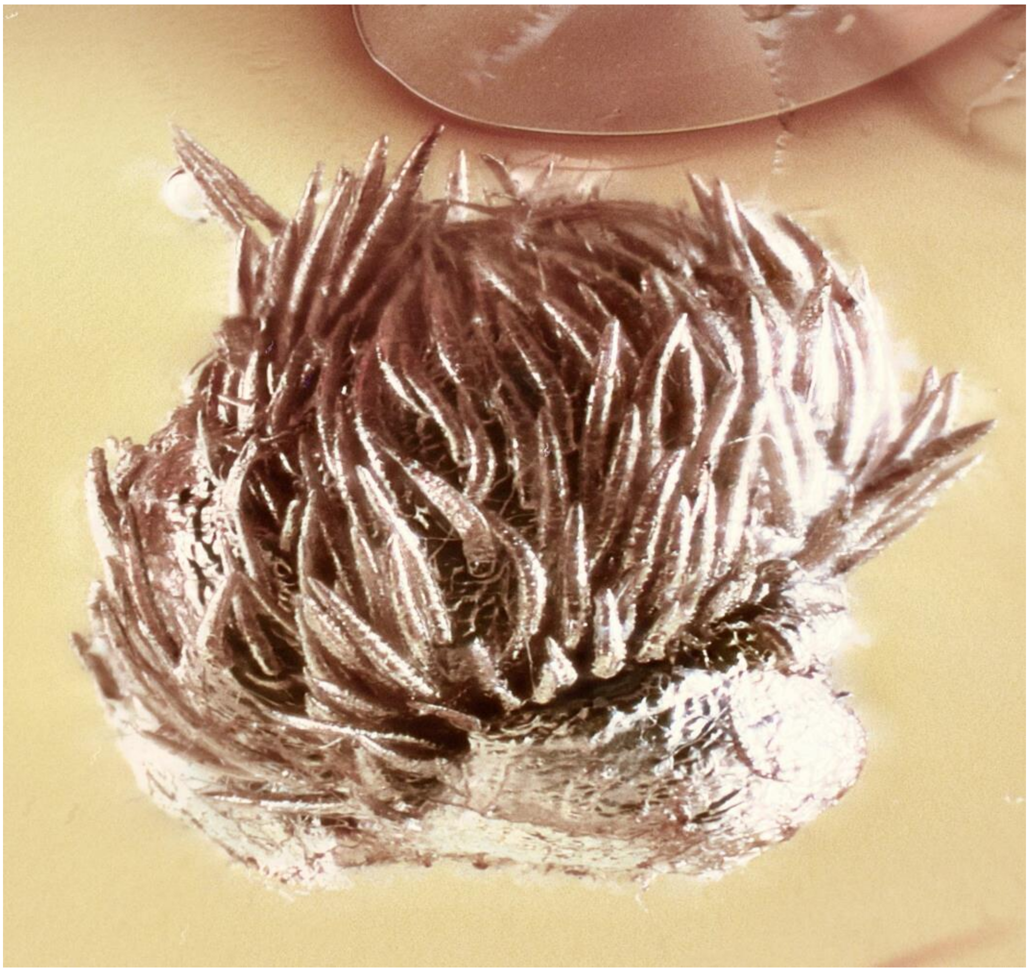
Appendix 1. High resolution image. Lacewing larva, springtail and wasp syninclusions in Burmese amber (Figs. 2A-2D).



Appendix 2. High resolution images. Long-legged fly, barklouse nymph, mite and plant moss identified in Baltic amber (Figs. 4A-4D and 5A-5B).







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