

A new genus of dance flies (Diptera: Empidoidea: Hybotidae) from Cretaceous Spanish ambers and introduction to the fossiliferous amber outcrop of La Hoya (Castellón Province, Spain) (#77358)

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A new genus of dance flies (Diptera: Empidoidea: Hybotidae) from Cretaceous Spanish ambers and introduction to the fossiliferous amber outcrop of La Hoya (Castellón Province, Spain)

Mónica M. Solórzano Kraemer^{Corresp., 1}, Bradley J. Sinclair², Antonio Arillo³, Sergio Álvarez-Parra^{4,5}

¹ Paläontologie und Historische Geologie, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

² Canadian Food Inspection Agency, Canadian National Collection of Insects, Ottawa, ON, Canada

³ Departamento de Biodiversidad, Ecología y Evolución, Facultad de Biología, Universidad Complutense de Madrid, Madrid, Spain

⁴ Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona, Barcelona, Barcelona, Spain

⁵ Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Barcelona, Spain

Corresponding Author: Mónica M. Solórzano Kraemer

Email address: monica.solorzano-kraemer@senckenberg.de

Hybotidae fly species, also known as dance flies, in Cretaceous ambers have been described from Lebanon, France, Myanmar, Russia, and Canada. Here we describe *Grimaldimyia coelica* **n. gen. et sp.**, and recognize other two species, remaining without name, in Spanish amber from the middle Albian El Soplao and lower Cenomanian La Hoya outcrops. The fore tibial gland is present in the new genus, which is characteristic of the family Hybotidae. We compare *Grimaldimyia coelica* **n. gen. et sp.** with the holotypes of *Trichinities cretaceous* Hennig, 1970 and *Ecommocyndromia difficilis* Schlüter, 1978, and clarify some morphological details present in the former two species. Further taxonomic placement beyond family of the here described new genus was not possible and remains *incertae sedis* within Hybotidae until extant subfamilies are better defined. We provide new paleoecological data of the hybotids, together with paleogeographical and life paleoenvironmental notes. A table with the known Cretaceous Hybotidae is provided. Furthermore, the La Hoya amber-bearing outcrop is described in detail, filling the information gap for this deposit.

A new genus of dance flies (Diptera: Empidoidea: Hybotidae) from Cretaceous Spanish ambers and introduction to the fossiliferous amber outcrop of La Hoya (Castellón Province, Spain)

Short Title: Hybotidae in Spanish ambers

Mónica M. Solórzano-Kraemer^{1*}, Bradley J. Sinclair², Antonio Arillo³, Sergio Álvarez-Parra^{4,5}

¹Paläontologie und Historische Geologie, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany.

²Canadian National Collection of Insects & Canadian Food Inspection Agency, OPL-Entomology, Ottawa, ON, Canada.

³Departamento de Biodiversidad, Ecología y Evolución, Facultad de Biología, Universidad Complutense, Madrid, Spain.

⁴Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona, Barcelona, Spain.

⁵Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Barcelona, Spain.

Corresponding Author:

Mónica M. Solórzano Kraemer¹

Senckenberganlage 25, 60325 Frankfurt am Main, Germany

Email address: monica.solorzano-kraemer@senckenberg.de

ORCID

Mónica M. Solórzano-Kraemer: <https://orcid.org/0000-0003-3065-119X>

Sergio Álvarez-Parra: <https://orcid.org/0000-0002-0232-1647>

Antonio Arillo: <https://orcid.org/0000-0002-4878-5797>

Bradley Sinclair: <https://orcid.org/0000-0001-6413-1606>

Abstract

Hybotidae fly species, also known as dance flies, in Cretaceous ambers have been described from Lebanon, France, Myanmar, Russia, and Canada. Here we describe *Grimaldipeza coelica* **n. gen. et sp.**, and recognize another two un-named species, in Spanish amber from the middle Albian El Soplao and lower Cenomanian La Hoya outcrops. The fore tibial gland is present in the new genus, which is characteristic of the family Hybotidae. We compare *Grimaldipeza coelica* **n. gen. et sp.** with the holotypes of *Trichinites cretaceous* Hennig, 1970 and *Ecommocyndromia difficilis* Schlüter, 1978, and clarify some morphological details present in the latter two species. Further taxonomic placement beyond family of the here described new genus was not possible and remains *incertae sedis* within Hybotidae until extant subfamilies are better defined. We provide new paleoecological data of the hybotids, together with paleogeographical and life paleoenvironmental notes. A table with the known Cretaceous Hybotidae is provided. Furthermore, the La Hoya amber-bearing outcrop is described in detail, filling the information gap for this deposit.

Keywords

Amber, new species, new genus, amber-bearing outcrop, *Trichinites*, *Ecommocyndromia*

Introduction

The Empidoidea Latreille, 1809 (Insecta: Diptera) contain more than 10,000 described species (Pape et al., 2011), representing a diverse lineage within the 166,859 described species in the order Diptera (Evenhuis and Pape, 2022). The Empidoidea (dance flies and long-legged flies) consist of five families: Empididae Latreille, 1809; Hybotidae Fallén, 1816; Atelestidae Henning, 1970; Dolichopodidae Latreille, 1809; and Brachystomatidae *sensu* Sinclair and Cumming, 2006 (Sinclair and Cumming, 2006). However, Wahlberg and Johanson (2018) returned the latter family to a lineage of the Empididae and elevated Ragadinae Sinclair, 2016 to family rank. A couple of additional families are sometimes also recognized in the Empidoidea (Pape et al., 2011). The fossils studied here belong to the Hybotidae, a well-defined monophyletic group (Sinclair and Cumming, 2006; Wahlberg and Johanson, 2018) ~~within the Empidoidea.~~

Most dance flies today are generalist predators, feeding on insects, but some also feed on dead insects (necrophagous). In addition, many species visit flowers and are known to feed on pollen and nectar (Downes and Smith, 1969). This behavior is also observable through the fossil record (Grimaldi and Engel, 2005). Predator insects can be abundant in Defaunation resin, copal and amber because they are attracted by arthropod or vertebrate trapped by the resin (Solórzano Kraemer et al., 2015, 2018).

The Hybotidae currently include seven subfamilies: Trichiniinae Chvála, 1983; Ocydromiinae Schiner, 1862; Oedaleinae Chvála, 1983; Tachydromiinae Meigen, 1822; Hybotinae Meigen, 1820; Stuckenbergomyiinae Sinclair, 2019; and Bicellariinae Sinclair and Cumming, 2006 (Sinclair and Cumming, 2006; Wahlberg and Johanson, 2018; Sinclair, 2019). The subfamily Trichiniinae remains poorly defined and its relationships with the Oedaleinae, Ocydromiinae or Bicellariinae, or even its position within the Hybotidae, need to be further evaluated (Sinclair and Cumming, 2006; Wahlberg and Johanson, 2018).

The fossil record of the Cretaceous Hybotidae or related species described in previous publications as *incertae sedis* is not extensive but diverse. Fossil species as bioinclusions have been described in amber from France, Lebanon, Myanmar, Russia, and Canada. Conversely, only one species based on a compression fossil is known from Orapa, Botswana (see Table 1).

The species here described shares characters with ~~the~~ genera *Trichinites* Hennig, 1970 and *Ecommocyndromia* Schlüter, 1978. *Trichinites cretaceous* Hennig, 1970 was described from Lebanese amber, which is Lower Cretaceous (Barremian, ~128 Ma) in age (Maksoud and Azar, 2020). It was described by Hennig (1970) based on a single female and placed as a stem-group to the subfamily group Ocydromioinea [Ocydromiinae+Hybotinae+Tachydromiinae], mainly based on wing characters. The position of the genus is currently assigned as the stem-group to the Hybotidae (Chvála, 1983; Grimaldi and Cumming, 1999).

Ecommocyndromia difficilis Schlüter, 1978 was described in amber from Bezonnais, France, which is Cenomanian (~100 Ma) in age (Schlüter, 1978; Perrichot et al., 2007). The most important

characters of this genus are the costa not circumambient, cell dm emitting three veins, and legs with pronounced setation. The fossil was placed within the Ocydromiinae, which at the time included all Hybotidae genera exclusive of Hybotinae and Tachydromiinae (Schlüter, 1978). Both Lebanese and French ambers were characterized within the group of *Agathis*-like (Araucariaceae) resins (Perrichot et al., 2007; Azar et al., 2010)

The specimens studied in this work come from the El Soplao and La Hoya amber-bearing outcrops (Fig. 1A), in Spain. The El Soplao outcrop is located in the western margin of the Basque-Cantabrian Basin (northern Iberian Peninsula). It belongs to the Las Peñas Formation, dated as lower–middle Albian based on foraminifera (García-Mondéjar, 1982), and the amber is most probably middle Albian in age. The sedimentary environment is related to a delta-estuary under marine influence (Najarro et al., 2009). El Soplao amber has been extensively studied and is one of the richest in bioinclusions in the Iberian Peninsula, yielding a diverse arthropod fauna (Najarro et al., 2010). The La Hoya locality (not to be mistaken with the Barremian compression outcrop of Las Hoyas, also in Spain) has been mentioned in several congress communications and scientific publications (Delclòs et al., 2007; Peñalver et al., 2007, 2010; Peñalver and Delclòs, 2010; Menor-Salván et al., 2016; Murillo-Barroso et al., 2018; Rodrigo et al., 2018; McCoy et al., 2021; Santer et al., 2022), but no detailed introduction has been published so far.

Here we describe more accurately the La Hoya outcrop together with a new genus and three species within Hybotidae are recognized, but only one species is named. We compare our specimens with the holotypes of *Trichinites cretaceous* and *Ecommocydromia difficilis*, and clarify some anatomical details of these species. Finally, we discuss their position within the Empidoidea.

Materials & Methods

Six specimens of dance flies included in amber have been examined for this work. From the El Soplao amber-bearing outcrop (Cantabria Autonomous Community, Spain): CES.404.1 ♂, CES.404.2 ♂, CES.439 ♂, CES.372 ♀; housed at the Colección Institucional del Laboratorio de la Cueva El Soplao in Celis, Cantabria (Acronym for the collections is CES); permissions of excavations PFC 83/08 and PFC 33/09 (Consejería de Cultura, Turismo y Deporte del Gobierno

de Cantabria). From the La Hoya amber-bearing outcrop (Castellón Province, Spain): MGUV-16348 (sex unknown) and MGUV-16349 ♀; housed at the Museu de la Universitat de València d'Història Natural (Burjassot, Valencia Province, Spain) (Acronym for the collections is **MGUV**); permission of excavation 2003/0593-V (Conselleria d'Educació, Cultura i Esport de la Generalitat Valenciana). Amber pieces were cut and embedded in synthetic epoxy resin (EPO-TEK 301) and then polished (Corral et al., 1999; Nascimbene and Silverstein, 2000; Sadowski et al., 2021). Color photographs and Z-stack images were performed under a Nikon SMZ25 microscope, using Nikon SHR Plan Apo 0.5x and SHR Plan Apo 2x objectives with a Nikon DS-Ri2 camera and NIS-Element software (version 4.51.00 www.microscope.healthcare.nikon.com) and a digital camera attached to an Olympus BX51 compound microscope. Black White (Infrared reflected photomicrographs) were taken with a Nikon Eclipse ME600D (see Brocke and Wilde, 2001 for precise technical information). Photographs were Z-stacked using the NIS-Element software. Drawings were made with the aid of an Olympus U-DA drawing tube attached to an Olympus BX50 compound microscope and digitized using a Wacom drawing tablet. Figures were assembled using Adobe Photoshop software (CS6 version 13.0 www.adobe.com).

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Synchrotron Radiation micro-Computed Tomography (SR μ -CT) scans were carried out; however, the specimens did not produce enough signal, and segmentation of the reconstructed scans was not successful.

The Fourier Transform Infrared Spectroscopy (FTIR) analysis of La Hoya amber was obtained using an IR PerkinElmer Frontier spectrometer that utilizes a diamond ATR system with a temperature stabilized DTGS detector and a CsI beam splitter at the Molecular Spectrometry Unit of the CCI-TUB (University of Barcelona, Spain).

The anatomical terminology of the specimens follows Cumming and Wood (2017).

Results

Systematic paleontology

The specimens are placed in the family Hybotidae, based on the following apomorphic ground plan characters: 1) Costa runs to just below the apex of the wing, ending near or beyond distal end of M_1 or M_{1+2} ; 2) Sc incomplete, not reaching the wing margin, ending freely in wing membrane; 3) R_{4+5} unbranched; 4) fore tibial gland present; 5) stylus with bare, terminal sensillum.

Order DIPTERA Linnaeus, 1758

Superfamily Empidoidea (*sensu* Chvála, 1983)

Family HYBOTIDAE Meigen, 1820

***Grimaldipeza* n. gen.** (Figs. 2–5, 7, and 8)

LSID urn:lsid:zoobank.org:act:23818B66-56D4-4D7B-BFA5-1EB7D6995462

Type species. *Grimaldipeza coelica* n. sp.

Etymology. The genus name is in honour of David A. Grimaldi (American Museum of Natural History, USA) for his persevering and remarkable legacy work on fossil insects, principally on Diptera and the suffix *myia*, meaning fly in Greek. The gender is feminine.

Diagnosis. Eyes meeting above antennae (holoptic) in males and dichoptic in females. Antenna with long, arista-like stylus, longer than postpedicel. R_{2+3} straight to costa. Cell dm slightly larger than cell cua, apices in same plane or linear. Cell dm with M_1 , M_2 and M_4 extending to wing

margin. Thoracic setae long and strong. Fore and hind tibiae more or less of the same thickness. Longitudinal furrow on mid and hind femora and tibiae. Fore tibial gland present. Symmetrical male hypopygium, slightly rotated. Hypandrium apically narrowly bilobed, with posterior apices pointed.

***Grimaldipeza coelica* n. sp.** (Figs. 2–4, and 5A–C)

LSID urn:lsid:zoobank.org:act:9028DF70-F0B3-4A2C-B677-64F51C8CEC33

Etymology. After the locality of Celis, close to the outcrop El Soplao in Cantabria Autonomous Community, Spain.

Diagnosis. As for the genus.

HOLOTYPE: CES.404.1 ♂. Housed at the Colección Institucional del Laboratorio de la Cueva El Soplao in Celis (Cantabria, SPAIN).

PARATYPES: CES.404.2 ♂, CES.439 ♂

Description

Body: Holotype male CES.404.1 (Fig. 2A–C) body length about 1.79 mm, wing 1.57 mm. Paratype male CES.404.2 (Fig. 2A right) body length 1.74 mm, wing 1.53 mm. Paratype male CES.439 (Fig. 4A–G) body length 1.78 mm, wing 1.42 mm.

Head. Eyes meeting above antennae (holoptic) (Fig. 3B); eyes do not meet below antenna (Fig. 3A); ommatrichia absent. Face flat level with eyes. Gena not extended below eye; ventral surface of head, posterior to mouth opening clothed in long, pale setulae. Two pairs of fine ocellar setulae, directed more upward than forward. One pair of outer vertical setae and one pair of inner vertical setae. Antenna inserted above middle of head; scape small, devoid of setulae; pedicel globose bearing long setulae; scape and pedicel similar in length; postpedicel pointed ovate to conical, apically tapered gradually to point, with two-articled apical arista-like stylus (Fig. 3A–C), longer than postpedicel; stylus 0.22 mm, pubescent with bare, terminal sensillum. Labrum large, almost

as long as proboscis, apex of labrum rounded. Proboscis half as long as head. Palpus round, bearing 3–4 long setae; palpifer not visible or not present. Labellum covered with short setae on base and 4 strong, short setae visible in specimen CES.439 (Fig. 4C and D).

Thorax. Notum humpbacked (Fig. 2B), notum with 4 irregular rows of acrostichal and dorsocentral setulae; 2 pairs of larger dorsocentral setae posteriorly. One long, strong supra-alar seta, 2 long, strong notopleural setae, and 1 postalar seta on each side (Fig. 3F). Scutellum with 2 pairs of long setae. Legs long and unmodified, hindlegs longest; none of legs raptorial. Fore and hind femora slightly thicker than mid femur. Mid and hind femora and tibiae with longitudinal furrow (Fig. 4F). All femora and tibiae armed with rows of long, strong setae (Figs. 2A and B, 3G). Tarsus of all legs bearing short, strong setae. Fore tibia with posteroventral gland (Fig. 5).

Wing. Hyaline; with fine microtrichia over entire membrane. Pterostigma absent. Costa terminates between R_{4+5} and M_1 (Fig. 4G); Sc apically evanescent, ending slightly before costal margin; Rs arising distant from level of humeral crossvein; R_1 ending at or slightly beyond mid-length of wing; R_{2+3} straight to C, ending closer to apex of R_1 than R_{4+5} ; R_{4+5} unbranched, parallel to M_1 ; cell dm slightly larger than cell cua, emitting three veins: M_1 , M_2 , and M_4 ; M_1 and M_4 only moderately divergent; CuA straight, aligned with apex of cell bm; apex of cell cua slightly truncate or acute. Anal lobe broad, well developed.

Abdomen. Abdomen scarcely broader near base, laterally compressed. Tergites and sternites bearing long, strong setae. Hypopygium symmetrical, slightly rotated (Figs. 3H–J, 4E and F). Hypandrium apically narrowly bilobed, with posterior apices pointed (Fig. 3H–J). Epandrium with pair of articulated surstyli; left surstylus slightly elongate, with inner long, strong setae. Cercus short, unmodified with pubescence.

Remarks. The description of *Trichinites cretaceus* was based on a female in Barremian amber from Jezzine (Lebanon) and is housed at the Staatliches Museum für Naturkunde (Stuttgart, Germany) (Holotype Nummer LB-617) (Fig. 6D). This holotype specimen was re-examined. *Grimaldipeza* n. gen. can be distinguished from *Trichinites* by the following combination of characters: position of vein r-m close to base of cell dm, R_{2+3} longer than in *Trichinites* and

extending straight to wing margin (*T. cretaceus* is sharply curved prior to joining costa, Fig. 6A). Apices of cell bm and cua are alignment in *Grimaldipeza* n. gen. In contrast, the apex of cell cua is obliquely projecting in *Trichinites*. *Trichinites* has an extra cell at the bifurcation of M_1 and M_2 , but this is most probably an aberrant feature, thus it is not a diagnostic feature of the species, and is absent in all other specimens studied here. In the new genus, the fore tibia is slightly broader than the mid and hind tibiae and the fore tibial gland is present, distinguishable in three of the four specimens (Fig. 5). Furthermore, *Trichinites* lacks the fore tibial gland and is larger than the new species here described (body length 2.99 mm), including the telescopic abdomen, whereas the maximum length of *Grimaldipeza coelica* n. gen. et n. sp. is 1.79 mm. The thorax of the paratype CES.439 appears somewhat flat, however, this is not considered here a differential character and could be due to the fossilization process.

Grimaldipeza species 1

(Fig. 7)

Female. Piece CES.372 ♀. Body length 1.68 mm. Wing 1.22 mm. Stylus 0.22 mm. Postpedicel 0.16 mm. Similar to *Grimaldipeza coelica* n. gen. et n. sp. male holotype, except for the following characters: eyes dichoptic (Fig. 7A and B); setae shorter and finer on thorax, abdomen and legs; labrum curved bearing pseudotracheae (Fig. 7C); proboscis 1/3 longer than head; thorax setae appears with seriated rings (Fig. 7B), possibly artifact of preservation; tergites bearing several shorter setae in comparison with males, first tergite with cluster of about 5 long setae on each side; apical abdominal segments exposed, gradually telescopic; cercus cylindrical, bearing 3 long setulae (Fig. 7F).

Grimaldipeza species 2

(Fig. 8)

Female. MGUV-16348 (sex unknown), **MGUV-16349** ♀. Part of the abdomen of MGUV-16348 is not preserved; however, all other characters, such as the length of the proboscis, which is as long as the head, and dichoptic eyes indicate that it could be a female. Specimen MGUV-16349 only shows the end of the abdomen, which is telescopic, and one wing partially and badly preserved.

MGUV-16348 and MGUV-16349 are included in the same amber piece as syninclusions. Similar to the male holotype of *Grimaldipeza coelica* n. gen. et n. sp. except for the following characters: stylus 0.19 mm; postpedicel 0.10 mm; eyes dichoptic (Fig. 8D); setae long, strong on thorax, abdomen and legs, somewhat longer than in *Grimaldipeza* sp. 1; labrum curved; proboscis 1/4 longer than head (Fig. 8D); tergites and sternites bearing several long setae; setae on anal lobe of wing longer than in *Grimaldipeza* sp. 1; apical abdominal segments exposed, gradually telescopic; cercus short, cylindrical.

Remarks. *Grimaldipeza* sp. 1 can be distinguished from *Grimaldipeza* sp. 2 by the tergites bearing several shorter setae and the proboscis 1/3 longer than head. *Grimaldipeza* sp. 2 can be distinguished from *Grimaldipeza* sp. 1 by the long and strong setae on the thorax, abdomen and legs, somewhat longer than in species 1 and the proboscis is as long as the head. As the females do not appear in any of the pieces containing males we cannot describe these as new species and they will remain unnamed until more specimens are found, that can be associated to the species with confidence.

Ecommocyndromia difficilis Schlüter, 1978
(Fig. 9)

Additional information to the original description:

Head. Antenna inserted above middle of head. Right antenna broken, only scape, pedicel and part of postpedicel preserved. Left antenna preserved but base not visible. Scape longer than pedicel; pedicel short, slightly broader than scape with one long seta visible; postpedicel on one side appears pointed ovate to conical, however (as described by Schlüter, 1978) left postpedicel conical, with two-articled apical arista-like stylus (Fig. 9E and F).

Thorax. Laterotergite bare. Presence of tibial gland on foreleg not possible to ascertain. On right fore tibia, gland appears present, in abnormal position (Fig. 9H), but could be artifact due to preservation. On left foreleg, gland not visible, or absent. Fore tibia with anterodorsal row of strong setae, nearly as long as width of tibia (Fig. 9G).

Abdomen. Shorter than thorax. Tergites and sternites bearing long, strong setae. Hypopygium nearly symmetrical, not rotated (Fig. 9C and D). Hypandrium apically narrowly bilobed, with posterior apices pointed (Fig. 9D). Epandrium with left surstylus broader, not articulated; long postgonites or phallic process (Fig. 9D). Cercus short, unmodified.

Remarks. In the original publication, the holotype of *E. difficilis* has the collection number Emp Ce Bez 1 (Paläontologisches Institut, FU-Berlin) (Fig. 9I). However, the holotype has been transferred to the Natur Museum für Naturkunde in Berlin, Germany under the Number MB.I.7927.

La Hoya amber-bearing outcrop

The La Hoya amber-bearing outcrop is located in the Penyalgosa Sub-basin within the Maestrazgo Basin in the eastern Iberian Peninsula (Salas and Guimerà, 1996). More than 30 amber outcrops have been reported in this basin, although only four of them are fossiliferous (Peñalver and Delclòs, 2010; Álvarez-Parra et al., 2021): Ariño, San Just, Arroyo de la Pascueta and La Hoya. The amber outcrop of La Hoya is close to the Cortes de Arenoso town (Castellón Province, Valencian Community) and was named after the Font de l'Hoya ravine, where it is located. The Arroyo de la Pascueta amber outcrop is only a few kilometers from La Hoya (Fig. 1A). The oldest mention of amber in the Valencian Community corresponds to Cavanilles (1797), who indicated the presence of “succino” near the Quesa town (Valencia Province); since then, the number of amber outcrops detected in the region has increased. The amber of this area was traditionally used as incense by shepherds, but the livestock grazing has declined in the last decades, furthermore the access to the outcrop is difficult, so this locality could be currently free of anthropic alteration (Rodrigo et al., 2018). The La Hoya amber outcrop was discovered in 1998 and the first paleontological excavation took place in October 2003. La Hoya amber corresponds to the only known fossiliferous amber from the Valencian Community, including: two cockroaches (Blattodea), one platygastid (Hymenoptera), one chironomid (Diptera), two hybotids (Diptera) here studied, and a few undetermined insect remains.

Geologically, the La Hoya amber outcrop is located at the top of the Cortes de Arenoso section (Barrón et al., submitted). This section has been dated as upper Albian–lower Cenomanian based on stratigraphic and palynological data, while the amber-bearing level is most probably lower Cenomanian (Upper Cretaceous) (Barrón et al., submitted). Therefore, La Hoya corresponds to the only known fossiliferous Cenomanian amber outcrop from the Iberian Peninsula, providing an interesting comparison framework with the Albian fossiliferous ambers from Iberia and with other Cenomanian ambers, such as those from the Hukawng Valley (Myanmar) and Charente-Maritime (France) (Grimaldi et al., 2002; Perrichot et al., 2007). The amber outcrops of San Just, Arroyo de la Pascueta, and La Hoya were initially assigned to the Escucha Formation (Delclòs et al., 2007), but they actually correspond to the Utrillas Group (Barrón et al., submitted). The amber-bearing level of La Hoya is a grey-black mudstone rich in organic matter about 50 cm thick at the top of grey mudstone about three meters thick (Fig. 1B). Below the grey mudstone there is a sandstone level, while above the amber-bearing level there are sandstone and limestone levels (Fig. 1B). The amber-bearing rock is tough, and the amber pieces are usually broken and crumbled, so amber extraction is challenging (Fig. 1C). The aerial amber pieces (related to resin produced in branches or trunks) are scarcer than the nearly rounded kidney-shaped pieces (related to resin produced in roots). The aerial amber mainly corresponds to flow-shaped pieces, instead of droplet- or stalactitic-shaped morphologies. The color of the amber pieces is reddish-yellow.

The FTIR spectrum of the aerial amber from the La Hoya outcrop (Fig. 10) shows the typical characteristics of the amber (Grimalt et al., 1988): carbon-hydrogen stretching band about 2950 cm^{-1} , a prominent carbonyl band about 1700 cm^{-1} , and bending motions carbon-hydrogen bands about 1470 cm^{-1} and 1380 cm^{-1} . There are also hydroxyl bands about 3500 cm^{-1} . The absence of exocyclic methylenic bands at 1640 cm^{-1} and 880 cm^{-1} indicates a high degree of maturation, related to the Cretaceous age of the amber (Alonso et al., 2000). The molecular composition of the La Hoya amber (through gas chromatography-mass spectrometry) was classified as Type 3, based on an absence of abietane type diterpenoids and higher proportion of amberene with relatively lower homoamberene (**III**) and trimethyltetralin (**II**) than the Type 1 amber (Menor-Salván et al., 2016). The amber Type 3 is compatible with an Araucariaceae origin (Menor-Salván et al., 2016; McCoy et al., 2021).

Finally, it is important to note that the La Hoya amber-bearing outcrop is designated as a LIG (*Lugar de Interés Geológico*, Site of Geological Interest), and it is protected under legislation for paleontological heritage (Rodrigo et al., 2018).

Discussion

Systematic position

Trichinities has been proposed as the sister group of the hybotids in which the fore tibial gland was not developed (Chvála, 1983). *Trichinities* was described from a single female with the following characters: arista-like stylus longer than postpedicel, with two, possibly three articles [Hennig (1970) suspected the distal basal article was an artifact and we can here confirm that the arista-like stylus of *Trichinities* consists of one basal article]. Fore tibial gland absent or not visible; notum with four irregular rows of acrostichal and dorsocentral setulae; two pairs of larger dorsocentral setae; wing with costal vein ending beyond apex of M_1 ; Sc incomplete; R_{4+5} not forked; cell dm with veins M_1 , M_2 and M_4 branching separately off apex of cell, reaching wing margin; cell cua moderately long, subequal to length of cell bm, truncate apically; CuA projecting slightly obliquely; CuA+CuP reaching wing margin but becoming evanescent; anal lobe large. Terminal segments of female telescoping, without acanthophorite spines; cerci long.

We compared the female of *T. cretaceus* with *Grimaldipeza* spp. and noticed several differences: fore tibial gland present (absent or not visible in *Trichinities*), terminal abdominal segments telescoping but compact in comparison with *Trichinities*, tergite 8, syntergite 9+10 and cerci are half as long as in *Trichinities* (Fig. 6A). The wings also present some differences, including the length and apex of cell cua and the setae in the anal area are much larger in *Grimaldipeza* n. gen. than in *Trichinities*, principally in *Grimaldipeza* sp. 2. Accordingly, the specimens described herein could not be classified within *Trichinities*.

The most distinctive features of this new fossil genus are: three veins emitted from cell dm; unbranched R_{4+5} ; truncate cell cua which is subequal in length with cell bm, both cells being apically aligned; and presence of the fore tibial gland. Furthermore, male specimens have symmetrical terminalia, which appears to be at most only slightly rotated. The presence of the fore

tibial gland immediately assigns the genus to the Hybotidae, along with the slender apical sensillum on the stylus. The genus is excluded from the subfamilies Hybotinae and Tachydromiinae by the presence of cell dm emitting three veins. The long cell cua and the linear alignment with cell bm, excludes it from the Ocydromiinae, but it is most similar to the genera *Bicellaria* Macquart, 1823 (Bicellariinae) and *Trichinomyia* Tuomikoski, 1959 (Trichininae) (Chvála, 1983; figs 204, 206). These two genera also have similar nearly symmetrical male terminalia. The Bicellariinae is a distinct monophyletic lineage, defined on the basis of the loss of cell dm and the branches of M evanescent near mid wing, whereas the Trichininae is defined on the basis of symplesiomorphies (Sinclair and Cumming, 2006): dichoptic females, antennal stylus about half as long or shorter than the postpedicel, cell dm emitting three veins, proboscis short and directed downwards, ventral apodeme and postgonites absent. The subfamily contains only two genera, *Trichina* Meigen, 1830 and *Trichinomyia*. However, the position of Trichininae within Hybotidae remains unresolved. *Grimaldipeza* spp. remains apart from this lineage on the basis of the elongate mouthparts and antennal stylus longer than the postpedicel. Furthermore, *Grimaldipeza* n. gen. can be separated from *Trichinomyia* by the thoracic hairs and slender bristles, and wings without pterostigma. The male terminalia of *Trichina* is somewhat similar to *Grimaldipeza coelica* n. gen. et n. sp., however the hypandrium in the latter seems to be symmetrically bilobed. Wing venation and mouthparts are similar to Oedaleinae; however, our genus can be excluded from the subfamily because of the long, apical antennal stylus, which is usually greatly shortened (shorter than postpedicel) in Oedaleinae.

The genus *Apterodromia* Oldroyd, 1949 was transferred from the Tachydromiinae to the tribe Ocydromiini (now subfamily Ocydromiinae) (Sinclair and Cumming, 2000) and excluded from Trichininae with the argument that an elongated cell cua represents the ground plan condition of the hybotid lineage and the male terminalia characters should be used. The male hypopygium of *Grimaldipeza coelica* n. gen. et n. sp. is symmetrical, not rotated, yet the genus *Trichinomyia*, classified in Trichininae by Sinclair and Cumming (2006) is hypothesized to be the sister group to the remaining Hybotidae on the basis of its symmetrical male hypopygium. Thus, we can assume that symmetrical male hypopygium and the absence of genital rotation in *Ecommocyndromia difficilis* and *Grimaldipeza coelica* n. gen. et n. sp. are primitive conditions. A similar condition

has recently been described in the Ocydromiinae genus *Pseudoscelolabes* Collin, 1933 (Barros et al., 2022).

The phylogenetic position of *Ecommocyndromia difficilis* remains uncertain in part mostly because several important characters are not visible, e.g., apex of the arista-like stylus, basal portion of the wings, and mouthparts. However, the wing venation possibly indicates a close relationship with *Grimaldipeza* n. gen. and *Trichinities*.

Ecology

The eyes of *Grimaldipeza* n. gen. are holoptic in males, and dichoptic in females; this condition indicates that males probably formed aerial mating swarms (Chvála, 1976). The form of the females' mouthparts differs from that of males. This could be because of a natural dimorphism, common in Empidoidea, where the females have more prominent mouthparts than the males (Bletchly, 1954). We cannot exclude that the females belong to different species because they are found in separate amber pieces. Consequently, they are not described here as new species. However, the morphology of the mouthparts indicates the well-known predatory feeding habits of the empidoids. Diptera are very abundant in Defaunation resin, copal, and amber, and Empidoidea are among the most abundant Diptera within Cretaceous ambers (e.g., Grimaldi and Cumming, 1999; Sinclair and Grimaldi, 2020; Ngô-Muller et al., 2021). We know that selected taxa trapped in resins represent the fauna living in and around the resin-producing tree and appear in resins because of their ecology and behavior (Solórzano Kraemer et al., 2018). In the case of the here described specimens, their capture in resin is most probably due to swarming and predator behaviors (Chvála, 1976; Daugeron, 1997).

The presence of *Grimaldipeza* n. gen. in the amber-bearing outcrops of El Soplao and La Hoya points out to a wide distribution of the genus in the Cretaceous Iberia Island, along the northern and eastern coasts. This kind of distribution is compatible with that of other taxa found in amber from the Maestrazgo Basin (such as San Just) and in amber from the Basque-Cantabrian Basin (such as El Soplao and Peñacerrada I). Species of Psocodea, Coleoptera, Hymenoptera, and Diptera have been found in San Just and amber-bearing outcrops of northern Iberia (Arillo et al., 2008; Ortega-Blanco et al., 2011a, b; Peris et al., 2014; Álvarez-Parra et al., 2022). Thus, these

paleogeographical distributions may indicate that the resiniferous forests in the Iberia Island were at least partly connected, not independently isolated, allowing the movement of entomofauna along the coastal forest environments. Furthermore, the finding of *Grimaldipeza* n. gen. in the El Soplao amber middle Albian in age, and La Hoya amber most probably lower Cenomanian in age, shows that this genus inhabited the Iberia Island for an interval of about seven million years (~107–100 Ma). The finding of nearly rounded kidney-shaped amber pieces in the same level together with aerial amber pieces in La Hoya amber-bearing outcrop implies a parautochthonous accumulation in a transitional environment (Álvarez-Parra et al., 2021), similarly to El Soplao (Najarro et al., 2010). The La Hoya FTIR spectrum (Fig. 10) does not show significant differences with the spectra of other ambers from the Maestrazgo Basin, such as San Just and Ariño (Álvarez-Parra et al., 2021). The molecular composition of the amber from La Hoya, San Just, and Ariño relates the resin-producing tree to the Araucariaceae (Menor-Salván et al., 2016; Álvarez-Parra et al., 2021). Thus, the paleoenvironment could be similar in the three areas (Barrón et al., submitted). Interestingly, the geochemical analysis of the El Soplao amber linked it to a resin-producing tree related to Cupressaceae or the extinct Cheirolepidiaceae, maybe the genus *Frenelopsis* (Menor-Salván et al., 2010). Therefore, the genus *Grimaldipeza* n. gen. could inhabit in forests with different plant compositions.

Conclusions

The relevance of the new findings consists in providing new characters to the fossil character-pool of Hybotidae. Furthermore, a new genus and species are described, highlighting the diversity of the family during the Cretaceous. This is critical in understanding the evolution of the family. The positions of *Grimaldipeza* n. gen., *Trichinites*, and *Ecommocyndromia* remain unresolved until the extant subfamilies are better defined and more specimens in Cretaceous amber are discovered that could provide more key information. Because Empidoidea, especially Hybotidae are frequent in amber, it is probably only a matter of time before new findings are discovered. Furthermore, delving into taphonomical, geochemical, and paleobotanical data of the amber-bearing outcrops in which these insects are found provide key information about their paleoenvironment and paleoecology.

The search for new characters in the fauna included in amber is supported by technologies such as μ -CT or SR μ -CT. However, not all the inclusions in the different ambers offer good results. In the case of the amber studied here, SR μ -CT, which normally offers a better contrast than μ -CT, did not provide any signal. This made the segmentation and therefore the visualization of the specimens impossible, thus the character search was limited to light microscopy.

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Additional Information and Declarations

Author Contributions

Mónica M. Solórzano-Kraemer, wrote the paper, performed the experiments, analyzed the data, prepared figures and/or tables, authored and reviewed drafts of the paper, and approved the final draft.

Bradley J. Sinclair, wrote the paper, analyzed the data, authored and reviewed drafts of the paper, and approved the final draft.

Antonio Arillo, analyzed the data, performed the experiments, prepared figures and/or tables, authored and reviewed drafts of the paper, and approved the final draft.

Sergio Álvarez-Parra, wrote the paper, analyzed the data, prepared figures and/or tables, authored and reviewed drafts of the paper, and approved the final draft.

References

- Almera J, Anadón P, Godoy A. 1977. Cartografía geológica y memoria explicativa. In: Barnolas A, ed. *Mapa geológico de España 1:50.000, Hoja 591* Mora de Rubielos. Madrid: Instituto Geológico y Minero de España, 28–23.
- Alonso J, Arillo A, Barrón E, Corral JC, Grimalt J, López JF, López R, Martínez-Delclòs X, Ortuño VM, Peñalver E, Trincão PR. 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Alava (northern Spain, Basque-Cantabrian Basin). *Journal of Paleontology* **74**:158–178. [https://doi.org/10.1666/0022-3360\(2000\)074<0158:ANFRWB>2.0.CO;2](https://doi.org/10.1666/0022-3360(2000)074<0158:ANFRWB>2.0.CO;2)
- Álvarez-Parra S, Pérez-de la Fuente R, Peñalver E, Barrón E, Alcalá L, Pérez-Cano J, Martín-Closas C, Trabelsi K, Meléndez N, López Del Valle R, Lozano RP, Peris D, Rodrigo A, Sarto i Monteys V, Bueno-Cebollada CA, Menor-Salván C, Philippe M, Sánchez-García A, Peña-Kairath C, Arillo A, Espílez E, Mampel L, Delclòs X. 2021. Dinosaur bonebed amber from an original swamp forest soil. *eLife* **10**:e72477. <https://doi.org/10.7554/eLife.72477>
- Álvarez-Parra S, Peñalver E, Nel A, Delclòs X. 2022. New barklice (Psocodea, Trogiomorpha) from Lower Cretaceous Spanish amber. *Papers in Palaeontology* **8**(3):e1436. <https://doi.org/10.1002/spp2.1436>
- Arillo A, Peñalver E, Delclòs X. 2008. *Microphorites* (Diptera: Dolichopodidae) from the Lower Cretaceous amber of San Just (Spain), and the co-occurrence of two ceratopogonid

- species in Spanish amber deposits. *Zootaxa* **1920**(1):29–40.
<https://doi.org/10.11646/ZOOTAXA.1920.1.2>
- Azar D, Gèze R, Acra F. 2010. Lebanese amber. In: Penney D, ed. *Biodiversity of fossils in amber from the major world deposits*. Manchester: Siri Scientific Press, 271–298.
- Barros LM, Soares MMM, Freitas-Silva RAP, Sinclair BJ, Ale-Rocha R. 2022. Revision of the New Zealand endemic genus *Pseudoscelolabes* Collin (Diptera: Hybotidae: Ocydromiinae). *Zootaxa* **5150**(4):516–528. <https://doi.org/10.11646/zootaxa.5150.4.3>
- Barrón E, Peyrot D, Bueno-Cebollada CA, Kvaček J, Álvarez-Parra S, Altolaguirre Y, Meléndez N. submitted. Biodiversity of ecosystems in an arid setting: the late Albian plant communities and associated biota from eastern Iberia. *PLOS ONE*.
- Bletchly JD. 1954. The mouth-parts of the dance fly, *Empis livida* L. (Diptera, Empididae). *Proceedings of the Zoological Society of London* **124**(2):317–334.
<https://doi.org/10.1111/j.1469-7998.1954.tb07785.x>
- Brocke R, Wilde V. 2001. Infrared video microscopy—an efficient-method for the routine investigation of opaque organic-walled microfossils. *Facies* **45**:157–164.
<https://doi.org/10.1007/BF02668109>
- Cavanilles AJ. 1797. *Observaciones sobre la historia natural, geografía, agricultura, población y frutos del Reyno de Valencia*. Madrid: Imprenta Real.
- Chvála M. 1976. Swarming, mating and feeding habits in Empididae (Diptera), and their significance in evolution of the family. *Acta Entomologica Bohemoslovaca* **73**:353–366.
- Chvála M. 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General Part. The families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomologica Scandinavica* **12**:1–279.
- Cockerell TDA. 1917. Insects in Burmese amber. *Annals of the Entomological Society of America* **10**(4):323–329. <https://doi.org/10.1093/aesa/10.4.323>
- Corral JC, López Del Valle R, Alonso J. 1999. El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, norte de España). Su colecta y preparación. *Estudios del Museo de Ciencias Naturales de Álava* **14**(2):7–21.
- Cumming JM, Wood DM. 2017. Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ, eds. *Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families*. Pretoria: SANBI Graphics & Editing, 89–133.

- Daugeron C. 1997. Evolution of feeding and mating behaviors in the Empidoidea (Diptera: Eremoneura). In: Grandcolas P, ed. *The origin of biodiversity in insects: tests of evolutionary scenarios*. Paris: Mémoires du Muséum National d'Histoire Naturelle, Zoologie, 163–182.
- Delclòs X, Arillo A, Peñalver E, Barrón E, Soriano C, López del Valle R, Bernárdez E, Corral C, Ortuño VM. 2007. Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *Comptes Rendus Palevol* **6**(1–2):135–149. <https://doi.org/10.1016/j.crpv.2006.09.003>
- Downes JA, Smith SM. 1969. New or little known feeding habits in Empididae (Diptera). *The Canadian Entomologist* **101**(4):404–408. <https://doi.org/10.4039/Ent101404-4>
- Evenhuis NL, Pape T. 2022. *Systema Dipterum* Update. *Fly Times* **68**:34.
- García-Mondéjar J. 1982. Aptiense y Albiense. In: Alonso A, Arias C, García A, Mas R, Rincón R, Vilas L, eds. *El Cretácico de España*. Madrid: Editorial Universidad Complutense de Madrid, 63–84.
- Grimaldi DA, Cumming JM. 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History* **239**:1–124.
- Grimaldi D, Engel MS. 2005. *Evolution of the Insects*. England: Cambridge University Press.
- Grimaldi DA, Engel MS, Nascimbene PC. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* **3361**:1–71. [https://doi.org/10.1206/0003-0082\(2002\)361<0001:FCAFMB>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2)
- Grimalt JO, Simoneit BRT, Hatcher PG, Nissenbaum A. 1988. The molecular composition of ambers. *Organic Geochemistry* **13**(4–6):677–690. [https://doi.org/10.1016/0146-6380\(88\)90089-7](https://doi.org/10.1016/0146-6380(88)90089-7)
- Hennig W. 1970. Insektfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). *Stuttgarter Beiträge zur Naturkunde* **214**:1–12.
- Jouault C, Ngô-Muller V, Zhang Q, Nel A. 2020. New empidoid flies (Diptera: Atelestidae; Dolichopodidae) from mid-Cretaceous Burmese amber. *Palaeoentomology* **3**(2):204–211. <https://doi.org/10.11646/palaeoentomology.3.2.10>
- Kovalev VG. 1974. A new genus of the family Empididae (Diptera) and its phylogenetic relationships. *Paleontological Journal* **8**:196–220.

- Kovalev VG. 1978. A new fly genus (Empididae) from the Cretaceous resinites of Taimyr. *Paleontological Journal* **12**:351–356.
- Maksoud S, Azar D. 2020. Lebanese amber: latest updates. *Palaeoentomology* **3**(2):125–155. <https://doi.org/10.11646/PALAEOENTOMOLOGY.3.2.2>
- McCoy VE, Barthel HJ, Boom A, Peñalver E, Delclòs X, Solórzano-Kraemer MM. 2021. Volatile and semi-volatile composition of Cretaceous amber. *Cretaceous Research* **127**:104958. <https://doi.org/10.1016/j.cretres.2021.104958>
- Menor-Salván C, Najarro M, Velasco F, Rosales I, Tornos F, Simoneit BR. 2010. Terpenoids in extracts of lower cretaceous ambers from the Basque-Cantabrian Basin (El Soplao, Cantabria, Spain): paleochemotaxonomic aspects. *Organic Geochemistry* **41**(10):1089–1103. <https://doi.org/10.1016/j.orggeochem.2010.06.013>
- Menor-Salván C, Simoneit BR, Ruiz-Bermejo M, Alonso J. 2016. The molecular composition of Cretaceous ambers: Identification and chemosystematic relevance of 1, 6-dimethyl-5-alkyltetralins and related bisnorlabdane biomarkers. *Organic Geochemistry* **93**:7–21. <https://doi.org/10.1016/j.orggeochem.2015.12.010>
- Murillo-Barroso M, Peñalver E, Bueno P, Barroso R, de Balbín R, Martiñón-Torres M. 2018. Amber in prehistoric Iberia: New data and a review. *PLOS ONE* **13**(8):e0202235. <https://doi.org/10.1371/journal.pone.0202235>
- Najarro M, Peñalver E, Rosales I, Pérez-de la Fuente R, Daviero-Gómez V, Gómez B, Delclòs X. 2009. Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): Palaeoenvironmental and palaeobiological implications. *Geologica Acta* **7**(3):363–388. <https://doi.org/10.1344/105.000001443>
- Najarro M, Peñalver E, Pérez-de la Fuente R, Ortega-Blanco J, Menor-Salván C, Barron E, Soriano C, Rosales I, López Del Valle R, Velasco F, Tornos F, Daviero-Gomez V, Gomez B, Delclòs X. 2010. Review of the El Soplao amber outcrop, Early Cretaceous of Cantabria, Spain. *Acta Geologica Sinica* **84**(4):959–976. <https://doi.org/10.1111/j.1755-6724.2010.00258.x>
- Nascimbene P, Silverstein H. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions. In: Grimaldi D, ed. *Studies on Fossils in Amber, with*

particular reference to the Cretaceous of New Jersey. Leiden: Backhuys Publishers, 93–102.

Ngô-Muller V, Engel MS, Garrouste R, Pouillon JM, Nel A. 2021. The first predatory dance fly of the subfamily Ocydromiinae with specialized, raptorial legs in mid-Cretaceous amber from Myanmar (Diptera: Hybotidae). *Cretaceous Research* **119**:104697.

<https://doi.org/10.1016/j.cretres.2020.104697>

Ortega-Blanco J, Delclòs X, Engel MS. 2011a. Diverse stigmaphronid wasps in Early Cretaceous amber from Spain (Hymenoptera: Ceraphronoidea: Stigmaphronidae). *Cretaceous Research* **32**(6):762–773. <https://doi.org/10.1016/j.cretres.2011.05.004>

Ortega-Blanco J, Peñalver E, Delclòs X, Engel MS. 2011b. False fairy wasps in early Cretaceous amber from Spain (Hymenoptera: Mymarommatoidea). *Palaeontology* **54**(3):511–523.

<https://doi.org/10.1111/j.1475-4983.2011.01049.x>

Pape T, Blagoderov V, Mostovski MB. 2011. Order Diptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.), *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* **3148**:222–229. <https://doi.org/10.11646/zootaxa.3703.1.3>

Peñalver E, Delclòs X. 2010. Spanish amber. In: Penney D, ed. *Biodiversity of fossils in amber from the major world deposits*. Manchester: Siri Scientific Press, 236–270.

Peñalver E, Delclòs X, Soriano C. 2007. A new rich amber outcrop with palaeobiological inclusions in the Lower Cretaceous of Spain. *Cretaceous Research* **28**(5):791–802.

<https://doi.org/10.1016/j.cretres.2006.12.004>

Peñalver E, Ortega-Blanco J, Nel A, Delclòs X. 2010. Mesozoic Evaniidae (Insecta: Hymenoptera) in Spanish amber: reanalysis of the phylogeny of the Evanioidea. *Acta Geologica Sinica-English Edition* **84**(4):809–827. <https://doi.org/10.1111/j.1755-6724.2010.00257.x>

Peris D, Davis SR, Engel MS, Delclòs X. 2014. An evolutionary history embedded in amber: reflection of the Mesozoic shift in weevil-dominated (Coleoptera: Curculionoidea) faunas. *Zoological Journal of the Linnean Society* **171**(3):534–553.

<https://doi.org/10.1111/zoj.12149>

Perrichot V, Néraudeau D, Nel A, De Ploë G. 2007. A reassessment of the Cretaceous amber deposits from France and their palaeontological significance. *African Invertebrates* **48**(1):213–227.

- Rodrigo A, Peñalver E, López del Valle R, Barrón E, Delclòs X. 2018. The heritage interest of the Cretaceous amber outcrops in the Iberian Peninsula, and their management and protection. *Geoheritage* **10**(3):511–523. <https://doi.org/10.1007/s12371-018-0292-1>
- Sadowski EM, Schmidt AR, Seyfullah LJ, Solórzano-Kraemer MM, Neumann C, Perrichot V, Hamann C, Milke R, Nascimbene PC. 2021. Conservation, preparation and imaging of diverse ambers and their inclusions. *Earth-Science Reviews* **220**:103653. <https://doi.org/10.1016/j.earscirev.2021.103653>
- Salas R, Guimerà J. 1996. Rasgos estructurales principales de la cuenca cretácica inferior del Maestrazgo (Cordillera Ibérica oriental). *Geogaceta* **20**:1704–1706.
- Santer M, Álvarez-Parra S, Nel A, Peñalver E, Delclòs X. 2022. New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea). *Cretaceous Research* **133**:105128. <https://doi.org/10.1016/j.cretres.2021.105128>
- Schlüter T. 1978. Zur Systematik und Palökologie harzkonservierter Arthropoda einer Taphozonose aus dem Cenomanium von NW-Frankreich. *Berliner Geo-wissenschaftliche Abhandlungen - Reihe A: Geologie und Palaontologie* **9**:1–150.
- Sinclair BJ. 2019. Revision of the southern African genus *Stuckenbergomyia* Smith, 1971 (Diptera, Empidoidea) and proposal of a new subfamily. *African Invertebrates* **60**:133–145.
- Sinclair BJ, Cumming JM. 2000. Revision of the genus *Apterodromia* (Diptera: Empidoidea), with a redefinition of the tribe Ocydromiini. *Records-Australian Museum* **52**(2):161–186. <https://doi.org/10.3853/j.0067-1975.52.2000.1313>
- Sinclair BJ, Cumming JM. 2006. The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa* **1180**(1):1–172. <https://doi.org/10.11646/zootaxa.1180.1.1>
- Sinclair BJ, Grimaldi DA. 2020. Cretaceous diversity of the relict genus *Alavesia* Waters and Arillo (Diptera: Empidoidea: Atelestidae). *American Museum Novitates* **3961**:1–40. <https://doi.org/10.1206/3961.1>
- Solórzano Kraemer MM, Delclòs X, Clapham M, Arillo A, Peris D, Jäger P, Stebner F, Peñalver E. 2018. Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. *Proceedings of the National Academy of Sciences* **115**(26):6739–6744. <https://doi.org/10.1073/pnas.1802138115>

- 712 Solórzano Kraemer MM, Solórzano KA, Stebner F, Bicke D, Rust J. 2015. Entrapment bias of
713 insects in Miocene amber revealed by trapping experiments in a tropical forest in
714 Chiapas, Mexico. *PLOS ONE* **10(3)**:e.0118820.
715 <https://doi.org/10.1371/journal.pone.0118820>
- 716 Wahlberg E, Johanson KA. 2018. Molecular phylogenetics reveals novel relationships within
717 Empidoidea (Diptera). *Systematic Entomology* **43(4)**:619–636.
718 <https://doi.org/10.1111/syen.12297>
- 719 Waters SB. 1989. A new Hybotine dipteran from the Cretaceous of Botswana. *Palaeontology*
720 **32(3)**:657–667.
721

TABLE AND FIGURE LEGENDS

TABLE

Table 1. Checklist of the known Cretaceous Hybotidae and related genera (Diptera: Empidoidea), with indication of the provenance and age. The new taxa here described are in bold. The genus *Cretoplatypalpus* is doubtfully assigned to Empidoidea sensu Jouault et al. (2020). The genus *Ecommocydromia difficilis* was originally assigned to Ocydromiinae but later to the Empididae s.s. by Grimaldi and Engel (2005) and as *incertae sedis* within Empidoidea sensu Ngô-Muller et al. (2021) and in the present work. * *Trichinites* has been here proposed as the sister group of the hybotids, it is here included for practical reasons.

FIGURE LEGENDS

Figure 1. The lower Cenomanian (Upper Cretaceous) amber-bearing outcrop of La Hoya (Maestrazgo Basin, Castellón Province, Spain). (A) Geographical location within the Iberian Peninsula of the El Soplao (middle Albian) and La Hoya amber outcrops, and geological location of the La Hoya outcrop; Cortes de Arenoso village and the fossiliferous Arroyo de la Pascueta amber outcrop (late Albian) are also indicated in the geological map. (B) Amber-bearing level of the La Hoya outcrop, constituted by grey-black mudstone rich in organic matter, at the top of the Cortes de Arenoso section (Barrón et al., submitted). (C) An amber piece in the rock of the La Hoya outcrop. Geological map in A modified and simplified from Almera et al. (1977).

Figure 2. *Grimaldipeza coelica* n. gen. et sp. (Diptera: Hybotidae), holotype male CES.404.1 and paratype male CES.404.2, from El Soplao outcrop, Cantabria, Spain (middle Albian in age). (A) Piece showing two specimens (holotype, left; paratype, right). (B) Habitus of holotype CES.404.1, lateral view. (C) Habitus of holotype CES.404.1, dorsal view. Scale bars 0.5 mm.

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TABLE

Subfamily	Genus and species	Provenance	Age	Reference
<i>Incertae sedis</i>	<i>Grimaldipeza coelica</i> n. gen. et n. sp.	El Soplao. Amber.	middle Albian (Early Cretaceous)	This paper
<i>Incertae sedis</i>	<i>Grimaldipeza</i> n. sp. 1	El Soplao. Amber.	middle Albian (Early Cretaceous)	This paper
<i>Incertae sedis</i>	<i>Grimaldipeza</i> n. sp. 2	La Hoya. Amber.	early Cenomanian (Late Cretaceous)	This paper
<i>Incertae sedis</i>	<i>*Trichinites cretaceous</i> Hennig, 1970	Jezzine (Lebanon). Amber.	Barremian (Early Cretaceous)	Henning (1970); Grimaldi and Cumming (1999)
<i>Incertae sedis</i>	<i>Ecommocyndromia difficilis</i> Schlüter, 1978	Écommoy (France). Amber.	Cenomanian (Late Cretaceous)	Schlüter (1978)
Hybotinae	<i>Pseudoacarterus orapaensis</i> Waters, 1989	Orapa (Botswana). Compression.	Turonian (Late Cretaceous)	Waters (1989)
Ocydromiinae	<i>Pouillonhybos venator</i> Ngô-Muller, Engel and Nel, 2021	Hukawng Valley (Myanmar). Amber.	early Cenomanian (Late Cretaceous)	Ngô-Muller et al. (2021)
Tachydromiinae	<i>Archiplatypalpus cretaceous</i> Kovalev, 1974	Yantardakh, Taimyr (Russia). Amber.	Santonian (Late Cretaceous)	Kovalev (1974); Grimaldi and Cumming (1999)
	<i>Cretoplatypalpus americanus</i> Grimaldi and Cumming, 1999	Cedar Lake (Canada). Amber.	Campanian (Late Cretaceous)	Grimaldi and Cumming (1999)
	<i>Cretoplatypalpus archaeus</i> Kovalev, 1978	Nizhnyaya Agapa (Russia). Amber.	late Cenomanian (Late Cretaceous)	Kovalev (1978); Grimaldi and Cumming (1999)
	<i>Electocyrtoma burmanica</i> Cockerell, 1917	Hukawng Valley (Myanmar). Amber.	early Cenomanian (Late Cretaceous)	Cockerell (1917); Grimaldi and Cumming (1999)
	<i>Mesoplatypalpus carpenteri</i> Grimaldi and Cumming, 1999	Cedar Lake (Canada). Amber.	Campanian (Late Cretaceous)	Grimaldi and Cumming (1999)

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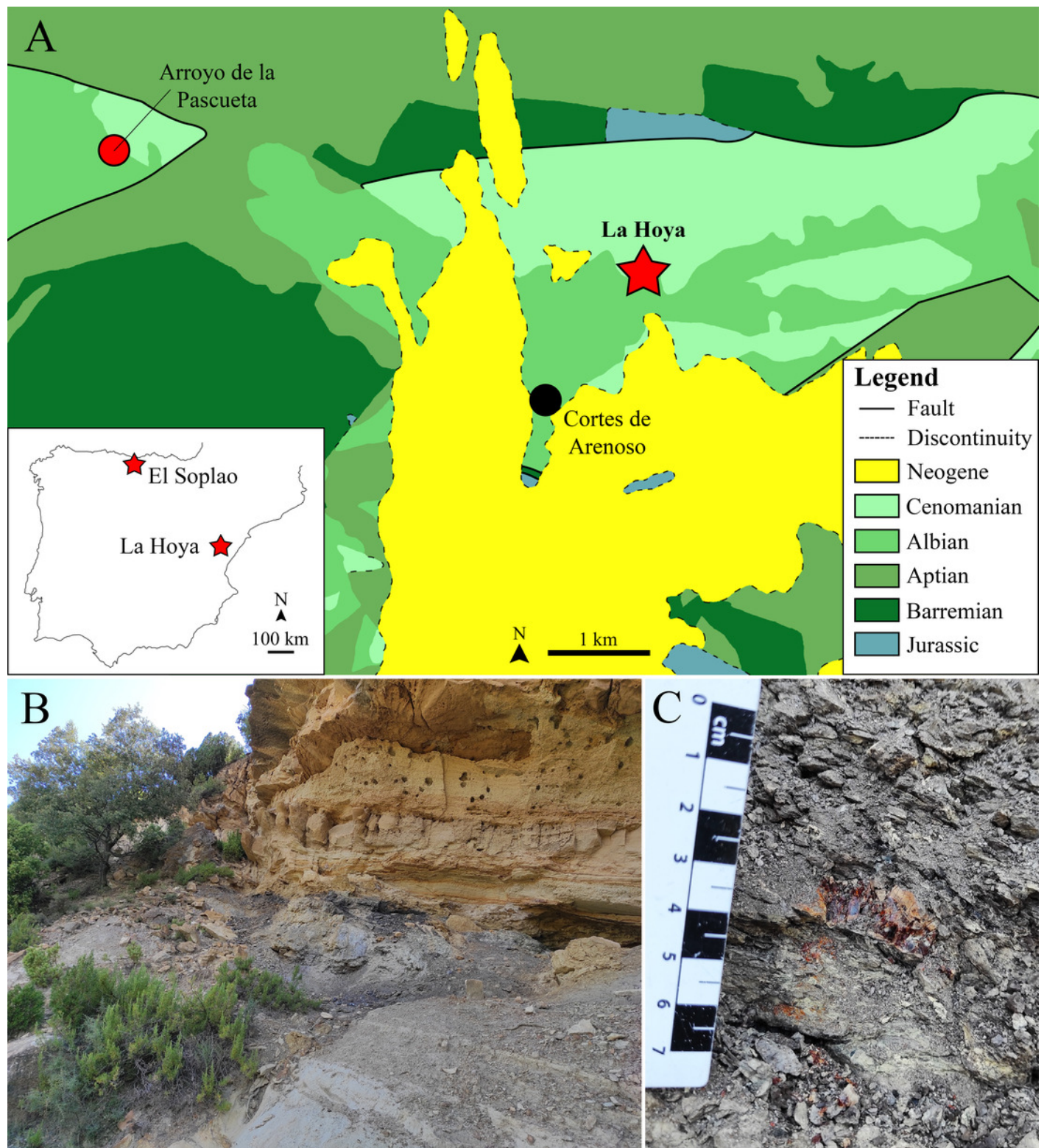


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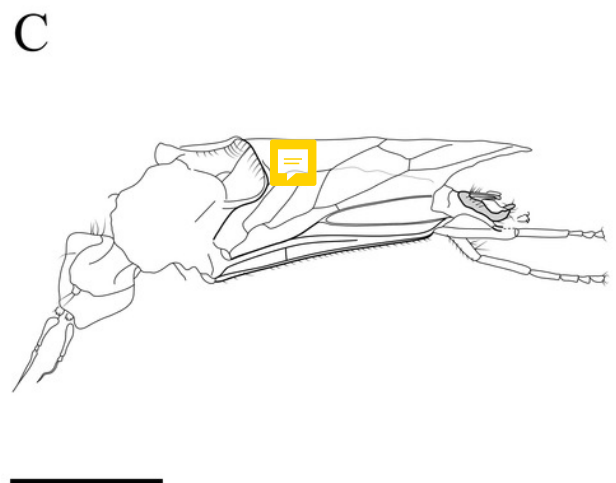
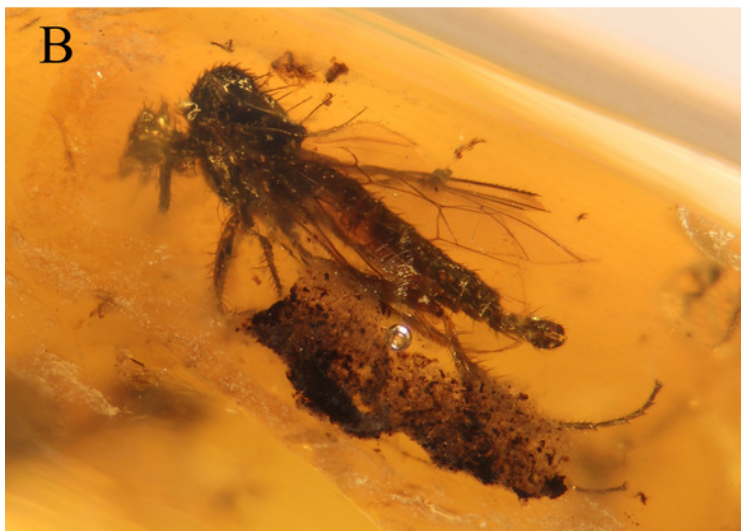
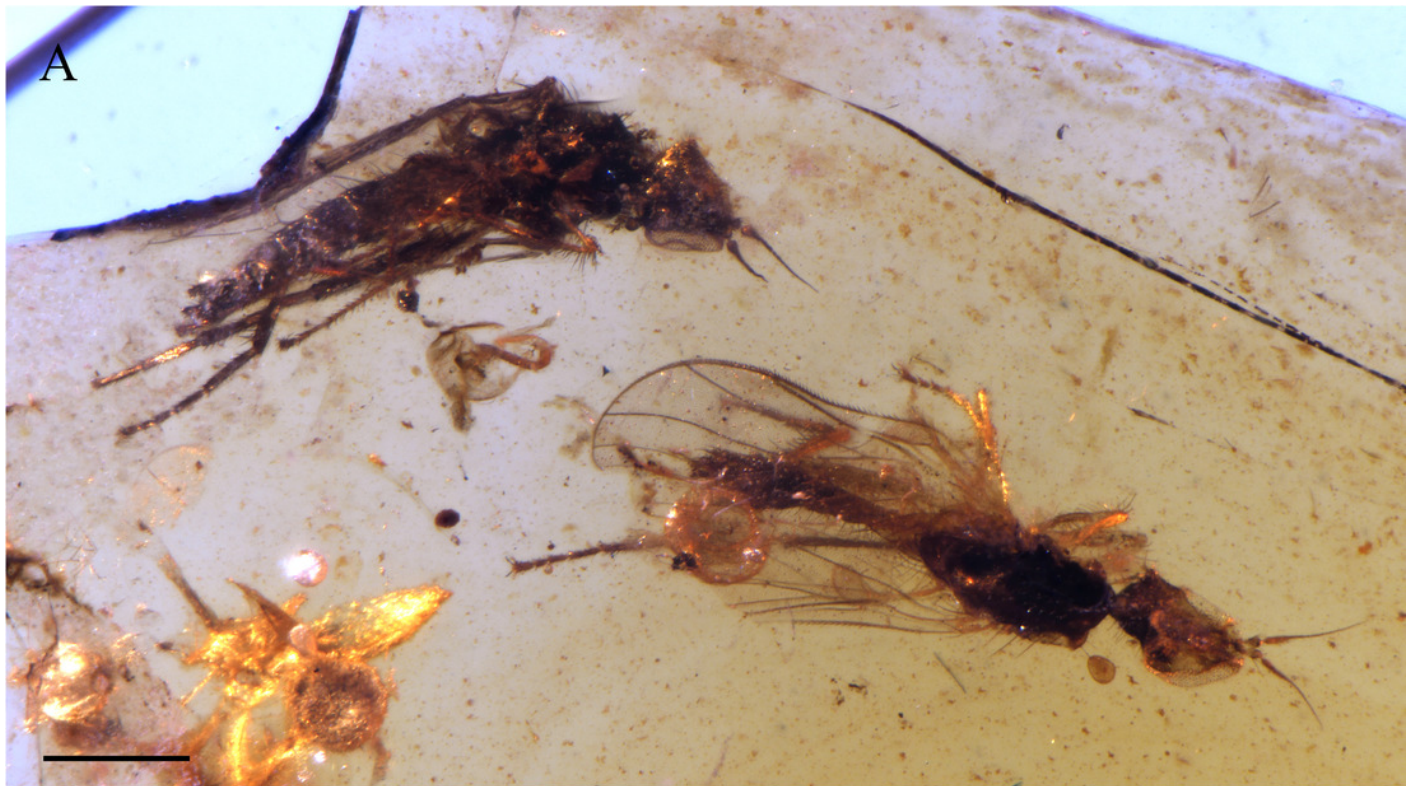


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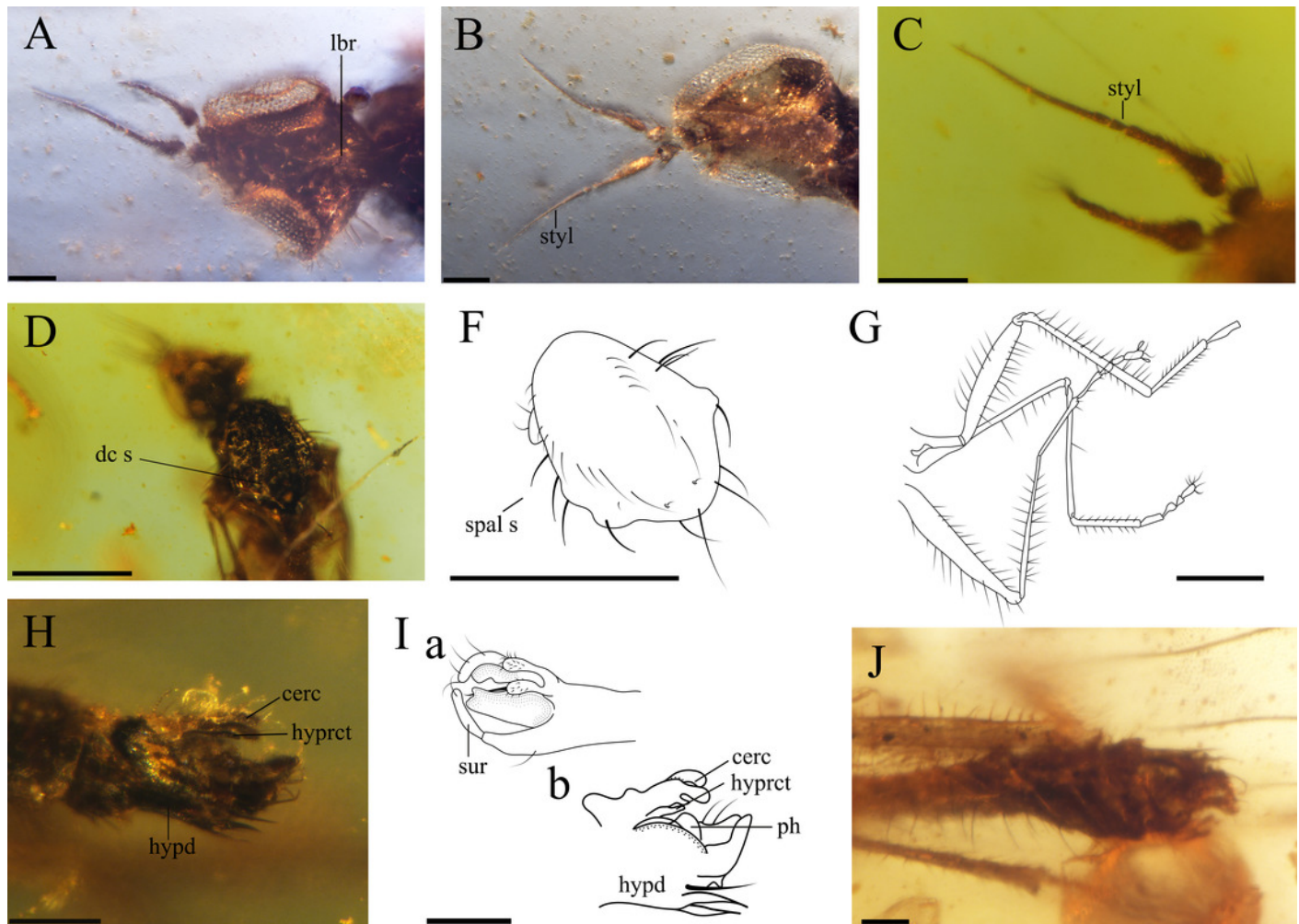


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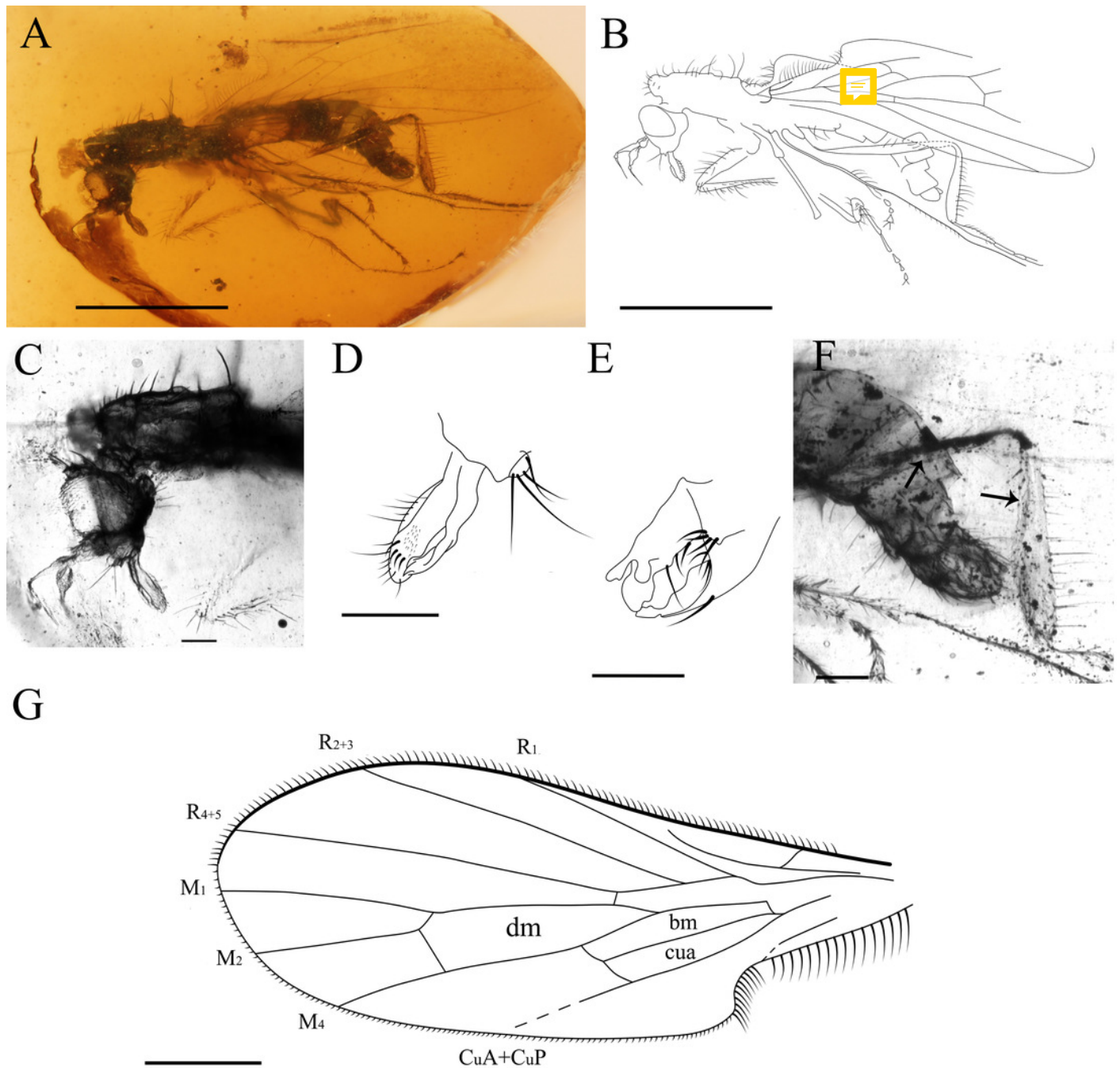


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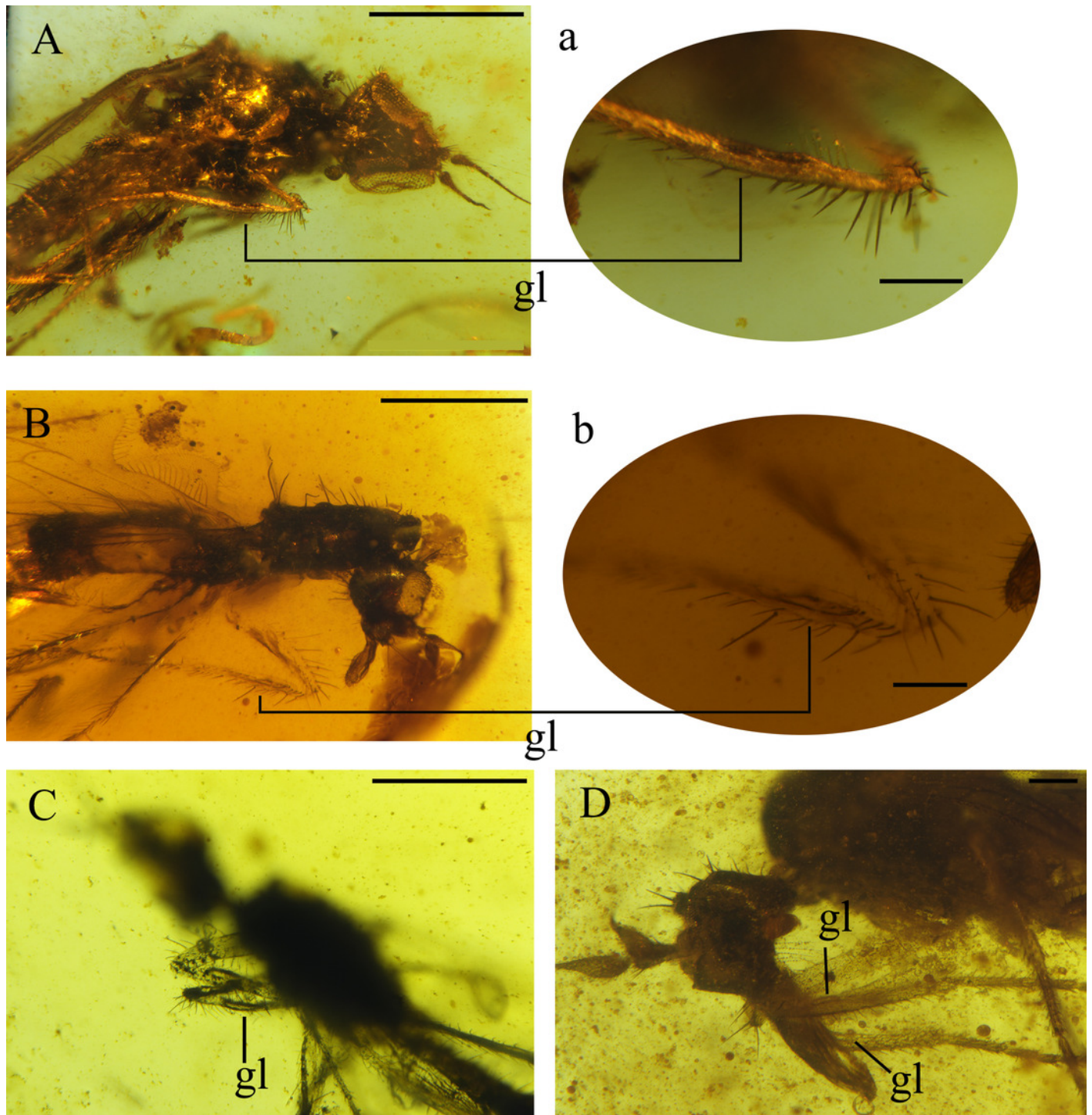


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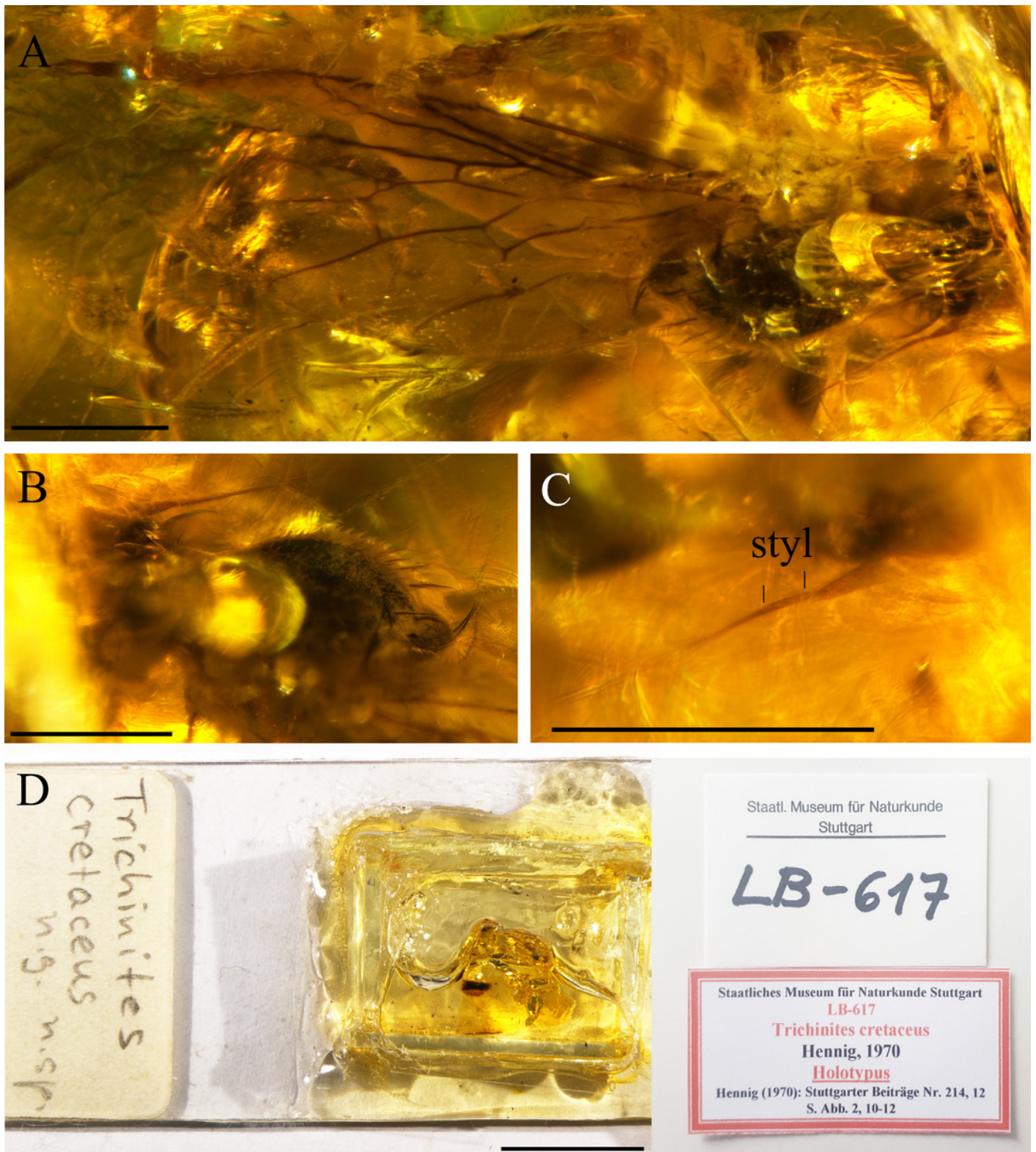


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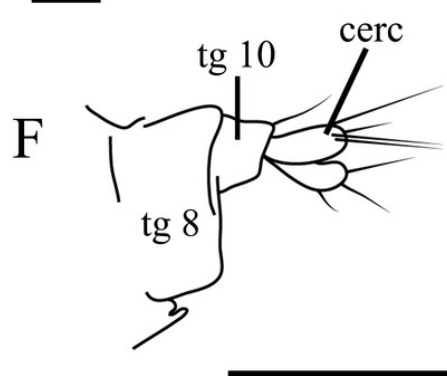
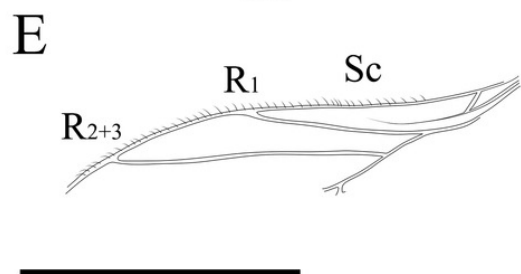
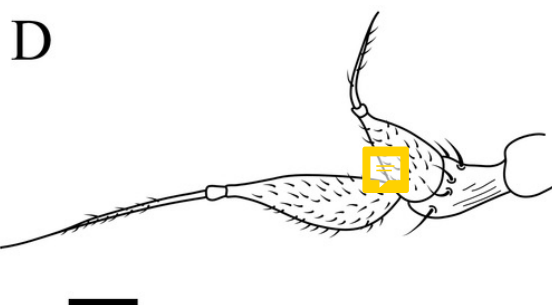
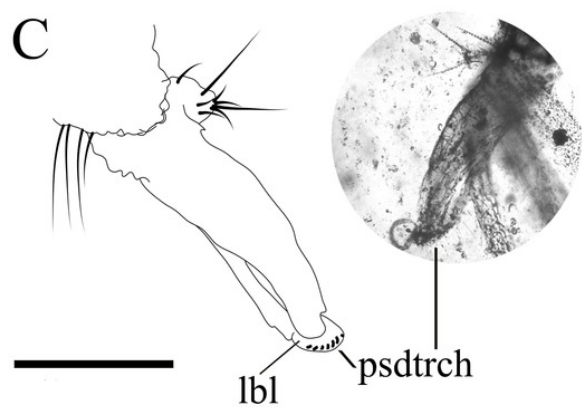
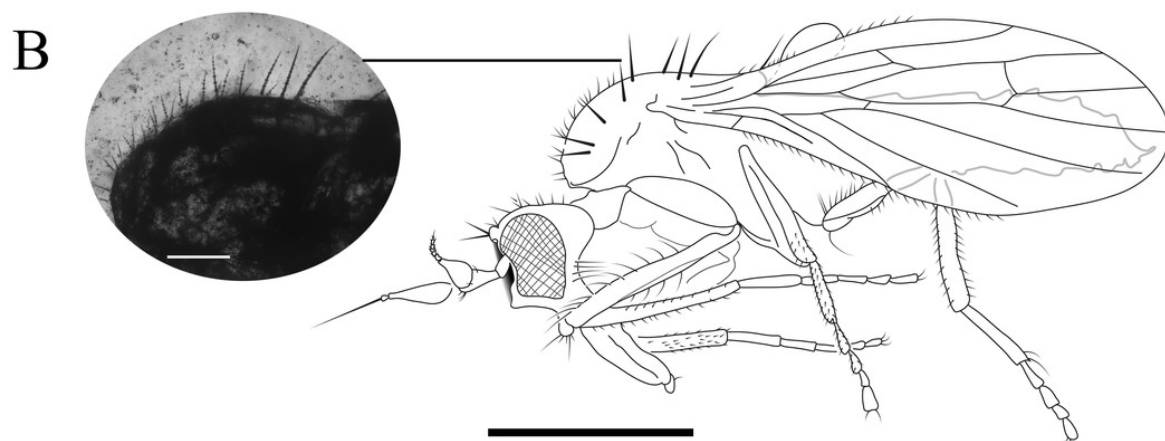
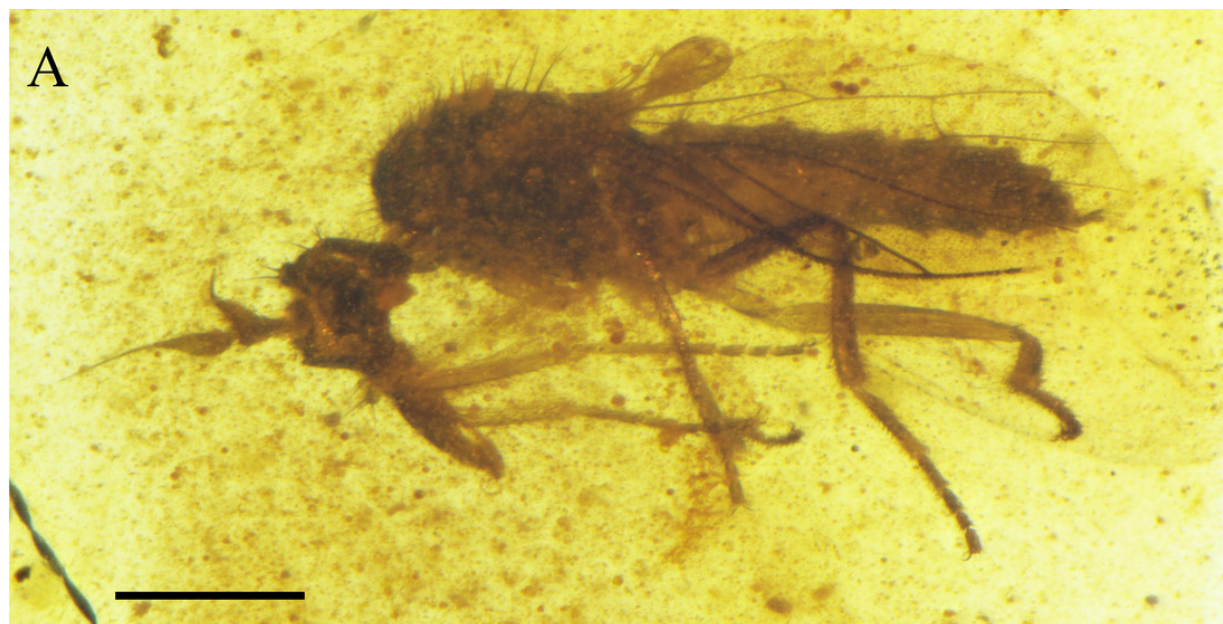


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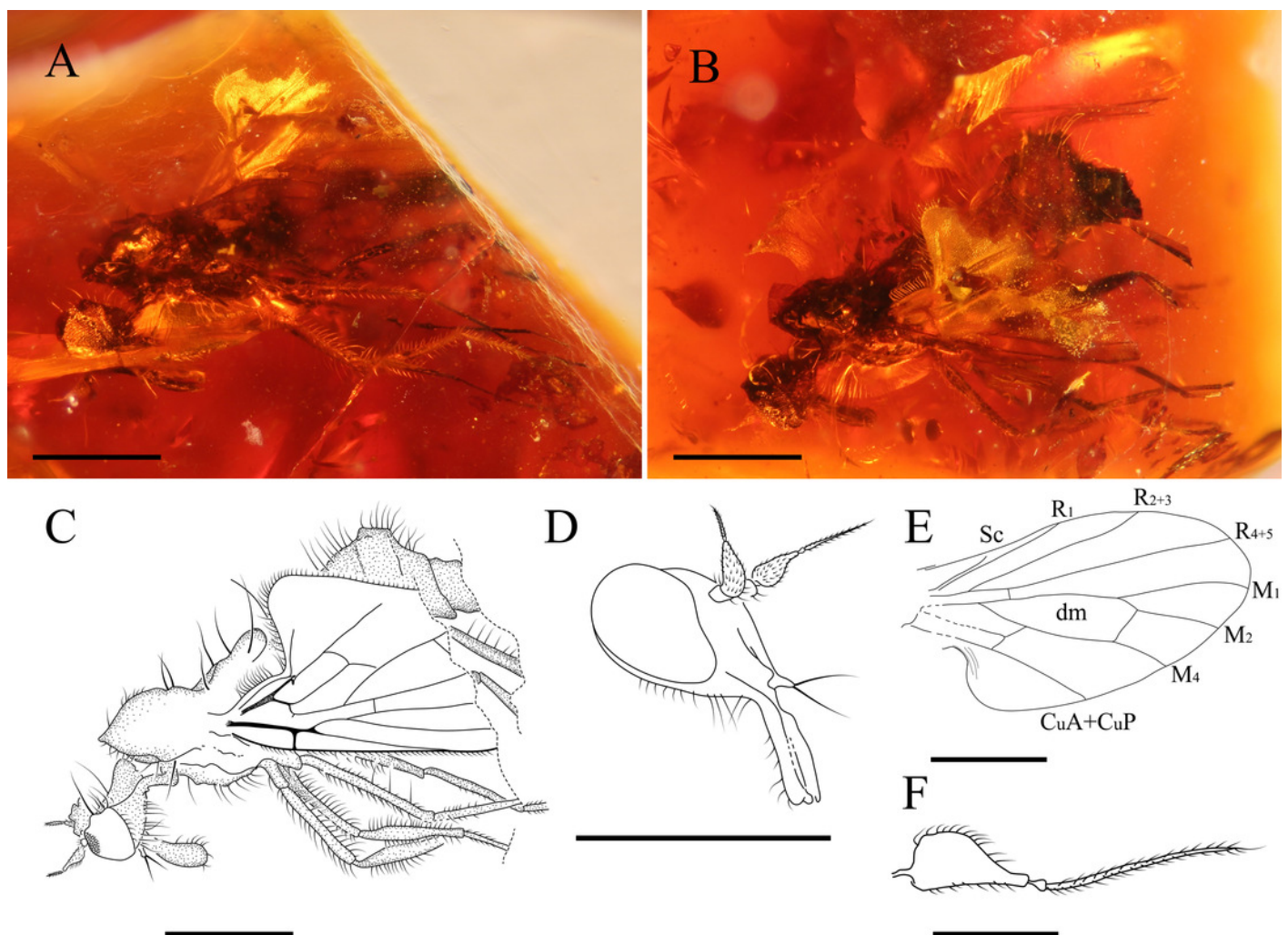


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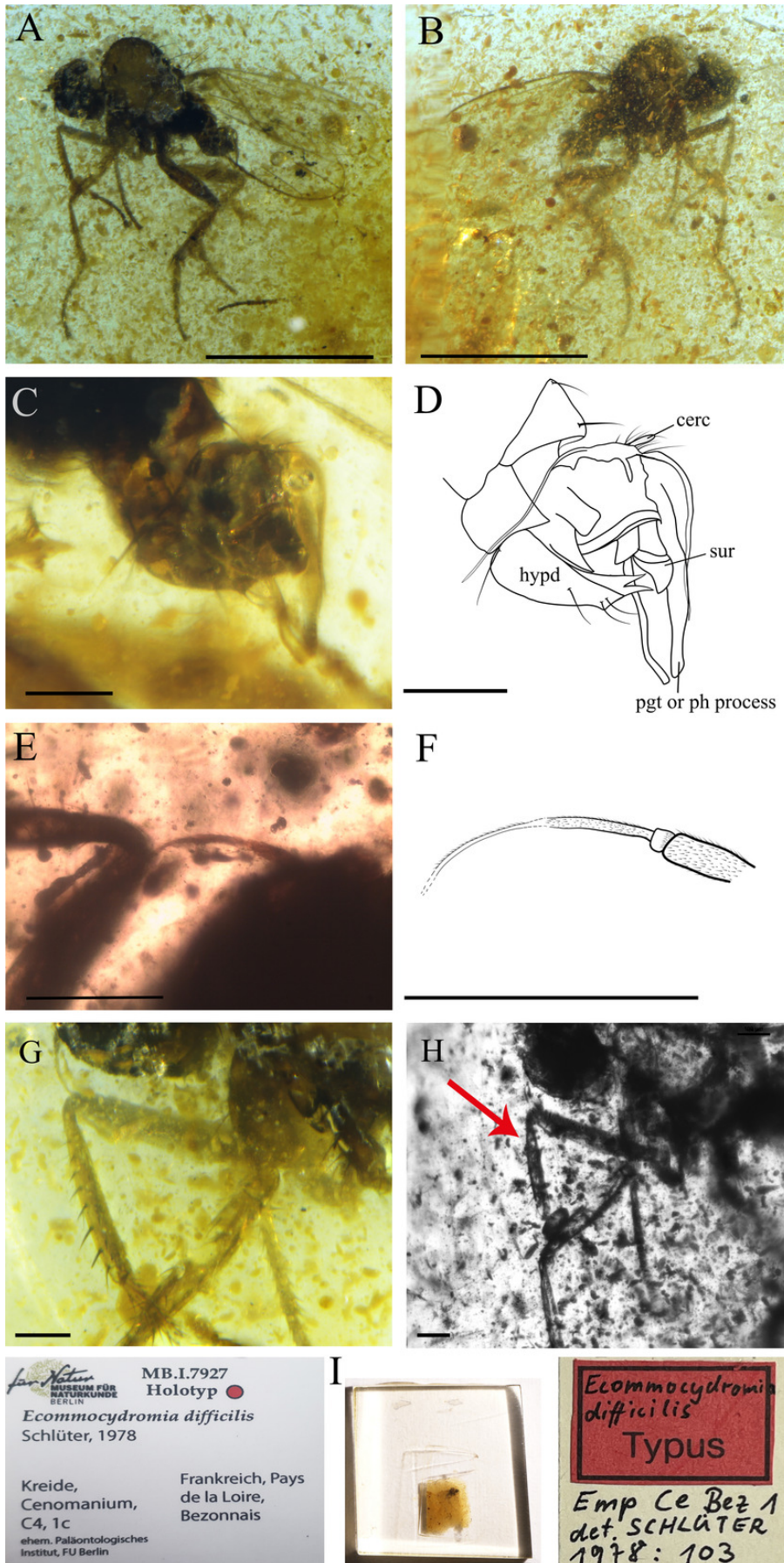


Figure 10

Figure 10.

Infrared spectroscopy spectrum (FTIR) from an aerial amber piece of La Hoya outcrop (Castellón Province, Spain). Resolution = 4 cm^{-1} .

