

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.

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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 (Martínez-Delclòs et al., 2004), 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 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

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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 intra-specific 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 3700 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 1200 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 (Montserrat 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

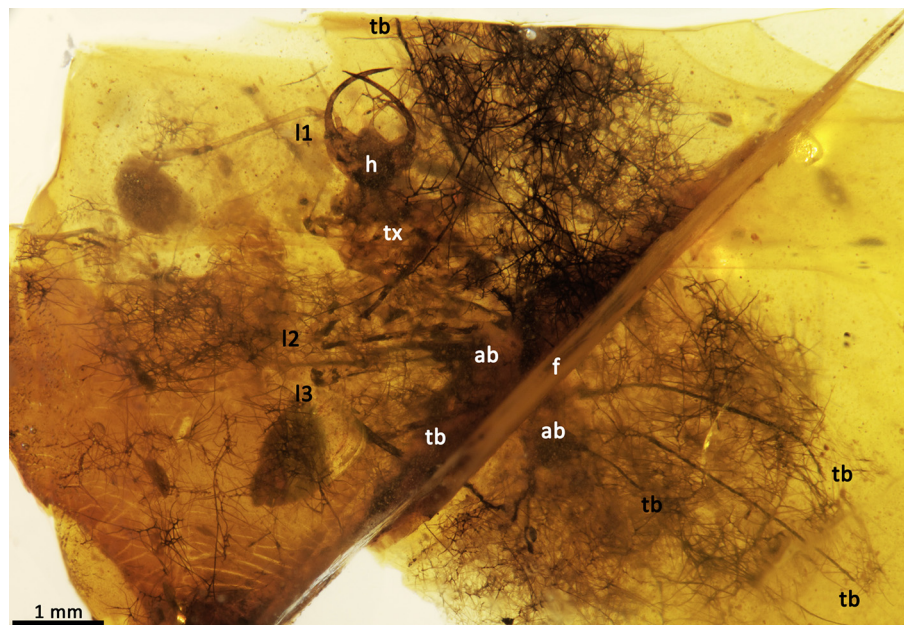


Fig. 1. Lateroventral habitus of *Hallucinochrysa diogenesi* Pérez-de la Fuente, Delclòs, Peñalver and Engel, 2012 (Neuroptera: Chrysopoidea), holotype, preserved together with its trash packet. Abbreviations: ab – abdomen; h – head; l1 – prothoracic leg; l2 – mesothoracic leg; l3 – metathoracic leg; 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.

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