

Supporting Information

Pérez-de la Fuente et al. 10.1073/pnas.1213775110

SI Text

Insect *H. diogenesi* gen. et sp. nov. Preservation and taphonomy. The holotype is almost complete, although both distal parts of antennae and some tubular tubercles are missing. A large, multiple amber fracture is crossing transversally the proximal part of the larval abdomen; thus, several tubular tubercles are obscured. The cuticle preservation differs significantly between some parts, possibly reflecting different degrees of chitinization: the head, legs, and tubular tubercles are very well preserved, but the thorax and the abdomen cuticle aspect is very weak. Tubular tubercles are preserved mainly erect, but a few of them are bent and/or partially collapsed in some portions. Apart from the larval specimen with its trash packet, the amber piece contains a brachyceran fly as a syninclusion (CES 418.2), suggesting that the resin exuded close to the branches in the aerial part of the plant where the larva gathered trichomes, instead of close to the ground.

The complete absence of air bubbles into the intricate, dense web that forms the trash packet of trichomes is indicative of emersion in a highly liquid resin. Nevertheless, the morphology and characteristics of other amber pieces from El Soplao are indicative of highly viscous resin. Apparently, both kinds of resin were produced by the same plant, most likely a cheirolepidiacean gymnosperm (1, 2). Because the resin of the piece in question was highly liquid and fossilized as clear amber, a detailed study of this complex bioinclusion has been possible.

Some parts of the larval body, mainly the tubular tubercles, contain pyrite deposits as thin crusts or clusters constituted by isolated cuboidal crystals (Fig. S1 *A*, *C*, and *D*). In the tubular tubercles, these thin crusts can obscure their real diameter (Fig. S1*D*). A few trichomes contain pyrite deposits as well. Pyrite mineralization in amber bioinclusions is not uncommon, mainly in Cretaceous ambers. That mineralization has been established, in part, as the origin of the exceptional preservation of diverse protist in Spanish Álava amber (3). The abundant presence of pyrite in the El Soplao organic-rich claystones, as in the other main Spanish amber outcrops, along with other evidence, indicates original suboxic conditions within the water-sediment interphase, where resins were originally deposited (4).

Description. The fossil sample is immature, probably a third instar. The body is campodeiform and gibbous (likely moderately gibbous). The body length is *ca.* 4 mm from the head, excluding the jaws, to the apex of abdomen, as preserved. The cephalic capsule is banana-shaped (i.e., very broad and short with frons heavily concave, 1.00 mm wide). The jaws are very long (*ca.* 1.20 mm), stylized, and highly recurved; the jaw apices have a few sensilla and serrated inner margins (Fig. S2*A*). Present are a distal depression on the ventral surface of the right jaw and a conical process on the dorsal surface of left jaw, with both structures at a similar distance from the apexes, together interpreted as a coupling system (Fig. S2*B*). The palpiger has two setae. The labial palpi are very gracile, having three palpomeres; the basal palpomere has short setae, except for two extremely long setae at the apex; the median palpomere is the longest (*ca.* 0.40 mm), without annulations; the distal palpomere is slightly club-shaped, bearing a terminal conical papilla (0.31 mm including papilla) (Fig. S2*C*). The relative length ratio of the median palpomere/distal palpomere is 1.35 (i.e., lower than in extant larvae). The antenna is gracile, fairly long despite missing distal parts; the scapus is elongated; the pedicel is cylindrical (0.13 mm long); the flagellum is filiform, straight, with a constant diameter; the flagellar base is bulbous. Ocular tubercles are very prominent, located on the most distolateral sides of the head, each with four

stemmata (Fig. S2*D*). Several cephalic setae are emerging from grooves, elongated (about as long as cephalic length) (Fig. S2*D*); at least five setae are emerging from the lateral sides of head, curving anteriorly, and some elongated setae are also present on the longitudinal head axis. No apparent color pattern nor epicranial marks are preserved. The cervix is conical and elongated. The prothorax is narrower than other thoracic segments. Setation on the dorsal surface is not conspicuous. Present are extremely elongated, highly setigerous tubular tubercles on the thorax and abdomen, apparently with the same development. The thorax has lateral and laterodorsal pairs of tubular tubercles on each segment (i.e., not simply one lateral pair) (Fig. S1*A*). Thoracic tubular tubercles have a broad insertion (Fig. S1*A* and *B*). Prothoracic pairs of tubular tubercles are anteriorly directed (Fig. S1*A*); mesothoracic and metathoracic pairs are more perpendicularly directed in relation to body axis. None of the thoracic tubular tubercles are preserved in complete length, with the longest preserved at 3.64 mm; the lateral and laterodorsal prothoracic tubular tubercles are 0.08 and 0.09 mm wide, respectively. The abdominal pairs of tubular tubercles become gradually thinner toward the apices. The total number of abdominal tubular tubercles is unknown because of the presence of a multiple fracture that obscures a large portion of the abdomen. The longest abdominal tubular tubercle is over 4 mm long, as preserved (incomplete). Tubular tubercles from the anterior abdominal segments are perpendicularly directed in relation to body axis, and those from the last segments are posteriorly directed. Tubular tubercles have setae along the entire length except the very base, which are shorter and sparser basally (setae of abdominal tubular tubercles are about 0.40 mm basally and up to *ca.* 0.75 mm apically) (Fig. S1*E*). Tubular tubercle setae emerge from tuberculated bases that are more conspicuous toward the tubular tubercle apex (Fig. S1*C*), smooth (without serrations), strongly tapering apically, with trumpet-shaped endings (Fig. S1*E* and *F*). The legs are distinctly large and robust; the prothoracic leg is 3.10 mm long (femur, 1.18 mm; tibia, 1.56 mm; tarsus, 0.36 mm); the mesothoracic leg is 3.23 mm long (femur, 1.49 mm; tibia, 1.42 mm; tarsus, 0.32 mm); the metathoracic leg is the largest (3.68 mm long), with a total length estimated (femur, 1.69 mm; tibia, 1.60 mm estimated; tarsus, 0.39 mm) as about 1.2 times longer than the prothoracic leg. The femora are almost glabrous. The trochanters have a few long setae, with an external, rounded process on all legs bearing a particularly elongated seta. Tibiae and tarsi have copious setae, with particularly elongated setae basally at each tibia. Tarsi have fused tarsomeres. The pretarsal claws are long, sharp, recurved at an almost right angle (not curving inward), with laminar basal expansions (Fig. S2*E* and *F*). Trumpet-shaped empodia are well developed (0.19 mm long) (Fig. S2*F* and *G*). Two long, fine pulvilli are present between the claws (0.19 mm long) (Fig. S2*F*). The last abdominal segment likely ends in a rather broad, depressed cone.

Phylogeny and fossil record of green lacewings and relatives. The superfamily Chrysopoidea comprises the extant family Chrysopidae and several allied, extinct lineages of lacewings. It is a matter of semantics whether these are all considered subfamilies within an expanded Chrysopidae s.l. or as families within a superfamily. Herein, we prefer to consider the fossil lineages at the family rank (5) (i.e., Mesochrysopidae Handlirsch, 1906; Limaiidae Martins-Neto & Vulcano, 1989; Allopteridae Zhang, 1991; Liasso-chrysiidae Nel, Delclòs & Hutin, 2005; and Tachynymphidae Nel, Delclòs & Hutin, 2005). Chrysopoidea first appeared in the Early Jurassic and reached maximum disparity and geographical dis-

tribution during the Late Jurassic/Early Cretaceous (5). The extinct families, excluding Limaiidae, did not cross the Cretaceous–Tertiary boundary. Chrysopoidea are closely related to the Hemerobiidae (5–7) or sometimes considered as allied to the Hemerobiidae and/or Osmyliidae (8, 9).

The first adult fossil record relatable to Chrysopidae *sensu stricto* is *Paralembochrysa splendida* Nel, Delclòs & Hutin, 2005 from Late Jurassic/Early Cretaceous compression rocks in Liaoning Province, China. Other than that dubious record, modern Chrysopidae have been exclusively recognized from the Cenozoic fossils (5). The monophyly of Chrysopidae is well supported, although relationships within the Neuroptera remain contentious (9–11). Significant advances have been made toward recovering stable relationships within the family (12–15). Today, the majority of species of Chrysopidae belong to the subfamily Chrysopinae, which appeared during the Late Eocene. It has been suggested that, apart from their adaptation to the Cenozoic climate (16), the appearance and widespread distribution of the Chrysopinae since the Eocene is related to the evolution of their auditory organs (alar tympanic organs), which detect bat echolocation and permit escape responses (17, 18).

The fossil record of green lacewing larvae is extremely scarce. A green lacewing larva carrying a trash packet of “stellate hairs” (oak trichomes) and other plant remains was figured from mid-Eocene Baltic amber but without further study (19). Also, another green lacewing larva from Baltic amber, originally described as a hemerobiid (20), was recognized with some trichomes in the vicinity as possible remains of a trash packet, although the exemplar is lost (21). Furthermore, a described chrysopid larva from Early Miocene Dominican Republic amber lacks a trash packet (22). On the other hand, the only previously known Cretaceous record in amber of the lineage is a neonate first instar larva from Late Cretaceous Canadian amber (Campanian), which was entrapped while emerging from its characteristic stalked egg (23) (Fig. 4). In contrast, adult green lacewings are well reported from impression/compression fossils (5), even though they are also outstandingly rare from amber deposits. In fact, up to now, only three green lacewing adults have been described from the Dominican Republic amber (22), and another one has been reported from Baltic amber (24). No chrysopid adults have yet been reported from Cretaceous amber. Therefore, the discovery described here also represents the earliest record in amber of the superfamily Chrysopoidea.

Morphological comparison. Several studies have reviewed larval morphology and anatomy (25–27). The morphological disparity of *H. diogenesi* with both known extinct and extant chrysopid larvae is very remarkable. The larva figured from Baltic amber carrying a trash packet (19) lacks extremely elongated tubercles and the legs are not particularly enlarged, whereas the larva described in 1856 by Hagen from Baltic amber, today lost, possessed “round, strongly constricted setigerous tubercles on the thorax” (21), although it is not certain to which larval stage the specimen corresponded. The immature from Miocene Dominican amber (22) shows tubercles on the thorax and abdominal segments I–VII that are spherical. Each tubercle bears four to six very long, thick setae, which are inserted into conspicuous nodules from the tubercle. In addition, the head is subquadrate, the jaws are short and relatively blunt, and the legs are not particularly enlarged, being only slightly longer than the cephalic capsule plus jaws. Its scarce tubercle setation and small body size (1.3 mm) could indicate that it was a first instar. Regarding the neonate reported from Late Cretaceous Canadian amber preserved as it emerged from its stalked egg (23), no other features are preserved to permit a more conclusive determination as to its later morphology, behavior, or ecology. Today, neonate larvae, after hatching through a slit formed at the egg cephalic pole by its egg-burster, remain clung to their stalked egg for several

hours until the body hardens and the jaws become operative (25), probably explaining this exceptional record.

Modern chrysopid larvae have palpi with a short basal palpomere, an annulated second palpomere distinctly more elongated than the others, and a shorter third palpomere slightly tapering distally (27). However, the three palpomeres of *H. diogenesi* are not so different in length, the annulations of the second palpomere are not present, and the elongated third palpomere does not taper distally but slightly expands. Also, the bizarre tubercle length and the special cephalic capsule morphology (i.e., banana-shaped head) of *H. diogenesi* are not found today in extant green lacewing diversity, even though they could represent highly variable characters because, today, they strongly depend on trash-carrying and feeding habits, respectively. Lastly, the coupling system of the jaws has not been described, to our knowledge, from any Recent chrysopid larvae.

Suprageneric-level assignment. The most conservative is to classify *H. diogenesi* as a Chrysopoidea of uncertain family. Exclusion of *H. diogenesi* from Chrysopidae *sensu stricto* is supported by the fact that, even though it shows the same bauplan that extant trash-carrying chrysopid larvae, it exhibits several unique characters, as noted above. Also, Chrysopidae *sensu stricto* are not recognized until the Cenozoic (5). It is interesting to note that the current high-level classification within Chrysopidae is almost solely based on adult characters (12), because parallelisms and convergence in larval traits are rampant across the family (28). However, larval anatomy and morphology have proven to be of great importance for recovering lower-level relationships within the family (29, 30).

On the other hand, it is not possible to assign the fossil to any extinct chrysopid family because nothing was known previously about the larval stages of nonchrysopid chrysopoids. Although there is evidence of the extinct chrysopid families Allopteridae and Tachynymphidae living in the Iberian Plate during the Early Cretaceous [i.e., adult rock fossils (5)], it is virtually impossible to relate adult forms with their larval counterparts.

Predatory habits. Whereas chrysopid adults have mainly carnivorous diets or feed on plant products, larvae are always voracious predators and mostly polyphagous but sometimes stenophagous (25, 31). As is true for all immature neuropterans, chrysopid larvae have sucking jaws, which inject salivary secretions and then absorb the liquified tissues and internal fluids (25). The common prey of extant green lacewing larvae are sternorrhynchans such as aphids, coccoids, and psyllids, but the prey range covers an extreme diversity of groups, including spiders, phytophagous mites, and other insects such as hemipterans, thrips, barklice, hymenoptera, or even termites (26), the majority of which are represented in Spanish Albian ambers (32). The potential diet of the fossil larva can be delimited. First, aphids, the main food for extant green lacewings, were extremely scarce in its paleoenvironment in comparison with coccoids, the relative abundance of which has been explained by the low paleoclimate seasonality (33). Second, insects associated with extant ferns are mainly hemipterans, beetles, and lepidopterans, with a high proportion of sap-feeders and specialist feeders restricted to ferns; it has been estimated that only 9,300 insect species are able to use ferns as a food source, compared with ~400,000 species of insects that use angiosperms (34). In addition, it has been demonstrated that the jaw length and cephalic width, which relates to more widely spaced jaws, are related with prey size (35); thus, the very long jaws of *H. diogenesi* (ca. 1.20 mm) and its especially broadened cephalic capsule suggest specialization or, at least, capacity to feed on large prey. The trumpet-shaped empodia allows an efficient anchoring to the substrate that is associated with not only better locomotion but also an increase of the ability to capture and retain active prey (36).

Trichomes from the Plant Host. Overview on trichomes. The filamentous plant remains composing the larval trash packet are rec-

ognized as plant trichomes because of their morphology, size range, microornamentation, and autofluorescence signals. Trichomes exhibit the greatest intra- and interspecific morphological variation among plant epidermal outgrowths, ranging from a few micrometers to several millimeters. Hundreds of different trichome morphologies have been documented from vegetative and reproductive structures of diverse vascular plants, having long been used for taxonomic purposes (37–40). According to their function, trichomes can be glandular or nonglandular and are characterized by numerous anatomical features such as surface morphology, wall thickness, unicellular/multicellular structure, and cell type (38, 41). Some of the more advanced trichome specializations include the nonglandular, hooked forms of *Loasaceae*, which entrap potential herbivores (42) or those with a completely cutinized wall as a xerophytic adaptation to prevent evapotranspiration and excessive solar radiation (43). In addition, trichomes can provide a variety of mechanical and/or chemical defense functions against herbivores or pathogens (44). Mature, nonglandular trichomes are composed of a thick cell wall and cuticle layer along with cytoplasmic content that usually disintegrates (40, 45). Despite being physiologically “dead,” the trichome function persists (41). The cell wall of nonglandular trichomes tends to be thick so as to protect any internal structures and is also often composed of lignin, cutin, or suberin (37, 41). Accordingly, trichomes preserve well in the fossil record, particularly as inclusions in amber, owing to their thick cuticles with chemical stability and resistance to biological degradation (46, 47).

The most abundant and frequently reported fossil trichomes are the “stellate hairs” from oaks (*Fagaceae*), which are characteristic of the mid-Eocene Baltic amber (24). Stellate trichomes have also been reported from Mexican amber (Early Miocene) and, along with those from the Baltic deposits, have been characterized using confocal laser microscopy (48). Cretaceous amber trichomes have been scarcely studied. Branched, nondendritic trichomes have been discovered in mid-Cretaceous Ethiopian amber and likely originate from ferns of the families *Cyatheaceae* and *Hymenophyllaceae* (49). Although the occurrence of trichomes has been reported in Cretaceous ambers from New Jersey, Myanmar, and Spain, they lack further characterization (50–52).

Morphological variability. For the basic description of the trichomes composing the larval trash packet refer to the main text. Overall, two basic morphologies of trichomes composing the larval trash packet were evident, in part because of different maturation degrees (Fig. S3A). The first, type I, has a straight axis, and the OSAs are close together, sometimes even in contact, whereas secondary branches emerge perpendicularly from the axis (Fig. S3A and B). In type II trichomes, much more abundant than type I, the axis is flexuose (i.e., zigzagged) and the OSAs tend to be well separated, with secondary branches arising at an angle of 70–120° relative to the main axis and always directed apically away from the blunt base or trichome insertion (Fig. S3B and Fig. S3A and C).

When comparing individual trichomes, the length of the trichome base (length between the blunt base of the axis and the first secondary branch) is relatively similar, ranging from 20 to 30 μm , whereas the total length of the axis is understandably more variable, ranging from 140 to 550 μm but normally is ca. 300 μm long. The length of an individual secondary branch is similarly quite variable, with some extending more than a millimeter in total length (2,200 μm the longest measured). A few long remains present in the trash packet could correspond to extremely long secondary branches from old, highly differentiated trichomes.

We recognized very similar trichome morphologies when examining several isolated trichomes from the Peñacerrada I outcrop (sample MCNA 10023; Fig. S3F and G), and one trichome adhered to the leg of an oonopid spider, *Orchestina* sp., from the San Just outcrop (sample CPT 4100) (53). Furthermore, we have

recognized in the bibliography very similar trichome morphologies in Late Albian Burmese amber (54).

Trichome identity. The morphology of the fossil trichomes is compared with those in extant plants to identify them. For that comparison, all of the plant groups that could produce trichomes and are present in the El Soplao outcrop were first considered. The plant meso- and macroremains (cuticles) from El Soplao belong to extinct conifers (cheirolepidiaceans and miroviaceans) and ginkgoaleans (1, 4). These lineages are also recognizable in the palynological record, along with other conifers (araucariaceans, cupressaceans/taxodiaceans, and pinaceans) and other vascular plants, such as leptosporangiate ferns, pteridospermophytes (caytonialeans and peltaspermaleans), and even early flowering plants (magnoliids and monocots) (1).

Among the leptosporangiate ferns, palynological evidence from the El Soplao outcrop demonstrates the presence of *Cyatheaceae/Dicksoniaceae*, *Gleicheniaceae*, *Schizaeaceae*, *Marsiliaceae*, and *Osmundaceae* (1). Among these, the presence of multiserial and even dendritic trichomes is well known for *gleicheniaceans* (55, 56), a lineage widespread during the Early Cretaceous (57–59). *Gleichenia chaloneri* Herendeen & Skog, 1998, an Albian species from England preserved as fusainized remains, shows dendritic trichomes associated with pinnules and sori (60) that are similar in shape and size to those recovered from El Soplao. *Gleicheniaceae* are known from El Soplao such as the spore species *Gleicheniidites senonicus* Ross, 1949 (1) and *Ornamentifera peregrina* (Bolchovitina, 1953) Bolchovitina, 1968 (Fig. S4).

In the gymnosperm lineages present in El Soplao, trichomes are either uncommon or nondendritic. Among *Cheirolepidaceae* the trichomes are principally found associated with cones, microsporophylls, and free leaves and, when known, are conical and nonbranched (61–65). In addition, although cycads exhibit a dense wool of very long trichomes covering the base of young leaves and cataphylls (i.e., ramentum), these are also nonbranched (66). Trichomes in Cretaceous magnoliids have nonbranched morphologies that are associated to inflorescences (66–70). Moreover, although there is evidence of dendritic trichomes in different groups of modern monocots, they are restricted primarily to inflorescences (71, 72), less available than leaf trichomes in terms of time and abundance for being potentially harvested by trash-carrying larvae. The possibility that the trichomes would have belonged to a eudicot, although less plausible because its presence has not been evidenced in El Soplao, should not be discarded. Among the basal eudicots, which radiated during the Early Cretaceous (73), dendritic trichomes can be found within the *Platanaceae* (74). Interestingly, there has been documented an extant chrysopid larva (*Ceraeochrysa lineaticornis*) that incorporates stellate trichomes to its trash packet exclusively gathered from *Platanus wrightii* leaves (*Platanaceae*) (75). Within rosids and asterids, the two main clades of the eudicots that radiated during the Late Cretaceous (73), dendritic trichomes are nowadays extremely diverse and can be widely found among very different groups (38, 40). In fact, dendritic trichomes with a flexuose main axis, thus with a high resemblance to those composing the trash packet from El Soplao’s larva, have been noted in the recent asterid families *Lamiaceae* and *Acanthaceae* (76–78). However, asterids have their first known occurrence in the Turonian of New Jersey (79, 80), and only molecular studies hypothesize their origin back to the Early Cretaceous (81, 82). In conclusion, apart from the *gleicheniacean* ferns, the remaining plant families known from El Soplao seem were not the sources of the trichomes harvested by *H. diogenesi*.

Paleoecological implications. Ecological studies have demonstrated that *gleicheniacean* ferns are primary succession pioneers, following wildfires or lava flows (83–85). Indeed, the *gleicheniacean* fossil record is well represented by charcoalified and fusainized remains, indicating that these ferns were present as colonizers in

fire-prone environments, at least since the Late Jurassic (60, 86, 87). Charcoal or fusinite are not only copiously present in the Spanish amber-bearing levels but also sometimes found as inclusions within amber (1, 32). Given the abundance of the amber deposits and their pervasiveness in the Albian outcrops of Spain (32), it seems evident that wildfires were a prominent feature of the forest functioning, promoting both resin production and subsequent erosion of partially burnt litter where the detached resin was primarily buried (1) and permitting the perpetual invasion of primary succession lineages such as Gleicheniaceae. The plant–insect relationship presented in this paper represents possible paleoecological evidence reinforcing this scenario. Additional evidence is the presence of an anaxylid woodwasp in Álava amber (88), a group whose extant representatives lay eggs in burnt coniferous trees shortly after wildfires, as well as the diversity of snakefly species in Spanish amber, including some preserved with charcoaled plant remains (89).

Trichome autofluorescence. Resistant biomacromolecules can be preserved in the fossil record (90–93). As has been detected from biological remains preserved in amber, some of these biomacromolecules maintain their autofluorescence (3, 48, 94–97). Although amber has its own autofluorescence when excited with UV light, the filters used permitted us to discriminate the autofluorescence produced by specific trichome biomolecules despite their low intensity. Autofluorescence of the trash packet trichomes was only detected with UV excitation (Ex/Em: 365/420–470 nm), although the blue emission recorded was mainly localized on the micropapillae on the wall's surface (Fig. 3G). Autofluorescence was also detected on the walls of germane trichomes found in other Spanish ambers, as Peñacerrada I amber (Fig. S3 F and G). This blue autofluorescence in the trichome cuticle indicates the presence of phenols, such as hydroxycinnamic acid and/or flavonoids (98–101). In some modern ferns, such as the genus *Pityrogramma*, flavonoids are known to pass through the cell wall and cuticle, crystallizing on the surface of trichomes, and apparently possess antimicrobial properties against plant pathogens (98).

Geological Context. The formation of the Basque-Cantabrian Basin (BCB), northern Spain, along with other Mesozoic basins of the Iberian Plate, is associated with the opening of the northern part of the Atlantic. During the Early Cretaceous, sedimentation of the basin was dominated by sandstones, limestones, and marls that were deposited in shallow marine and freshwater environments. During the Early-to-Middle Albian, at the end of the rift stage, deltaic and estuarine systems developed and evolved vertically into a deltaic system dominated by a fluvial–deltaic environment with siliciclastic input, represented by the Escucha Formation (102). In general, the amber localities of the BCB are related to paralic environments in the eastern region (Escucha Fm.), or paralic-marine environments in the western region (Las Peñas Fm.) (32). Spanish Cretaceous amber is principally found in localities distributed in a curvilinear arc from the east to the north along the Iberian Peninsula, which corresponds approximately to the seashore during the Early Cretaceous (103).

Three main amber-bearing outcrops are found in the BCB: Moraza, also named Peñacerrada I, in Burgos Province, and Peñacerrada II in Álava Province, both at the eastern BCB and known together as Álava amber (32, 104); and El Soplao in the Autonomous Community of Cantabria, at the western BCB (4). All of these amber-bearing outcrops are Albian in age, despite the first and second cited were formerly dated as Late Aptian to Early Albian. Other important Spanish outcrops of Albian age are Arroyo de la Pascueta and San Just in Teruel Province (50, 105, 106). All of these deposits originated in deltaic environments and contain abundant, exceptionally well-preserved plant cuticles.

The El Soplao amber-bearing deposit is geographically localized near the municipality of Rábago (Cantabria). Stratigraphically, it

occurs in the Las Peñas Fm., a nonmarine to transitional marine siliciclastic unit that is interleaved within a regressive–transgressive, carbonate-dominated marine sequence of Early Aptian to Late Albian age; Las Peñas Fm. corresponds to the regressive stage of that sequence during the Early Albian (4, 32). Strata of the El Soplao outcrop are located in a unit of heterolithic sandstones–siltstones and carbonaceous mudstones related to broadly coastal delta–estuarine environments (4). A level of organic-rich clays, 0.7–2.5 m thick, contains the amber pieces together with dinoflagellates, spores of vascular cryptogames, pollen grains of gymnosperms and angiosperms, abundant gymnosperm plant cuticle remains, fusinized wood, and marine or brackish-water invertebrates such as gastropods and bivalves. Serpulids and bryozoans encrusting some amber surfaces have been also found (1). The taphonomic data indicates that the amber had a parautochthonous origin in which paleofires promoted both resin production and erosion of the litter containing resin pieces (1, 107). Until now, this amber has yielded more than 500 arthropod bioinclusions belonging to arachnids (acari and spiders) and insects of 11 recognized orders: Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Hymenoptera, and Diptera. Stalactite-shaped amber pieces, very rich in bioinclusions because of their aerial origin (90), are especially abundant in the outcrop, as well as amber pieces with a very characteristic blue-violet fluorescence (2, 4).

Data used in Fig. 4. Note that FEC indicates fossil evidence of camouflage, and FR indicates fossil range. The ranges shown in Fig. 4 for those categories that contain more than one family correspond to the family underlined in the descriptions below. Fossil groups are marked with a dagger (†). The oldest records and group ranges are calibrated by geochronology (108).

Echinoderms (Phylum Echinodermata). Sea urchins (Class Echinoidea) attach stones, as well as animal and plant debris, to their body using their ambulacral podia (109–111) [FEC: absent; FR: Ordovician to Recent (112)].

Gastropods (Phylum Mollusca, Class Gastropoda). Euomphalid gastropods (Family †Euomphalidae) agglutinated exoskeletons to their shell, presumably with mucous secretion (113) [FEC: Early Devonian (114); FR: Early Devonian (inferred appearance in the Late Cambrian) to Late Permian (115)]. Xenophorid gastropods (Clade Littorinimorpha: Family Xenophoridae) agglutinate exoskeletons, stones, and sand grains to their shell with mucous secretion (116) [FEC: Cenomanian (Late Cretaceous), Eocene, Oligocene, Early Miocene (114); FR: Late Cretaceous to Recent (116, 117)]. Scaliolid and turritellid gastropods (Clade Sorbeoconcha: Superfamily Cerithioidea: Family Scaliolidae, Turritellidae) agglutinate sand grains and other debris to their shell with mucous secretion (118, 119) [FEC: Eocene (Scaliolidae), Late Miocene (Turritellidae) (119, 120); FR: Early Cretaceous to Recent (Turritellidae), Late Cretaceous to Recent (Scaliolidae) (117, 119)]. Enid gastropods (Clade Stylommatophora: Family Enidae) agglutinate soil or lichens to their shell with mucous secretion (121, 122) [FEC: absent; FR: Eocene to Recent (123)].

Arthropods (Phylum Arthropoda). Sand-covering spiders (Class Arachnida: Order Araneae: Family Paratropididae, Microstigmatidae, Pisauridae, Sicariidae, Homalonychidae, Zodariidae) attach sand grains to specialized body setae (124, 125) [FEC: absent; FR: Eocene to Recent (Pisauridae, Zodariidae), Miocene to Recent (Microstigmatidae, Sicariidae), no fossil record (Paratropididae, Homalonychidae) (126)]. Decorating crabs (Class Malacostraca: Order Decapoda: Family Dromiidae, Dorippidae, Homolidae, Xanthidae, and families within the superfamily Majoidea) attach animal and plant debris, stones, or living organisms to hooked body setae or specialized pereopods (127–130) [FEC: absent; FR: Late Jurassic to Recent (Homolidae), Late Cretaceous to Recent (Dorippidae), Paleocene (inferred appearance in the

Jurassic) to Recent (Dromiidae), Early Eocene (inferred appearance in the Cretaceous) to Recent (Majoidea), Late Eocene to Recent (Xanthidae) (131)].

Insects (camouflage only in immature stages) (Class Insecta). Assassin bugs (Order Hemiptera: Family Reduviidae) attach animal and vegetal debris to glandular or mechanically specialized body setae (132) [FEC: Early Miocene, Dominican and Mexican amber (114, 133); FR: Early Cretaceous to Recent (54)]. Barklice (Order Psocoptera: Family Psocidae, Troctopsocidae) attach debris (and their own feces) with silk to glandular body setae (134, 135) [FEC: Early Miocene, Dominican amber (114); FR: Late Jurassic to Recent (54)].

Neuropterans (Order Neuroptera). Neuropterans attach animal and vegetal debris to specialized body setae and setose tubercles (136–138): owlflies [Family Ascalaphidae; FEC: Early Miocene, Dominican amber (22); FR: Eocene (inferred appearance around limit Jurassic to Cretaceous) to Recent (54)]; split-footed lacewings [Family Nymphidae; FEC: absent; FR: Jurassic to Recent (54)]; green lacewings [Family Chrysopidae and extinct allies (i.e., Superfamily Chrysopoidea); FEC: Albian, Spanish amber; Middle Eocene, Baltic amber (19); FR: see below].

Case-building insects (marked with asterisks in Fig. 4). Leaf beetles (Order Coleoptera: Family Chrysomelidae) build a case with their own feces, incorporating plant debris, using salivary secretions (139) [FEC: Middle Eocene, Baltic amber; Early Miocene, Dominican amber (140); FR: Late Cretaceous to Recent (54)]. Tineid moths (Order Lepidoptera: Family Tineidae, Psychidae) build a case with their own feces, incorporating plant debris, using silk (141) [FEC: Middle Eocene, Baltic amber; Early Miocene, Dominican amber (54, 114); FR: Eocene (inferred appearance in the Cretaceous) to Recent (54)]. Caddisflies (Order Trichoptera) build a case with sand grains or animal and plant debris using silk (142) [FEC: very common in the fossil

record, known since the Early Jurassic (54, 143); FR: Early Triassic to Recent (54)].

Other invertebrates cover themselves with exogenous elements. Sea anemones and polychaetes actively select exogenous elements and attach them to their body structures (column and tube, respectively) but without proven camouflaging implications (144–146). Moreover, phoronids and sand-cementing bivalves agglutinate exogenous elements to their body structures (tube and shell, respectively) but passively (147–150).

Lower Box in Fig. 4. Spanish amber contained *H. diogenesi* gen. et sp. nov., which has the oldest trash-carrying behavior and trumpet-shaped empodia (this report). Canadian amber contained stalked eggs (23). Baltic amber contained a figured green lacewing larva carrying a trash packet of “stellate hairs” (oak trichomes) and other plant remains (19) and a lost specimen of a larva with some trichomes in the vicinity as possible remains of a trash packet, which was described originally as Hemerobiidae but possibly belonging to Chrysopidae according to a subsequent interpretation (20, 21). Dominican amber contained a complete larva with trumpet-shaped empodia and setigerous tubercles but without evidence of trash packet (22).

The localities where adult Chrysopoidea have been described are as follows: the Early Jurassic of Luxembourg; the Late Jurassic of Germany, Kazakhstan, and China; the Early Cretaceous of Brazil, Spain, Russia, Mongolia, and China; the Late Cretaceous of Russia; the Paleocene/Eocene of Denmark; the Late Eocene of France; the Late Eocene of England; the Eocene and Late Eocene/Early Oligocene of the United States; the Oligocene of Germany; the Late Oligocene of France; the Early Miocene of Spain; the Miocene of Hungary; and the Middle Miocene of Russia (5). The trumpet-shaped empodia can be considered an adaptation to capture and retain active prey because of an efficient anchoring to the substrate (36).

- Najarro M, et al. (2010) Review of the El Soplao amber outcrop, Early Cretaceous of Cantabria, Spain. *Acta Geol Sin* 84:959–976.
- Menor-Salván C, et al. (2010) Terpenoids in extracts of Lower Cretaceous ambers from the Basque Cantabrian Basin (El Soplao, Cantabria, Spain): Paleochemotaxonomic aspects. *Org Geochem* 41(10):1089–1103.
- Ascaso C, et al. (2005) Fossil protists and fungi amber and rock substrates. *Mikropaleontol* 51:59–72.
- Najarro M, et al. (2009) Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain). *Geol Acta* 7:363–387.
- Nel A, Delclòs X, Hutin A (2005) Mesozoic chrysopterid-like Planipennia: A phylogenetic approach (Insecta: Neuroptera). *Ann Soc Entomol Fr* 41(1):29–69.
- Winterton SL, Hardy NB, Wiegmann BM (2010) On wings of lace: Phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. *Syst Entomol* 35:349–378.
- Beutel RG, Friedrich F, Aspöck U (2010) The larval head of Nevrothidae and the phylogeny of Neuroptera (Insecta). *Zool J Linn Soc* 158(3):533–562.
- Aspöck U, Plant JD, Nemeschkal HL (2001) Cladistic analysis of Neuroptera and their position within Neuropterida (Insecta: Holometabola: Neuroptera). *Syst Entomol* 26(1):73–86.
- Aspöck U (2002) Phylogeny of the Neuropterida (Insecta: Holometabola). *Zool Scr* 31: 51–55.
- Haring E, Aspöck U (2004) Phylogeny of the Neuropterida: A first molecular approach. *Syst Entomol* 29:415–430.
- Aspöck U, Aspöck H (2008) Phylogenetic relevance of the genital sclerites of Neuropterida (Insecta, Holometabola). *Syst Entomol* 33:97–127.
- Brooks SJ, Barnard PC (1990) The green lacewings of the world: A generic review (Neuroptera: Chrysopidae). *Bull Br Mus Nat Hist Ent* 59(2):117–286.
- Brooks SJ (1997) An overview of the current status of Chrysopidae (Neuroptera) Systematics. *Deutsche Entomol Z* 44:267–275.
- Winterton S, de Freitas S (2006) Molecular phylogeny of the green lacewings (Neuroptera: Chrysopidae). *Aust J Entomol* 45:235–243.
- Haruyama N, Mochizuki A, Duelli P, Naka H, Nomura M (2008) Green lacewing phylogeny, based on three nuclear genes (Chrysopidae, Neuroptera). *Syst Entomol* 33:275–288.
- Archibald SB, Makarkin VN, Greenwood DR (2011) Cenozoic climates and the evolution of green lacewings (Neuroptera: Chrysopidae). *Ber Geol Bund* 85:34.
- Miller LA, Olesen J (1979) Avoidance behavior in green lacewings. I. Behavior of free flying green lacewings to hunting bats and ultrasound. *J Comp Physiol* 131:113–120.
- Resh VH, Cardé RT (2009) *Encyclopedia of Insects* (Academic, London), 2nd Ed.
- Weitschat W (2009) Jäger, gejagte, parasiten und blinde passagiere - momentaufnahmen aus dem Bernsteinwald [Predator, prey, parasites and stowaways - snapshots of the amber forest]. *Denisia* 26:243–256. German.
- Hagen H (1856) *Die im Bernstein Befindlichen Organischen Reste der Vorwelt. Zweiter Band, II* [Organic remains in amber, second volume, II], ed Berendt GC (Nicholaischen Buchhandlung, Berlin), pp 41–125. German.
- MacLeod EG (1970) The Neuroptera of the Baltic Amber. I. Ascalaphidae, Nymphidae, and Psychopsidae. *Psyche (Stuttg)* 77:147–180.
- Engel MS, Grimaldi DA (2007) The neuropterid fauna of Dominican and Mexican amber (Neuropterida: Megaloptera, Neuroptera). *Am Mus Novit* 3587:1–58.
- Engel MS, Grimaldi DA (2008) Diverse Neuropterida in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). *Nova Suppl Entomol Keltern* 20:1–86.
- Weitschat W, Wichard W (2002) *Atlas of Plants and Animals in Baltic Amber* (Verlag Dr. Friedrich Pfeil, Munich).
- Canard M, Séméria Y, New TR (1984) *Biology of Chrysopidae* (Dr. W. Junk Publishers, The Hague).
- McEwen PK, New TR, Whittington AE (2001) *Lacewings in the Crop Environment* (Cambridge Univ Press, Cambridge, UK).
- Tauber CA (1974) Systematics of North American chrysopterid larvae: *Chrysopa carnea* group (Neuroptera). *Can Entomol* 106:1133–1153.
- Tauber CA (1975) Larval characteristics and taxonomic position of the lacewing genus *Suaris*. *Ann Entomol Soc Am* 68(4):695–700.
- Tauber CA, Albuquerque GS, Tauber MJ (2008) *Gonzaga nigriceps* (McLachlan) (Neuroptera: Chrysopidae): Descriptions of larvae and adults, biological notes, and generic affiliation. *Proc Entomol Soc Wash* 110(2):417–438.
- Tauber CA, Tauber MJ, Albuquerque GS (2008) A new genus and species of green lacewings from Brazil (Neuroptera: Chrysopidae: Leucochrysin). *Ann Entomol Soc Am* 101(2):314–326.
- Millbrath LR, Tauber MJ, Tauber CA (1993) Prey specificity in *Chrysopa*: An interspecific comparison of larval feeding and defensive behaviour. *Ecology* 74(5):1384–1393.
- Peñalver E, Delclòs X (2010) *Biodiversity of Fossils in Amber from the Major World Deposits*, ed Penney D (Siri Scientific Press, Manchester, UK), pp 236–270.
- Peñalver E, Wegierek P (2008) A new genus and species of the family Tajmyraphidiidae (Hemiptera: Sternorrhyncha) in Early Cretaceous amber from Peñacerrada I (Spain). *Alavesia* 2:187–192.
- Cooper-Driver GA (1978) Insect-fern associations. *Entomol Exp Appl* 24(3):310–316.
- Tauber CA, Ruberson JR, Tauber MJ (1995) Size and morphological differences among the larvae of two predacious species and their hybrids (Neuroptera: Chrysopidae). *Ann Entomol Soc Am* 88(4):502–511.

36. Kirby MA (1984) Progress in world's neuropterology, *Proceedings of the 1st International Symposium on Neuropterology*, eds Gepp J, Aspöck H, Hölzel H (Graz, Austria), pp 261–265.
37. Fahn A (1990) *Plant Anatomy* (Pergamon, Oxford), 4th Ed.
38. Uphof JCT (1962) *Plant Hairs* (Gebrüder Borntraeger, Berlin).
39. Theobald WL, Krahulik JL, Rollins RC (1979) *Anatomy of the Dicotyledons*, eds Metcalfe CR, Chalk L (Clarendon, Oxford), Vol 1, pp 40–53.
40. Glover BJ, Martin C (2000) *Plant Trichomes*, Advances in Botanical Research: Incorporating Advances in Plant Pathology, eds Hallahan DL, Gray JC (Academic, San Diego; London), Vol 31, pp 193–217.
41. Werker E (2000) *Plant Trichomes*, Advances in Botanical Research: Incorporating Advances in Plant Pathology, eds Hallahan DL, Gray JC (Academic, San Diego; London), Vol 31, pp 1–35.
42. Eisner T, Eisner M, Hoebeke ER (1998) When defense backfires: Detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. *Proc Natl Acad Sci USA* 95(8):4410–4414.
43. Fahn A, Cutler DF (1992) *Xerophytes* (Gebrüder Borntraeger, Berlin).
44. Müller C (2006) *Biology of the Plant Cuticle*, Annual Plant Reviews, eds Riederer M, Müller C (Blackwell, Oxford), Vol 23, pp 398–422.
45. Evert RF (2006) *Esau's Plant Anatomy. Meristemes, Cells and Tissues of Plant Body: Their Structure, Function and Development* (Wiley, Hoboken, NJ), 3rd Ed.
46. Edwards D, Edwards DS, Rayner R (1982) *The Plant Cuticle*, eds Cutler D, Alvin KL, Price CE (Academic, London), pp 341–362.
47. Gupta NS, Collinson ME, Briggs DEG, Evershed RP, Pancost RD (2006) Reinvestigation of the occurrence of cutan in plants: Implications for the leaf fossil record. *Paleobiology* 32:432–449.
48. Clark ND, Daly C (2010) Using confocal laser scanning microscopy to image trichome inclusions in amber. *J Paleontol* 84:1–7.
49. Schmidt AR, et al. (2010) Cretaceous African life captured in amber. *Proc Natl Acad Sci USA* 107(16):7329–7334.
50. Peñalver E, Delclòs X, Soriano C (2007) A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretac Res* 28:791–802.
51. Grimaldi D, Shedirinsky A, Wampler P (2000) *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, ed Grimaldi D (Backhuys Publishers, Leiden, The Netherlands), pp 1–76.
52. Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. *Am Mus Novit* 3361:1–71.
53. Saupe EE, et al. (2012) New *Orchestina* (Simon 1882) (Oonopidae, Araneae) from Cretaceous ambers of Spain and France: First spiders imaged using phase-contrast X-ray synchrotron microtomography. *Palaeontology* 55(1):127–143.
54. Grimaldi D, Engel MS (2005) *Evolution of the Insects* (Cambridge Univ Press, Cambridge, UK).
55. Hooker WJ (1846) *Species Filicum* (W. Pamplin, London), Vol 1.
56. Holtum RE (1959) *Flora Malesiana. Ser. II. Pteridophyta* (Nijhoff, The Hague), Vol 1.
57. Bolchovitina NA (1966) Distribution of the ferns of the Family Gleicheniaceae in the past. *The Palaeobotanist* 15:11–15.
58. Skog JE (2001) Biogeography of Mesozoic leptosporangiate ferns related to extant ferns. *Brittonia* 53(2):236–269.
59. Pryer KM, et al. (2004) Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *Am J Bot* 91(10):1582–1598.
60. Herendeen PS, Skog JE (1998) *Gleichenia chaloneri* - a new fossil fern from the Lower Cretaceous (Albian) of England. *Int J Plant Sci* 159(5):870–879.
61. Watson J (1977) Some Lower Cretaceous conifers of the Cheirolepidiaceae from the U.S.A. and England. *Palaeontology* 20(4):715–749.
62. Kvaček J (2000) *Frenelopsis alata* and its microsporangiate and ovuliferous reproductive structures from the Cenomanian of Bohemia (Czech Republic, Central Europe). *Rev Palaeobot Palynol* 112(1–3):51–78.
63. Gomez B, et al. (2002) *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ genera from the Lower Cretaceous of Spain. *Palaeontology* 45:997–1036.
64. Axsmith BJ, Jacobs BF (2005) The conifer *Frenelopsis ramosissima* (Cheirolepidiaceae) in the Lower Cretaceous of Texas: Systematic, biogeographical, and paleoecological implications. *Int J Plant Sci* 166(2):327–337.
65. Yang X-J, Guignard G, Thévenard F, Wang Y-D, Barale G (2009) Leaf cuticle ultrastructure of *Pseudofrenelopsis dalatzensis* (Chow et Tsao) Cao ex Zhou (Cheirolepidiaceae) from the Lower Cretaceous Dalazi Formation of Jilin, China. *Rev Palaeobot Palynol* 153:8–18.
66. Hermesen EJ, Taylor TN, Taylor EL, Stevenson DW (2006) Cataphylls of the Middle Triassic cycad *Antarcticycas schopfi* and new insights into cycad evolution. *Am J Bot* 93(5):724–738.
67. Crepet WL, Nixon KC (1998) Two new fossil flowers of magnoliid affinity from the Late Cretaceous of New Jersey. *Am J Bot* 85(9):1273–1288.
68. Takahashi M, Herendeen PS, Crane PR (2001) Lauraceous fossil flower from the Kamikitaba Locality (Lower Coniacian; Upper Cretaceous) in Northeastern Japan. *J Plant Res* 114:429–434.
69. Crepet WL, Nixon KC, Gandolfo MA (2005) An extinct calycanthoid taxon, *Jerseyanthus calycanthoides*, from the Late Cretaceous of New Jersey. *Am J Bot* 92(9):1475–1485.
70. von Balthazar M, Pedersen KR, Crane PR, Stampanoni M, Friis EM (2007) *Potomacanthus lobatus* gen. et sp. nov., a new flower of probable Lauraceae from the Early Cretaceous (Early to Middle Albian) of eastern North America. *Am J Bot* 94(12):2041–2053.
71. Simpson MG (1990) Phylogeny and classification of the Haemodoraceae. *Ann Miss Bot Gard* 77(4):722–784.
72. Zomlefer WB, Whitten WM, Williams NH, Judd WS (2003) An overview of *Veratrum* s.l. (Liliales: Melanthiaceae) and an infrageneric phylogeny based on ITS sequence data. *Syst Bot* 28(2):250–269.
73. Taylor TN, Taylor EL, Krings M (2009) *Paleobotany: The Biology and Evolution of Fossil Plants* (Academic, Hoboken, NJ), 2nd Ed.
74. Carpenter RJ, Hill RS, Jordan GJ (2005) Leaf cuticular morphology links Platanaceae and Proteaceae. *Int J Plant Sci* 166(5):843–855.
75. Eisner T, Carrel JE, Van Tassel E, Hoebeke ER, Eisner M (2002) Construction of a defensive trash packet from sycamore leaf trichomes by a chrysoiid larva (Neuroptera: Chrysopidae). *Proc Entomol Soc Wash* 104(2):437–446.
76. Navarro T, El Oualidi J (2000) Trichome morphology in *Teucrium* L. (Labiatae). A taxonomic review. *Anal Jard Bot Mad* 57(2):277–297.
77. Daniel TF (2003) A reconsideration of *Megalostoma* (Acanthaceae), a new species, and recognition of a new section of *Justicia*. *Proc Calif Acad Sci* 54(21):371–380.
78. Salmaki Y, Zarre S, Jamzad Z, Bräuchler C (2009) Trichome micromorphology of Iranian *Stachys* (Lamiaceae) with emphasis on its systematic implication. *Flora* 204: 371–381.
79. Gandolfo MA, Nixon KC, Crepet WL (1998) *Tylerianthus crossmanensis* gen. et sp. nov. (aff. Hydrangeaceae) from the Upper Cretaceous of New Jersey. *Am J Bot* 85(3): 376–386.
80. Martínez-Millán M, Crepet WL, Nixon KC (2009) *Pentapetalum trifasciculandricus* gen. et sp. nov., a thealean fossil flower from the Raritan Formation, New Jersey, USA (Turonian, Late Cretaceous). *Am J Bot* 96(5):933–949.
81. Bremer K, Friis EM, Bremer B (2004) Molecular phylogenetic dating of asterid flowering plants shows early Cretaceous diversification. *Syst Biol* 53(3):496–505.
82. Martínez-Millán M (2010) Fossil record and age of the Asteridae. *Bot Rev* 76:83–135.
83. Walker LR, Boneta W (1995) Plant and soil responses to fire on a fern-covered landslide in Puerto Rico. *J Trop Ecol* 11:473–479.
84. Gillison AN (1969) Plant succession in an irregularly fired grassland area - Doma Peaks Region, Papua. *J Ecol* 57(2):415–428.
85. Russell AE, Raich JW, Vitousek PM (1998) The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawaii. *J Ecol* 86:765–779.
86. Collinson ME (2002) The ecology of Cretaceous ferns. *Rev Palaeobot Palynol* 119:51–68.
87. Van Konijnenburg-Van Cittert JHA (2002) Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia. *Rev Palaeobot Palynol* 119:113–124.
88. Ortega-Blanco J, Rasnitsyn AP, Delclòs X (2008) First record of anaxyelid woodwasps (Hymenoptera: Anaxyelidae) in Lower Cretaceous Spanish amber. *Zootaxa* 1937: 39–50.
89. Pérez-de Fuente R, Peñalver E, Delclòs X, Engel MS (2012) Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera). *Zookeys* 204:1–40.
90. Martínez-Delclòs X, Briggs DEG, Peñalver E (2004) Taphonomy of insects in carbonates and amber. *Palaeogeogr Palaeoclimatol Palaeoecol* 203:19–64.
91. Van Bergen PF, et al. (1995) Resistant biomacromolecules in the fossil record. *Acta Bot Neerl* 44:319–342.
92. Stankiewicz BA, Briggs DEG, Evershed RP, Flannery MB, Wuttke M (1997) Preservation of chitin in 25-million-year-old fossils. *Science* 276:1541–1543.
93. Briggs DEG (1999) Molecular taphonomy of animal and plant cuticles: Selective preservation and diagenesis. *Philos Trans R Soc London Ser B* 354:7–17.
94. Ascaso C, Wierzbosch J, Corral C, López del Valle R, Alonso J (2003) New applications of light and electron microscopic techniques for the study of microbiological inclusions in amber. *J Paleontol* 77:1182–1192.
95. Koller B, Schmitt JM, Tischendorf G (2005) Cellular fine structures and histochemical reactions in the tissue of a cypress twig preserved in Baltic amber. *Proc Biol Sci* 272(1559):121–126.
96. Compton SG, et al. (2010) Ancient fig wasps indicate at least 34 Myr of stasis in their mutualism with fig trees. *Biol Lett* 6(6):838–842.
97. Speranza M, et al. (2010) *Microscopy: Science, Technology, Applications and Education*, eds Méndez-Vilas A, Diaz J (Formatex Research Center, Badajoz, Spain), Vol II, pp 1135–1145.
98. Peterson RL, Vermeer J (1984) *Biology and Chemistry of Plant Trichomes*, eds Rodriguez E, Healey PL, Mehta I (Plenum, New York), pp 71–94.
99. Lang M, Stober F, Lichtenthaler HK (1991) Fluorescence emission spectra of plant leaves and plant constituents. *Radiat Environ Biophys* 30(4):333–347.
100. Spring O (2000) *Plant Trichomes*, Advances in Botanical Research: Incorporating Advances in Plant Pathology, eds Hallahan DL, Gray JC (Academic, San Diego; London), Vol 31, pp 153–174.
101. Pfündel EE, Agati G, Cerovic ZG (2007) *Biology of the Plant Cuticle*, Annual Plant Reviews, eds Riederer M, Müller C (Blackwell, Oxford), Vol 23, pp 216–249.
102. Martínez-Torres LM, Pujalte V, Robles S (2003) Los yacimientos de ámbar del Cretácico Inferior de Peñacerrada (Álava, Cuenca Vasco-Cantábrica): estratigrafía, reconstrucción paleogeográfica y estructura tectónica [Amber deposits from the Early Cretaceous of Peñacerrada (Álava, Basque-Cantabrian Basin): stratigraphy, paleogeographic reconstruction and tectonic structure]. *Est Mus Cienc Nat Álava* 18: 9–32. Spanish.
103. Delclòs X, et al. (2007) Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *C R Palevol* 6:135–149.
104. Alonso J, et al. (2000) A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (northern Spain, Basque-Cantabrian Basin). *J Paleontol* 74:158–178.
105. Gomez B, Barale G, Martín-Closas C, Thévenard F, Philippe M (1999) Découverte d'une flore à Ginkgoales, Bennettitales et Coniferales dans le Crétacé inférieur de la Formation Escucha (Chaîne Ibérique Orientale, Teruel, Espagne) [Discovery of a flora with Ginkgoales, Bennettitales and Coniferales in the Lower Cretaceous of the Escucha Formation (Eastern Iberian Ranges, Teruel, Spain)]. *Neues Jb Geol Paläont Mh* 1999:661–675. French.

106. Gomez B, Martin-Closas C, Barale G, Thévenard F (2000) A new species of *Nehvizdya* (Ginkgoales) from the Lower Cretaceous of the Iberian Ranges (Spain). *Rev Palaeobot Palynol* 111(1–2):49–70.
107. McKellar RC, et al. (2011) Insect outbreaks produce distinctive carbon isotope signatures in defensive resins and fossiliferous ambers. *Proc Biol Sci* 278(1722): 3219–3224.
108. Ogg JG, Ogg G, Gradstein FM (2008) *The Concise Geologic Time Scale* (Cambridge Univ Press, Cambridge, UK).
109. Levin LA, Gooday AJ, James DW (2001) Dressing up for the deep: agglutinated protists adorn an irregular urchin. *J Mar Biol Assoc UK* 81:881–882.
110. Kehas AJ, Theoharides KA, Gilbert JJ (2005) Effect of sunlight intensity and albinism on the covering response of the Caribbean sea urchin *Tripneustes ventricosus*. *Mar Biol* 146:1111–1117.
111. Dumont CP, Drolet D, Deschênes I, Himmelman JH (2007) Multiple factors explain the covering behaviour in the green sea urchin, *Strongylocentrotus droebachiensis*. *Anim Behav* 73(6):979–986.
112. Smith AB, Savill JJ (2001) *Bromidechinus*, a new Ordovician echinozoan (Echinodermata), and its bearing on the early history of echinoids. *Trans R Soc Edinb Earth Sci* 92:137–147.
113. Boucot AJ (1990) *Evolutionary Paleobiology of Behavior and Coevolution* (Elsevier, Amsterdam).
114. Boucot AJ, Poinar GO, Jr. (2010) *Fossil Behaviour Compendium* (CRC, Boca Raton, FL).
115. Bandel K, Fryda J (1998) The systematic position of the Euomphalidae. *Senck Leth* 78(1/2):103–131.
116. Ponder WF (1983) A revision of the Recent Xenophoridae of the world and of the Australian fossil species (Mollusca, Gastropoda). *Aust Mus Mem* 17:1–126.
117. Bandel K (1993) Caenogastropoda during Mesozoic times. *Scripta Geol* 2(Spec Issue): 7–56.
118. Ponder WF (1994) *The Malacofauna of Hong Kong and Southern China III*, ed Morton B (Honk Kong Univ Press, Hong Kong), pp 215–239.
119. Allmon WD (2011) Natural history of turrilline gastropods (Cerithioidea: Turritellidae): A status report. *Malacologia* 54(1–2):159–202.
120. El-Nakal HA, Bandel K (1991) Geographical distribution of the small gastropod genus *Scaliola*. *Micropaleontol* 37(4):423–424.
121. Allgaier C (2007) Active camouflage with lichens in a terrestrial snail, *Napaeus (N.) barquini* (Gastropoda, Pulmonata, Enidae). *Zoolog Sci* 24(9):869–876.
122. Yanes Y, Martín J, Delgado JD, Alonso MR, Ibáñez M (2009) Active disguise in land snails: *Napaeus badius* (Gastropoda, Pulmonata, Enidae) from the Canary Islands. *J Conchology* 40(2):143–148.
123. Mordan PB (1984) *World-Wide Snails. Biogeographical Studies on Non-marine Mollusca*, eds Solem A, van Bruggen AC (E. J. Brill, Leiden, The Netherlands), pp 124–133.
124. Domínguez K, Jiménez M-L (2005) Mating and self-burying behavior of *Homalonychus theologus* Chamberlin (Araneae, Homalonychidae) in Baja California Sur. *J Arachnol* 33(1):167–174.
125. Duncan RP, Autumn K, Binford GJ (2007) Convergent setal morphology in sand-covering spiders suggests a design principle for particle capture. *Proc Biol Sci* 274(1629):3049–3056.
126. Dunlop JA, Penney D, Jekel D (2012) *The World Spider Catalog, Version 13.0*, ed Platnick NI (American Museum of Natural History, New York). Available at <http://research.amnh.org/entomology/spiders/catalog/index.html>. Accessed December 1, 2012.
127. Lamberts AE, Garth JS (1977) Coral-crab commensalism in xanthids. *Pac Sci* 31(3): 245–247.
128. Lavaleye MSS, den Hartog JC (1995) A case of associated occurrence of the crab *Lauridromia intermedia* (Laurie, 1906) (Crustacea: Decapoda: Dromiidae) and the actinian *Nemanthus annamensis* Carlgren, 1943 (Anthozoa: Actiniaria: Nemanthidae). *Zool Med Leiden* 69:121–130.
129. Hultgren K, Stachowicz J (2011) *Animal Camouflage*, eds Stevens M, Merilaita S (Cambridge Univ Press, Cambridge, UK), pp 214–238.
130. Capezzuto F, et al. (2012) Occurrence and behaviour of *Paromola cuvieri* (Crustacea, Decapoda) in the Santa Maria di Leuca cold-water coral community (Mediterranean Sea). *Deep-Sea Res* 59:1–7.
131. Brösing A (2008) A reconstruction of an evolutionary scenario for the Brachyura (Decapoda) in the context of the Cretaceous-Tertiary boundary. *Crustaceana* 81(3): 271–287.
132. Weirauch C (2006) Anatomy of disguise: Camouflaging structures in nymphs of some reduviidae (Heteroptera). *Am Mus Novit* 3542:1–18.
133. Wu RJC (1996) *Secrets of a Lost World: Dominican Amber and Its Inclusions* (R. J. C. Wu, Santo Domingo, Dominican Republic).
134. Betz BW (1983) The biology of *Trichadenotecnium alexanderae* Sommerman (Psocoptera, Psocidae). 1. Habitat, life stages and events. *Entomol News* 94:152–158.
135. Lienhard C (1988) Three new extra-neotropical species of Troctopsocidae (Insecta: Psocoptera). *J Nat Hist* 22(3):575–587.
136. New TR (1982) The larva of *Nymphes* Leach (Neuroptera: Nymphidae). *Neurop Int* 2(2):79–84.
137. Henry CS (1976) Some aspects of the external morphology of larval owlflies (Neuroptera: Ascalaphidae), with particular reference to *Ululodes* and *Ascaloptynx*. *Psyche (Stuttg)* 83(1):1–31.
138. Henry CS (1977) The behavior and life histories of two North American ascalaphids. *Ann Entomol Soc Am* 70(2):179–195.
139. Brown CG, Funk DJ (2010) Antipredatory properties of an animal architecture: how complex faecal cases thwart arthropod attack. *Anim Behav* 79:127–136.
140. Chaboo CS, Engel MS, Chamorro-Lacayo ML (2009) Maternally inherited architecture in tertiary leaf beetles: paleoichnology of cryptocephaline fecal cases in Dominican and Baltic amber. *Naturwissenschaften* 96(9):1121–1126.
141. Davis DR, Robinson GS (1998) *Handbook of Zoology. Part 35. Lepidoptera, Moths and Butterflies*, eds Kristensen N, Fischer M (de Gruyter, Berlin), Vol 1, pp 91–118.
142. Holzenthal RW, Blahnik RJ, Prather AL, Kjer KM (2007) Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. *Zootaxa* 1668:639–698.
143. Rasnitsyn AP, Quicke LJ (2002) *History of Insects* (Kluwer, Dordrecht, The Netherlands; Boston; London).
144. Hart CE, Crowe JH (1977) The effect of attached gravel on survival of intertidal anemones. *Trans Am Microsc Soc* 96(1):28–41.
145. Berke SK, Woodin SA (2008) Tube decoration may not be cryptic for *Diopatra cuprea* (Polychaeta: Onuphidae). *Biol Bull* 214(1):50–56.
146. Brown PL, Ellis DV (1971) Relation between tube-building and feeding in *Neoamphitrite robusta* (Polychaeta: Terebellidae). *J Fish Res Board Can* 28(10): 1433–1435.
147. Emig CC (1982) The biology of Phoronida. *Adv Mar Biol* 19:1–89.
148. Taylor JD, Glover EA, Braithwaite CJR (1999) Bivalves with 'concrete overcoats': *Granicorium* and *Samarangia*. *Acta Zool* 80:285–300.
149. Braithwaite CJR, Taylor JD, Glover EA (2000) Marine carbonate cements, biofilms, biomineralization, and skeletogenesis: some bivalves do it all. *J Sediment Res* 70(5): 1129–1138.
150. Sartori AF, Harper EM (2009) Sticky bivalves from the Mesozoic: clues to the origin of the anomalodesmatan arenophilic system. *Lethaia* 42:486–494.

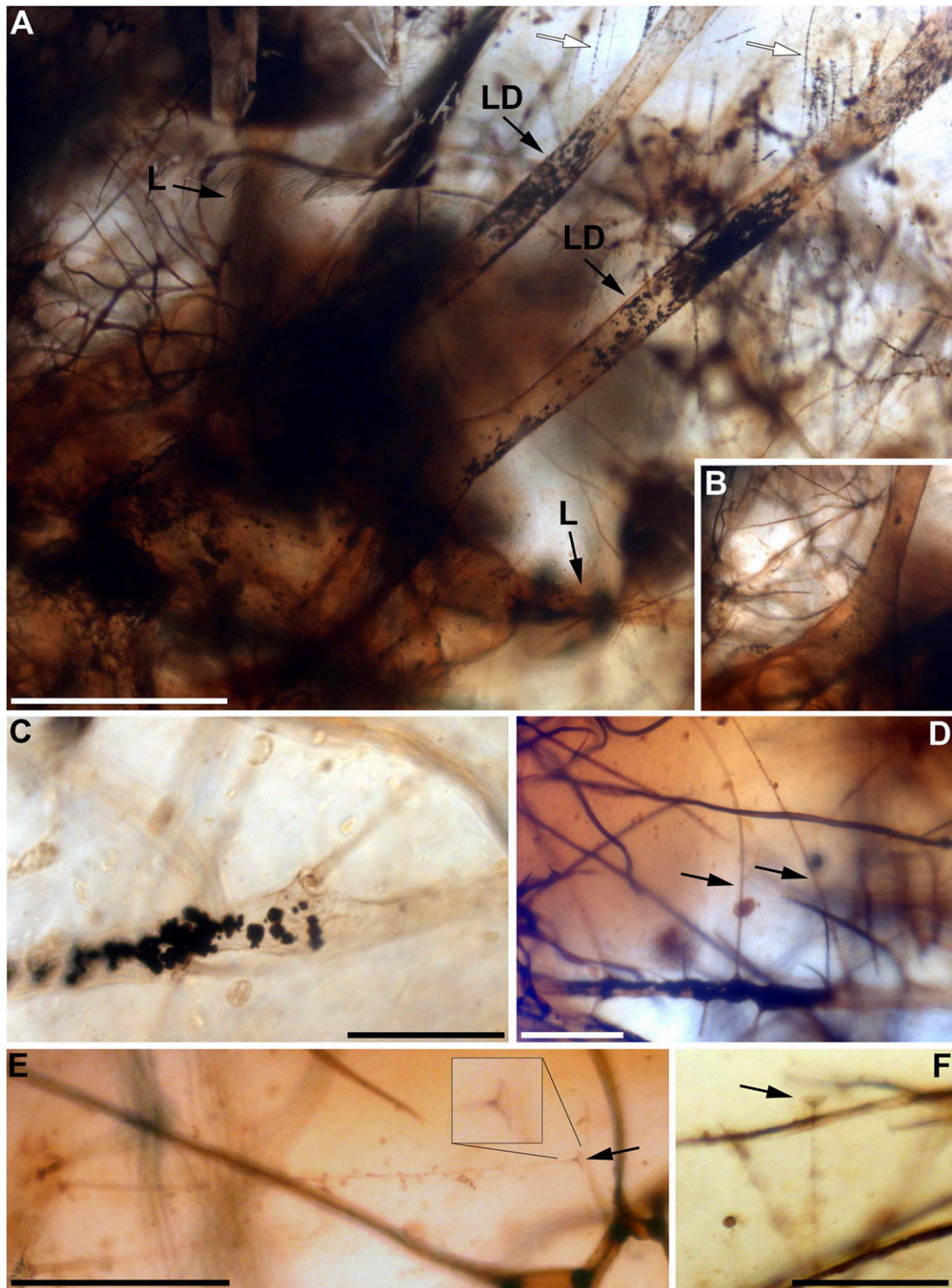


Fig. 51. Tubular tubercles of *H. diogenesi* gen. et sp. nov. (A) Lateral (L) and laterodorsal (LD) pairs of prothoracic tubular tubercles in dorsal view; laterodorsal pair showing some subbasal setae (white arrows). (B) Insertion of the left prothoracic lateral tubular tubercle (same scale as in A). (C) Apex of an abdominal tubular tubercle showing a setal insertion and pyrite crystals (black deposits). (D) Right metathoracic lateral tubular tubercle showing curved setae (arrows) and pyrite crusts in some parts of the tubular tubercle (black portions). (E) Erect seta emerging from a thoracic tubular tubercle, showing its trumpet-shaped ending (arrow), magnified at the inset. (F) Trumpet-shaped ending (arrow) of another tubular tubercle seta. (Scale bars: A, 0.5 mm; C, 0.05 mm; D and E, 0.2 mm; F, 0.1 mm.)

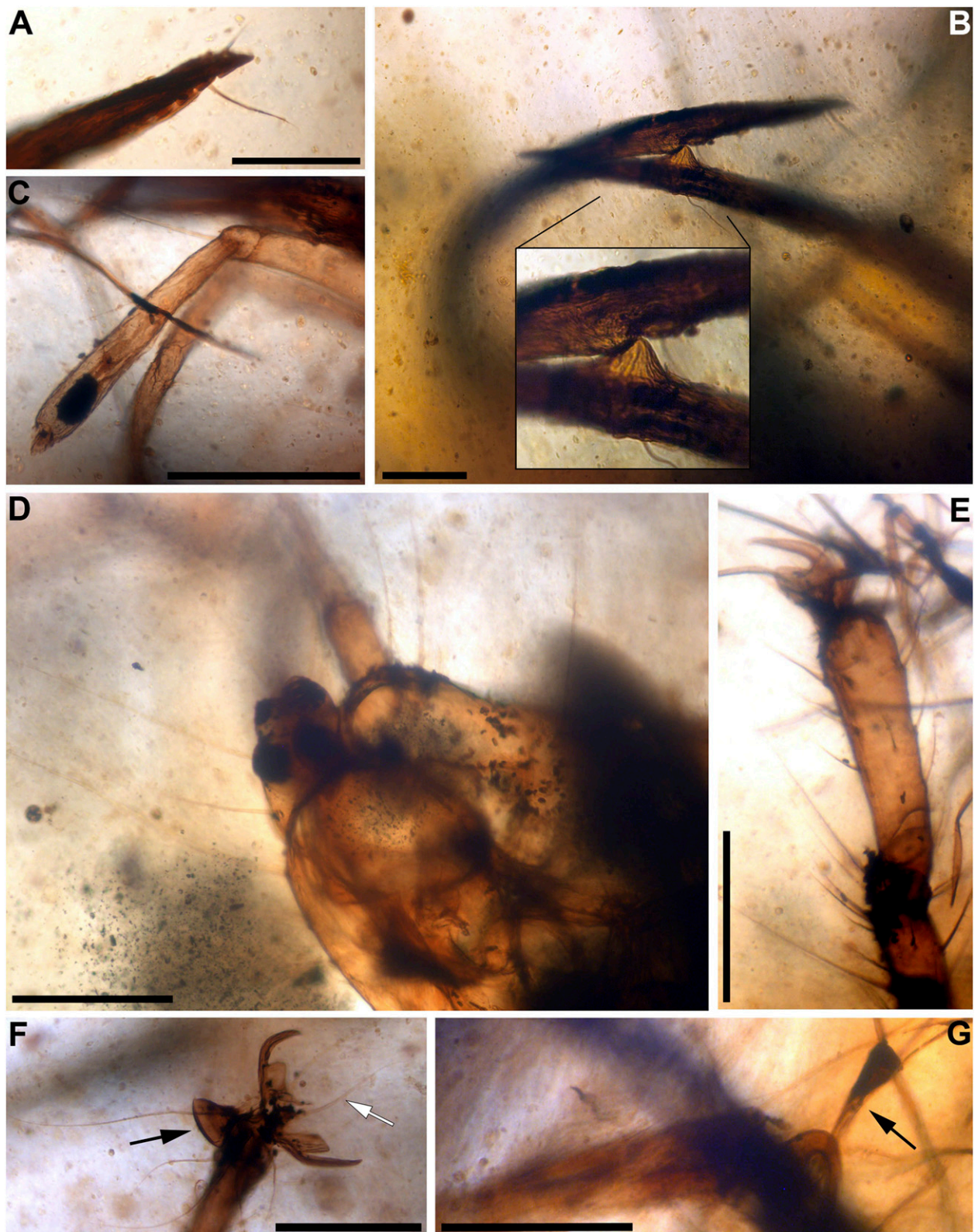


Fig. S2. Anatomical head and leg details of *H. diogenesi* gen. et sp. nov. (A) Apex of the right jaw showing serration on inner margin and distal sensilla. (B) Coupling system at jaw apices, with *Inset* showing a magnification of this structure. (C) Terminal left labial palpomere, showing a distal conical papilla. (D) Head in ventral view showing prominent ocular tubercle with four stemmata, antennal pedicel, and long setae emerging from grooves. (E) Right prothoracic tarsus showing pretarsal claws in lateral view. (F) Left prothoracic pretarsal claws in ventro-oblique view with conspicuous basal expansions, fine pulvilli (white arrow pointing to the left pulvillus) and distal pad of the trumpet-shaped empodium, distorted by preservation (black arrow). (G) Left metathoracic tarsus showing part of a pretarsal claw in lateral view and the trumpet-shaped empodium (arrow). (Scale bars: A and B, 0.1 mm; C–G, 0.2 mm.)

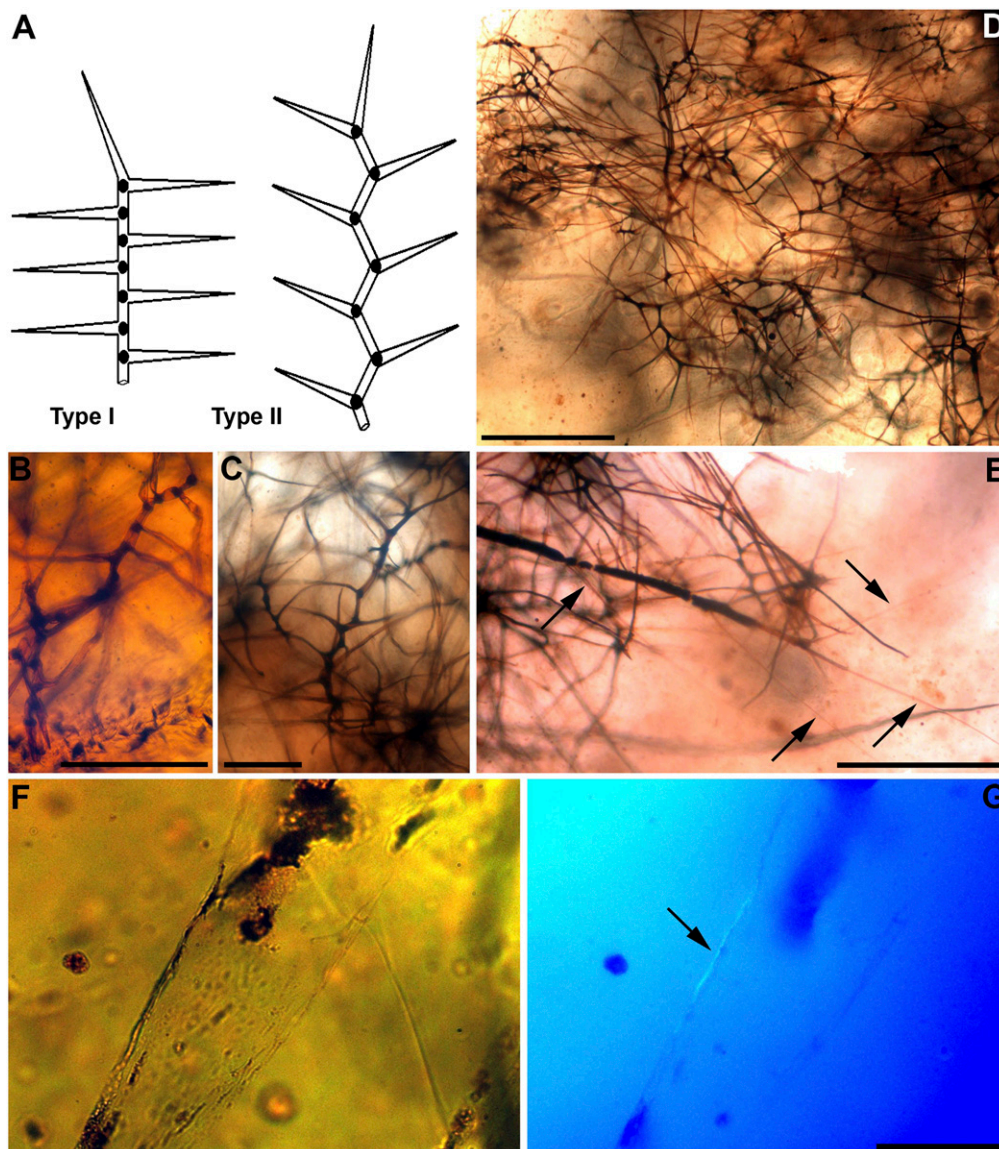


Fig. 53. Further morphological features of the trichomes of gleicheniacean fern affinity from the trash packet of *H. diogenesi* and autofluorescence of a germane trichome from Álava amber (MCNA 10023). (A) Two types of trichomes outlined within text. (B) Trichomes type I. (C) Trichome type II. (D) Detail of the trash packet showing abundant trichomes. (E) Several trichomes entangled among setae (arrows) of an abdominal tubular tubercle. (F) Detail of a trichome branch from Álava amber, at same scale as G. (G) Same detail as F under fluorescence microscopy (arrow indicates autofluorescence signal). (Scale bars: B and C, 200 μm ; D and E, 500 μm ; G, 25 μm .)

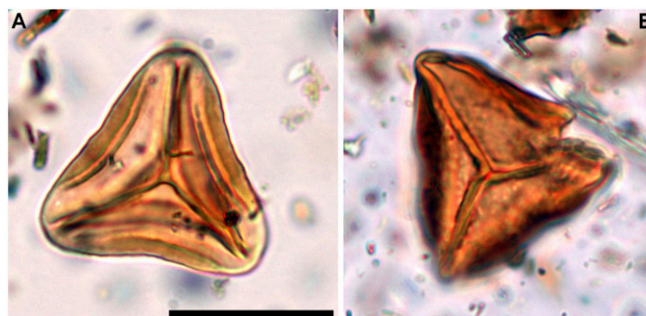
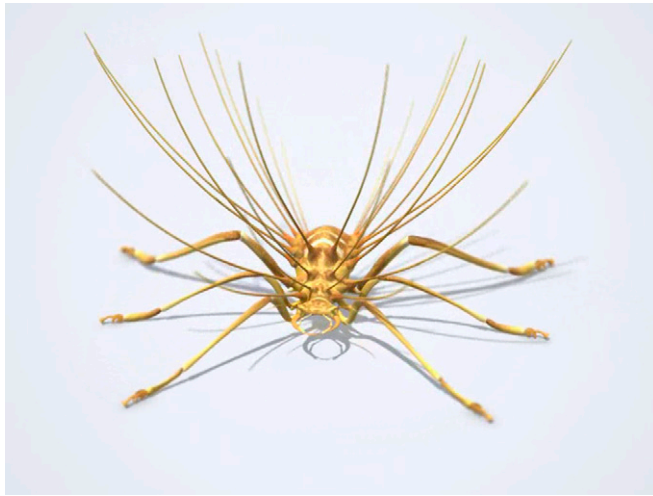
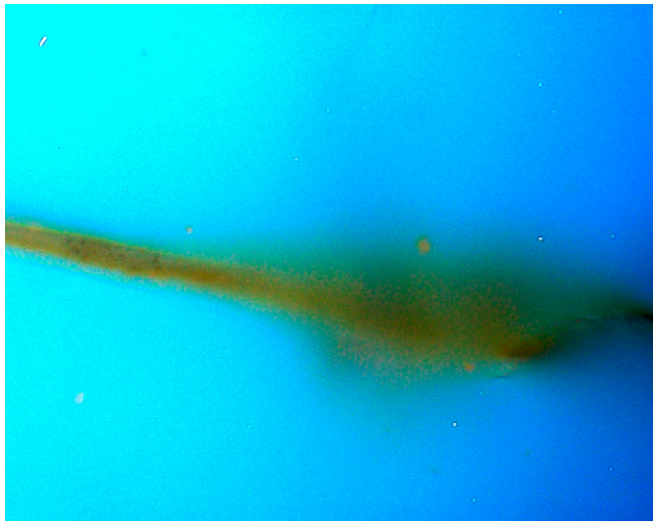


Fig. 54. Fern spores of gleicheniacean fern affinity from the amber-bearing sediments of the El Soplao outcrop. (A) *Gleicheniidites senonicus*. (Scale bar: 20 μm .) (B) *Ornamentifera peregrina*. Both A and B are at the same scale.



Movie S1. Morphological and locomotive reconstruction of *H. diogenesi*.

[Movie S1](#)



Movie S2. Micropapillae from a trichome within the trash packet of *H. diogenesi* under fluorescence microscopy.

[Movie S2](#)