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ARTHROPOD STRUCTURE AND DEVELOPMENT – SPECIAL VOLUME

A defensive behavior and plant-insect interaction in Early Cretaceous amber – the case of the immature lacewing *Hallucinochrysa diogenesi*

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ABSTRACT

Amber holds special paleobiological significance due to its ability to preserve direct evidence of biotic interactions and animal behaviors for millions of years. Here we review the finding of *Hallucinochrysa diogenesi* Pérez-de la Fuente, Delclòs, Peñalver and Engel, 2012, a morphologically atypical larva related to modern green lacewings (Insecta: Neuroptera) that was described in Early Cretaceous amber from the El Soplao outcrop (northern Spain). The fossil larva is preserved with a dense cloud of fern trichomes that corresponds to the trash packet the insect gathered and carried on its back for camouflaging and shielding, similar to that which is done by its extant relatives. This finding supports the prominent role of wildfires in the paleoecosystem and provides direct evidence of both an ancient plant-insect interaction and an early acquisition of a defensive behavior in an insect lineage. Overall, the fossil of *H. diogenesi* showcases the potential that the amber record offers to reconstruct not only the morphology of fossil arthropods but, more remarkably, their lifestyles and ecological relationships.

Keywords: fossil; reconstruction; insect; larva; Neuroptera

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1. Introduction

Amber – fossil resin – is a unique source of paleontological data on terrestrial arthropods and their environments, offering the most exquisite fossil preservation in deep time (Grimaldi and Engel, 2005; Labandeira, 2014). The resin often was able to protect small organisms (principally arthropods) from decay and disarticulation shortly after they became entombed, particularly as such resins have antiseptic and antimicrobial properties that hamper decomposition. Additionally, tissues of resin-included organisms dehydrate soon after they are trapped, leading to a process of mummification that normally ensures the fidelity of the fossilized structures down to the ultrastructural level (Martínez-Delclòs et al., 2004). Although most amber inclusions are preserved only as cuticle due to autolysis of internal tissues by endogenous bacteria (ibid.), soft tissues can also be preserved (e.g., Henwood, 1992; Pohl et al., 2008; Soriano et al., 2010; Perreau and Tafforeau, 2011; Labandeira, 2014). Moreover, resin entrapment and infilling, either partially or completely, protects inclusions from collapsing, preserving their three-dimensional structure. As a result of this exceptional morphological preservation, reliable inferences about the likely habits of the ancient organisms and the environments in which they lived can be extracted. Furthermore, the study of amber physicochemical properties provides information on its botanical source and the environment in which the resin was secreted, allowing for accurate assessment of the processes that permitted fossilization. Nevertheless, what makes the amber record most remarkable is

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its potential to preserve direct evidence of biotic interactions and complex behaviors for millions of years. This results from the ability of resin to encapsulate "small fragments" of the ecosystem in a relatively fast and unaltered way – in this sense, each amber piece can be considered a snapshot of the past. This ability is what distinguishes amber from other fossiliferous materials with a stability measured in millions of years, even others of exceptional preservation, such as some shales. A plethora of paleobiotic interactions, both intra- and interspecific, are known from the amber record (for a review, see Arillo, 2007). Among intraspecific interactions, there are cases of "frozen" reproductive behavior, such as mating and brood care, and social behaviors, such as cooperative feeding in social insects or gregarious habits (e.g., Weitschat and Wichard, 1998; Grimaldi and Engel, 2005; Engel, 2009). Among the intraspecific interactions, direct evidence of predation, parasitism, mutualism, or defensive behaviors are known (e.g., Janzen, 2002; Engel, 2005; Peñalver et al., 2012).

Although the oldest amber with arthropod inclusions comes from the Triassic of Italy (Schmidt et al., 2012), fossil resin with abundant biological content is not known until the Early Cretaceous. From that epoch, the most significant ambers in terms of their paleobiotic diversity and abundance are found in –from west to east– Spain, France, Lebanon, and Myanmar (see review in Penney, 2010). In Spain, more than a hundred amber-bearing localities, mostly Cretaceous, have been discovered to date (Peñalver and Delclòs, 2010). From these localities, nine have provided amber with inclusions, although only three have done so significantly, i.e., the outcrops of Peñacerrada I (Burgos Province; Alonso et al., 2000), San Just (Teruel Province; Peñalver et al., 2007), and El Soplao (Cantabria Autonomous Community; Najarro et al., 2009, 2010). More than 3,700 bioinclusions have been recovered from these three localities, which are dated to the Albian, ~105 million years ago (Peñalver and Delclòs, 2010; Barrón et al., 2015). In the El Soplao outcrop, amber is found embedded in sandstones and claystones that are associated with lignite, similar to the two deposits mentioned above, with accumulations of plant remains and marine to brackish invertebrates such as gastropods or bryozoans, indicating that the resin was deposited in delta-estuarine environments. Paleobotanical and chemotaxonomical data suggest that resin from which the El Soplao amber derives was secreted by conifers belonging to the extinct family Cheirolepidiaceae and, in some cases, another unidentified botanical source (Menor-Salván et al., 2010).

Several animal lineages possess a behavior by which they actively harvest and carry a wide variety of organic and/or inorganic remains on their bodies for protective purposes. Although some gastropods and sea urchins show this habit (Ponder, 1983, 1994; Allgaier, 2007; Dumont et al., 2007), arthropods exhibiting this behavior also possess associated morphological adaptations aimed at increasing the potential of retaining the exogenous elements, i.e., the presence of specialized setae, commonly hooked, and often also cuticular projections of their body dorsum. This is the case of decorating crabs (Hultgren and Stachowicz, 2011), sand-covering spiders (Duncan et al., 2007), some oribatid mites (Subías, 2012; Arillo and Subías, 2015 pers. comm.), some ants (Hölldobler and Wilson, 1986), and some immature forms from a few insect groups, i.e., assassin bugs (Weirauch, 2006), barklice (Betz, 1983; Lienhard, 1988), and lacewings and their relatives (Henry, 1977; Eisner et al., 1978; New, 1982). Among the latter, in green lacewing larvae, the term "trash-carrying" has been commonly used to refer to the described behavior.

Green lacewings (Neuroptera: Chrysopidae) have a nearly cosmopolitan distribution and comprise around 1,200 described species (Brooks and Barnard, 1990). Their larvae are voracious predators, generally feeding on a wide variety of prey, which have been used widely as biological control agents (Canard et al., 1984). They use their sickle-shaped jaws to pierce their prey, inject salivary secretions, and then absorb the internal fluids and liquefied tissues. Not all green lacewing larvae are trash carriers – trash-carrying is present in different lacewing lineages, and their related morphological adaptations are helping elucidate the phylogenetic relationships within the family (Monserrat and Díaz-Aranda, 2012; Tauber et al., 2014). Trash-carrying larvae, unlike the "naked" morphotypes, tend to have humped bodies as an adaptation to carry great loads and pairs of setigerous tubercles on their backs for ensnaring the trash packet elements (McEwen et al., 2001). This trash packet can be composed of single or multiple types of materials, both animal (prey corpses, exuviae, shells, waxy secretions, etc.) and non-animal (bark, trichomes, terrestrial algae, lichens, etc.) in origin (Tauber et al., 2014). The trash-packet provides a

two-fold defense – a camouflage that prevents visual and tactile detection from both predators and prey, and a physical shield that can be actively moved towards the predator in instances where the larva is attacked (McEwen et al., 2001; Tauber et al., 2014).

A four-millimeter-long immature green lacewing preserved together with its trash packet was discovered in the Spanish amber locality of El Soplao (Figs 1, 2, 3, Anim. 1; see above). This discovery is exceptional not only because fossil immature green lacewings are highly rare in the fossil record, but also because evidence of trash-carrying (in a broad sense) is also extremely scarce in the record of Arthropoda. The fossil was described as *Hallucinochrysa diogenesi* Pérez-de la Fuente, Delclòs, Peñalver and Engel, 2012 (Pérez-de la Fuente et al., 2012a), after the mind-boggling aspect of the fossil and the Greek philosopher Diogenes of Sinope, whose name has been used for the human psychological disorder characterized by the compulsive accumulation of trash. The present paper reviews this discovery and its paleobiological implications, showcasing the amount and quality of the paleoecological and paleoethological information that can be extracted from amber inclusions, and which can be used to obtain highly reliable reconstructions.

2. Material and methods

The holotype of *H. diogenesi* (CES 418.1) was isolated within a small piece of transparent amber and embedded in a regular prism of epoxy resin (EPO-TEK 301) for optimal viewing and curation (Nascimbene and Silverstein, 2000). The specimen is housed at the laboratory of the institutional El Soplao collection in El Soplao cave, Celis (Cantabria, northern Spain). The holotype is almost complete, although the distal parts of both antennae and some tubular tubercles are missing. A large, multi-planed fracture transversally crosses the larval abdomen, obscuring several tubular tubercles.

An Olympus BX51 transmitted-light microscope was used to study the insect in dorsal, ventral, and lateral views. Photography of the specimen used both a ColorView IIIu digital camera attached to an Olympus BX51 and a Nikon D1X digital camera attached to an Infinity K-2 long-distance microscope lens. Merged images were obtained with Helicon Focus v.5.3. The three-dimensional reconstruction was performed with the LightWave 3D computer graphics program (NewTek). Movement patterns, body coloration, antennal length, and number of abdominal tubular tubercle pairs (see below) were reconstructed as in modern trash-carrying green lacewing representatives, e.g., *Mallada desjardinsi* (Navás).

3. Morphofunctional interpretation

The morphological singularity of *H. diogenesi* compared to known diversity of green lacewing larvae, both fossil and extant, is remarkable. The most striking differences in the fossil are the highly specialized adaptations for carrying debris. First, *H. diogenesi*'s thorax and abdomen bear pairs of extremely elongate setigerous tubercles (= tubular tubercles; see Figs 1, 2, Anim. 1) dorsally, which exceed the body length. In extant green lacewing trash-carrying larvae, these tubercles are not developed in such an extreme form, never being more elongate than the body width. Also, the fossil bears two pairs of tubular tubercles on each thoracic segment (lateral and laterodorsal pairs), and these tubercles are similarly developed as to those on the abdomen. Conversely, only the laterodorsal thoracic tubercle pairs are well-developed in other known trash-carrying larvae, in which thoracic tubercles are often much more developed than those of the abdomen. The second remarkable adaptation of *H. diogenesi* to trash carrying is that the setae on the tubular tubercles show expanded, trumpet-shaped endings. Although this particular morphology of setae is unknown from other extinct and extant green lacewings, in which hooked ends and serrated margins are the most specialized setal adaptations for trash-carrying, it is known to be present in other neuropteran groups (New, 1982; McEwen et al., 2001). Additionally, and unlike any previously described green lacewing larvae, the fossil's head is broad, short, and with a strongly convex frons that resembles a banana (Fig. 3), its three labial palpomeres are not distinctly unequal in length, and the specimen lacks annulations on the second palpomere. The degree of tubercle development and setation indicates that the

specimen most likely corresponds to an advanced (third) instar. For a full description of the fossil larva see Pérez-de la Fuente et al. (2012a).

Based on the former characters, *H. diogenesi* was interpreted as a highly specialized, probably derived, trash-carrying morphotype, rather than representing the basal condition for the lineage that gave rise to modern green lacewings. For this reason, the fossil was not formally included in this family but left unclassified at familial level within the superfamily Chrysopoidea Schneider, 1851, which apart from modern green lacewings includes several extinct lineages known since the Early Jurassic (Nel et al., 2005). No other immature specimens assignable to any fossil chrysopoid lineage have been previously reported in the literature, as a few previous records of green lacewing larvae are only known from Cenozoic amber deposits and clearly fit within the diversity of modern green lacewings (Hagen, 1856; MacLeod, 1970; Engel and Grimaldi, 2007, 2008; Weitschat, 2009).

The dense and complete trash packet gathered by *H. diogenesi* (Figs 1 and 3) is exclusively composed of nonglandular, multicellular plant trichomes (Fahn, 1990; Evert, 2006), as indicated by their morphology, size range, ultrastructure, and autofluorescence signals (Pérez-de la Fuente et al., 2012a). These trichomes are tangled with the specialized setae of the larva's tubular tubercles. Trichomes show an oval cross-section (up to 30 µm thick), a micropapillate surface, and a thick hyaline layer that corresponds to their cell wall. They have a branched, dendritic morphology, with a blunt insertion base and an axis from which several secondary branches alternatively emerge in a single plane. The trichomes show variation in part attributable to different stages of growth – the axis goes from straight in the less developed forms to zigzagged in the more mature forms, in which secondary branches are directed apically and arranged with more space between them (Fig. 4). After an exhaustive literature comparison (see Pérez-de la Fuente et al., 2012a), the most plausible attribution is that these trichomes belong to the fern family Gleicheniaceae, a group widespread during the Early Cretaceous (Skog, 2001). Very similar trichomes were reported in a gleicheniacean described from the Albian of England (Herendeen and Skog, 1998). The family is present in the El Soplao outcrop sediments as two spore species attributed to these ferns (Najarro et al., 2010; Pérez-de la Fuente et al., 2012a).

Green lacewing larvae construct their trash packet using their jaws to gather debris in successive loads that are placed on the dorsum by bowing the head backwards as the rest of the body arches forwards (Jones, 1941; Eisner and Silberglied, 1988). Larvae are also capable of reallocating the elements of the trash-packet using their mouthparts and through peristaltic movements of their body (Eisner et al., 2002). In the trash packet of *H. diogenesi*, trichomes are often found in clusters with the same orientation, indicating that they were pulled out from the plant together by the larva. The extreme elongation of *H. diogenesi*'s tubercles suggests that it had its own stereotyped movements for constructing the trash packet. Trichomes were loaded into a dorsal basket shaped by the tube-like tubercles of the larva (Fig. 2, Anim. 1), which due to its extreme elongation would have allowed the construction of a thicker trash-packet, perhaps as a defense against a particular group of Cretaceous predators with an elongate piercing or sucking proboscis, such as true bugs, or elongate ovipositors, such as parasitoid wasps (Grimaldi and Engel, 2005). The trumpet-shaped endings of the tubercle setae acted as anchoring points among surfaces of trichomes, and the particular branched morphology of the trichomes added cohesion to the trash packet.

4. Paleobiological implications

This finding provides direct evidence that trash-carrying behavior, understood as actively harvesting and carrying exogenous materials for the purposes of camouflage and physical protection, has remained in stasis for more than 100 million years in the green lacewing lineage. Not only that, but it represents the earliest trash-carrying record known to date in the fossil record of arthropods (see Pérez-de la Fuente et al., 2012a). Previous fossil evidence of this behavior has only been reported from other immature insects in Cenozoic amber, i.e., in assassin bugs, barklice, and owlflies from Miocene Dominican and Mexican ambers (Wu, 1996; Engel and Grimaldi, 2007; Boucot and Poinar Jr., 2010), and in green lacewings from

Eocene Baltic amber (Weitschat, 2009). A similar behavior is present in case-building insect larvae like caddisflies (indirect camouflage), with records known since the Jurassic (Grimaldi and Engel, 2005).

Hallucinochrysa diogenesi and its trichome-based trash-packet showcase an ancient plant-insect interaction, in which the structures used by a fern to protect itself from herbivores (trichomes) are used by a predator to protect itself and provide camouflage from both its predators and prey. As the lacewing larva fed on the fern's hervibores, the fern could have invested a part of its defensive structures in the lacewing. For this reason, it seems reasonable to consider that both the fern and the insect obtained a mutual benefit from their interaction. Further evidence, however, is required to regard the described plant-insect relationship as a result of a symbiotic interaction, even if the relationship seems to have been specific to this fern: *H. diogenesi*'s trash packet is solely composed of the described trichomes, suggesting that the larvae might have exclusively fed on herbivores living in these ferns. In this regard, the predatory habits of these immature insects can be delimited. First, although the prey range for extant green lacewing larvae covers a high diversity of arachnid and insect groups (McEwen et al., 2001), their most common prey are sternorrhynchan hemipterans such as aphids, coccoids, and psyllids. Aphids, however, were scarce in the paleoenvironment in comparison with coccoids, and their low relative abundance has been attributed to a low climatic seasonality during the Cretaceous (Peñalver and Wegierek, 2008). Second, insects associated with ferns today are mainly hemipterans, beetles, and lepidopterans, with a high proportion of specialist feeders restricted to ferns (Cooper-Driver, 1978). Third, the broadened cephalic capsule of *H. diogenesi*, together with its long jaws, suggest specialization or, at least, ability to feed on large prey, as both cephalic width and jaw length are related to prey size (Tauber et al., 1995).

Lastly, evidence exists that indicates fires were important agents controlling the dynamics of the Iberian Cretaceous amber forest. Charcoal has been copiously found in the sediments associated with El Soplao amber (and other coetaneous Spanish deposits), and charcoalified plant fibers were discovered as inclusions within the amber (Najarro et al., 2010; Pérez-de la Fuente et al., 2012b). Fires induced resin production by damaging the resin-producing trees (in the same manner by which systemic and pandemic insect outbreaks similarly induce resin production: McKellar et al., 2011), and promoted resin accumulation after burning the plant mass due to increased erosion of the soil in which resin was primarily buried. In that sense, *H. diogenesi* and its trash packet composed by fern trichomes with gleicheniaceous affinity supports that scenario. Gleicheniacean ferns are today primary succession pioneers following wildfires or lava flows (Gillison, 1969; Walker and Boneta, 1995; Russell et al., 1998) and this was most likely the same in the past due to their abundance as charcoalified remains since the Late Jurassic (Herendeen and Skog, 1998; Collinson, 2002; Van Konijnenburg-Van Cittert, 2002). There also exists among the paleoentomological record further evidence supporting the presence of paleofires in the Iberian Cretaceous amber forests (Ortega-Blanco et al., 2008; Pérez-de la Fuente et al., 2012b).

Overall, the evolutionary, behavioral, paleoecological, and paleoenvironmental information that *H. diogenesi* provides represents a nice example of how the extraordinary paleobiological potential that amber holds can be reliably aimed at reconstructing the past and "give life" to fossils.

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Figure captions

Figure 1. Lateroventral habitus of *Hallucinochrysa diogenesi* Pérez-de la Fuente, Delclòs, Peñalver and Engel, 2012 (Neuroptera: Chrysopoidea), holotype, preserved together with its trash packet. Abbreviations: ab – abdomen; h – head; l1 – prothoracic leg; l2 – mesothoracic leg; l3 – metathoracic leg; tb – tubular tubercle; tx – thorax. Only the legs from the right side of the body and well-visible tubercles in the image have been tagged. Legs tagged at the femoro-tibial joint. A multiple fracture (f) is transversally crossing the abdomen. The image was obtained by combining photographs taken at successive focal planes.

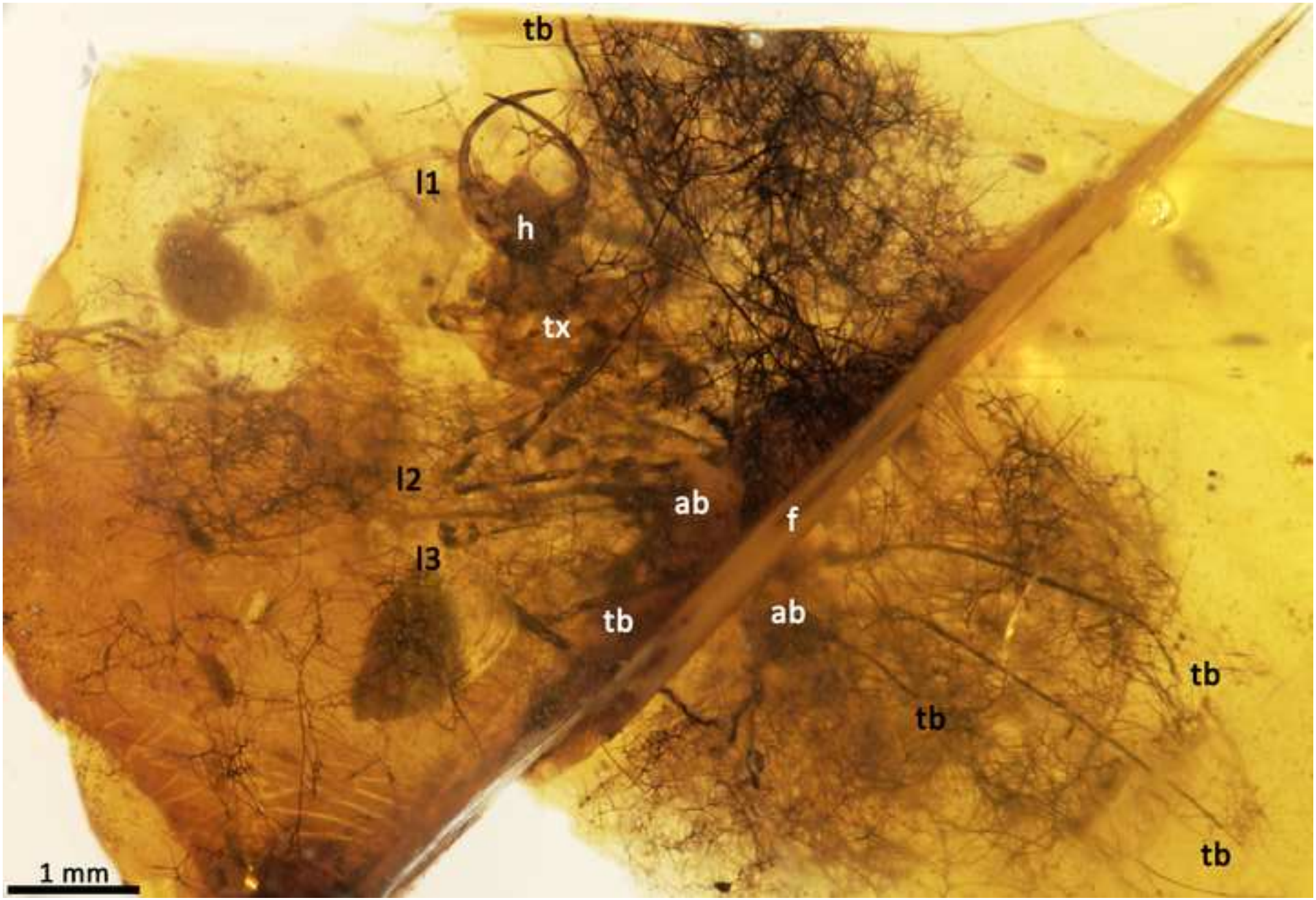
Figure 2. Reconstruction of *H. diogenesi* depicting its life aspect. A) Dorsolateral view. B) Frontal view. C) Sagital view. Head and leg setation have been omitted for clarity. Tubular tubercle setae have been modified for improved visibility (these setae are variable in length in the fossil, usually longer than modeled, and their trumpet-shaped endings are somewhat smaller than as shown here). Length of antennae, body coloration, and number of abdominal tubular tubercle pairs are based on extant larvae. (Author: J.A. Peñas.)

Figure 3. Detail of the head and the right prothoracic leg of *H. diogenesi* in lateroventral view; note also the abundant trichomes from its trash packet. Abbreviations: a – antenna; fe – femur; lp – labial palpi; o – ommatidium; ta – tarsus; tb – tubular tubercle; ti – tibia. A circular fracture is crossing the head (f). The image was obtained combining pictures taken at successive focal planes.

Figure 4. Detail of two trichomes from the trash-packet of *H. diogenesi*. These two trichomes appear to be tangled with one another and show different stages of development, the left one (A) being a more mature form than the one at right (B).

Animation 1. Morphological and locomotive reconstruction of *Hallucinochrysa diogenesi*. See figure 2 caption for additional information.

Figure



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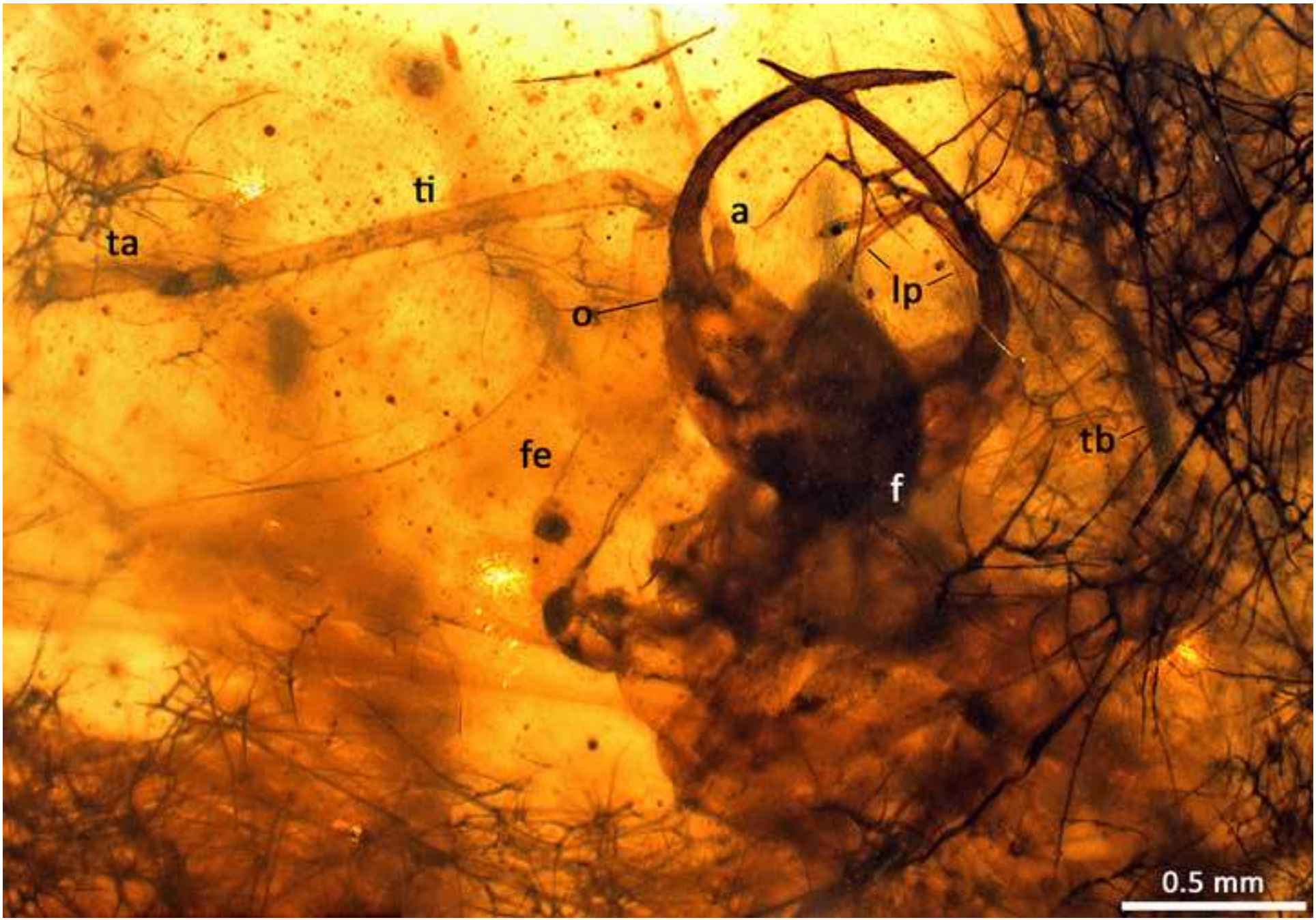

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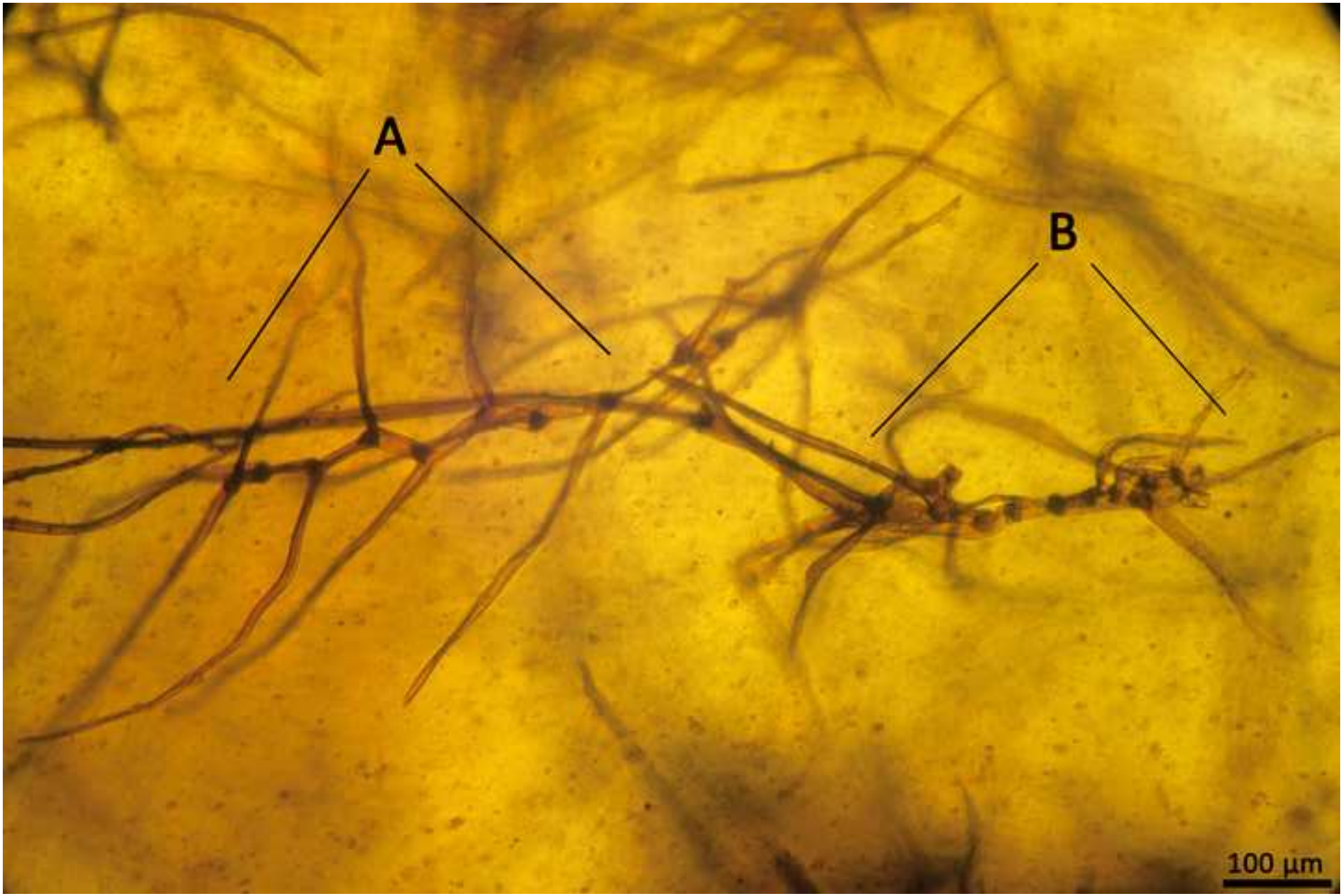

Video Still